OVARIAN CYCLING FREQUENCY AND BATCH FECUNDITY IN THE QUEENFISH, *SERIPHUS POLITUS*: ATTRIBUTES REPRESENTATIVE OF SERIAL SPAWNING FISHES

E. E. DeMartini and Robert K. Fountain[1]

ABSTRACT

Egg production by *Seriphus politus* near San Diego in southern California was studied during 1978-79. Spawning frequency was estimated on the basis of incidence of females with hydrated eggs. Estimates of annual egg production were an order of magnitude greater than estimates based on conventional methods.

Seriphus politus spawns during March-August, and females mature at 10.0-10.5 cm standard length in their first spring or second summer following birth. Planktonic eggs are spawned between late afternoon and early evening. Spawning is asynchronous among females, but has monthly peaks in intensity during the waxing (first quarter) of the moon. Fecundity is proportional to size and is better correlated with weight than with length of female. Individuals spawn once a week on average, regardless of body size. Larger females begin spawning earlier in the season and continue spawning after the smallest females have ceased. Recruit spawners and the largest repeat spawners produce about 12 to 24 batches of eggs during their respective spawning seasons. The average-sized female spawns about 300,000 eggs in a year. Relative fecundity is an increasing function of body size. Larger females produce larger eggs, and all females produce larger eggs earlier in the season. Implications of these life-history attributes are discussed.

The croakers (family Sciaenidae) are a major component of the nearshore fish fauna of southern California (Frey 1971), yet little is known about their fecundity patterns or other details of their reproductive biology (Skogsberg 1939). Seven species of croakers occur off southern California (Miller and Lea 1972). General information on breeding seasonality and size at sexual maturity exists for white seabass, *Atractoscion nobilis* (Clark 1930); black croaker, *Cheilotrema saturnum* (Limbaugh 1961; Fitch and Lavenberg 1975); California corbina, *Menticirrhus undulatus* (Fitch and Lavenberg 1971; Frey 1971); and spotfin croaker, *Roncador stearnsi* (Frey 1971). The general seasonal nature of spawning is known for yellowfin croaker, *Umbrina roncador* (Frey 1971). Additional data on ovarian cycling exist only for white croaker, *Genyonemus lineatus*, and for queenfish, *Seriphus politus* (Goldberg 1976).

The queenfish is an abundant, small species that is a major component of the sport fish catch on piers in southern California (Frey 1971); the species moreover provides forage for several fishes important to the sport and commercial fisheries in the area (Young 1963; Feder et al. 1974). It is the purpose of this paper to document the fecundity and ovarian cycling patterns of queenfish and to relate these results to what we feel are some general reproductive characteristics of serial spawning fishes.

MATERIALS AND METHODS

Field Sampling

Fish were sampled at nearshore (5-20 m) depths, 0.5-3 km from shore, between San Clemente and Oceanside, Calif. (Figure 1), using a lampara net (560 m long × 25 m deep, mesh: 15 cm in wings to 1.25 cm in center bag), fished surface-to-bottom by a commercial vessel. Fish were caught at standard times of day (1-6 h after dawn) and night (1-6 h after sunset) on surveys conducted at fortnightly (September 1978-February 1979; September 1979) or weekly (March-August 1979) intervals. Six daytime and five nighttime net hauls were made each survey.

---

[1]Marine Science Institute, University of California, Santa Barbara, CA 93106.
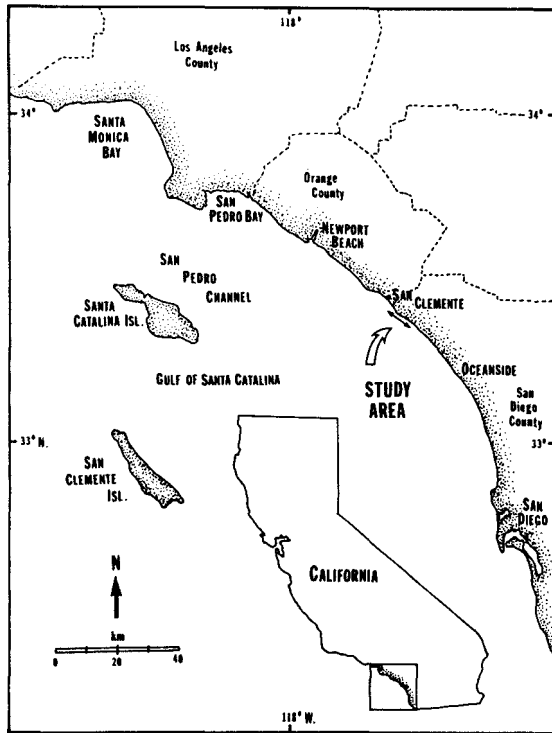
FIGURE 1.— Map of the study area.

Analysis of Fish and Ovaries

A maximum of two aliquots of 50 fish each were sacrificed from each net haul to determine size (standard length, SL, in millimeters) and sex composition. At most 15 females per 5 mm length class in each haul were measured and their ovaries excised and weighed (0.01 g) while fresh. Fresh (ovary-free) body weight (0.1 g) was recorded for subsampled, mature fish of a range of lengths. One or both ovaries of each mature pair were fixed and preserved in modified Gilson's fluid (Bagenal and Braum 1971) for 1-3 mo. Gonads were classified either as immature or mature according to several gross criteria (vasculariza-

tion, oocyte appearance, Table 1) of Bagenal and Braum (1971). Gonad maturity also was estimated using a gonad index, $GI = W/SL^3 \times C$ (Moser 1967), where W = weight of both ovaries in grams, SL = standard length in millimeters, and the constant $C = 10^8$. The median diameter (random axis) was determined for oocytes present in the largest size-frequency mode in ripening ovaries (Stage 2, Table 1) of each of 10-15 fish from pooled monthly samples. Oocyte maturation size was inferred from a plot of median oocyte diameter versus gonad index (Higham and Nicholson 1964). For select ripe (Stage 3, Table 1) females, both ovaries were reweighed after Gilson's preservation, a tissue sample ($\overline{X} = 3.4 \pm 1.0\%$ (SE), range 1.0-7.2% of the weight of both ovaries) weighed, and the numbers of oocytes in the largest size-frequency mode estimated for both ovaries by gravimetric method (Bagenal and Braum 1971). Tissue samples from either ovary of a pair were used, as the right and left ovaries of S. politus are, on average, equivalent in weight (paired t-test, $n = 20$ ovary pairs, $0.4 > P > 0.3$) and in the size-frequency distribution of oocytes (Kolmogorov-Smirnov 2-sample test, $n = 5$ ovary pairs, $P > 0.1$). Tissue samples for fecundity analysis were taken from the anterior one-third of the ovary. For other select Stage 2 and 3 fish, the second ovary of a pair was fixed in 10% Formalin[2] for 2 wk, sectioned at 0.008 mm, stained with Harris' hematoxylin and eosin, and a slide mount examined at 60-240× to validate classification as nonhydrated or hydrated based on the gross ovarian characteristics listed in Table 1. The latter tissue samples were also taken from the anterior one-third of the ovary. No difference existed in the frequency distribution of oocyte maturation states within anterior, central, or posterior regions of the queenfish ovary (Smirnov 3-sample test, $n = 5$ ovary pairs, $P > 0.1$; Conover 1971).

---

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

TABLE 1.—Gross characteristics of various stages in the queenfish ovarian cycle.

Egg stages within the ovary		Gross appearance of ovary and oocytes
1	Vestigial (= immature or inactive)	Ovaries avascular; oocytes not visible to naked eye. Ovaries uniform whitish-yellow.
2	Nonhydrated (= ripening)	Ovaries vascular and oocytes visible to the naked eye. Oocytes uniformly small, opaque, and straw-yellow throughout entire ovary.
3	Hydrated (= ripe)	Many small, opaque oocytes plus a minority of large, hyaline oocytes present throughout ovary. The two egg types together produce a speckled, translucent-opaque appearance, yellowish-orange to orange, throughout ovary.
4	Ovulated (= running)	A band of small, opaque, straw-yellow oocytes present along dorsal ridge of ovary; many large, hyaline oocytes visible within lumen of ovary. Most of ovary uniform yellowish-orange or orange.
5	Residual (= spent)	Ovary slightly blood-shot and deflated (partially spent) to very blood-shot, completely collapsed and flaccid (totally spent). A small number of large, ovulated eggs usually visible in lumen of ovary. Most oocytes present are small and opaque.

RESULTS

Spawning Season and Gonad Maturation

Queenfish ovaries accelerate development in February when daylight lengthens beyond 10 h and nearshore water temperatures are 15°-16° C. Ovaries increase to their maximum relative weight in April-May and decline through August until a resting stage recurs in September (Figure 2A). During February-September, nearshore water temperatures in general increase to 17°-19° C, although aperiodic bouts of upwelling (13°-14° C water) occur (J. Reitzel[3]). Ovaries mature at a

GI of 40, when the diameter of Gilson's fluid-fixed (nonhydrated) oocytes reaches 350 μm (Figure 3).

Body Size and Time of Spawning

The first sexual maturation of females begins at a length of 10-10.5 cm. The proportion of sexually active females increases with body size until, at a length of about 12 cm SL, virtually all females are spawning by midseason (Table 2). Larger females (>12 cm, age II and older, DeMartini et al.[4]) start spawning earlier and finish spawning later in the year than fish ≤12 cm SL (Table 2, Figure 4). Duration of spawning varies from 3 mo for first

[3]Reitzel, J. 1979. Physical/chemical oceanography. *In* Interim Report of the Marine Review Committee of the California Coastal Commission. Part II: Appendix of Technical Evidence in Support of the General Summary, March 12, 1979, p. 6-23. Unpubl. rep. Marine Review Committee Research Center, 533 Stevens Avenue, Suite E-36, Solana Beach, CA 92075.

[4]DeMartini, E. E., K. M. Plummer, and T. O. Moore. Age and growth of the queenfish (*Seriphus politus*), with back-calculated length-at-age estimates based on sections of otolith sagittae. Manuscr. in prep. Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106.
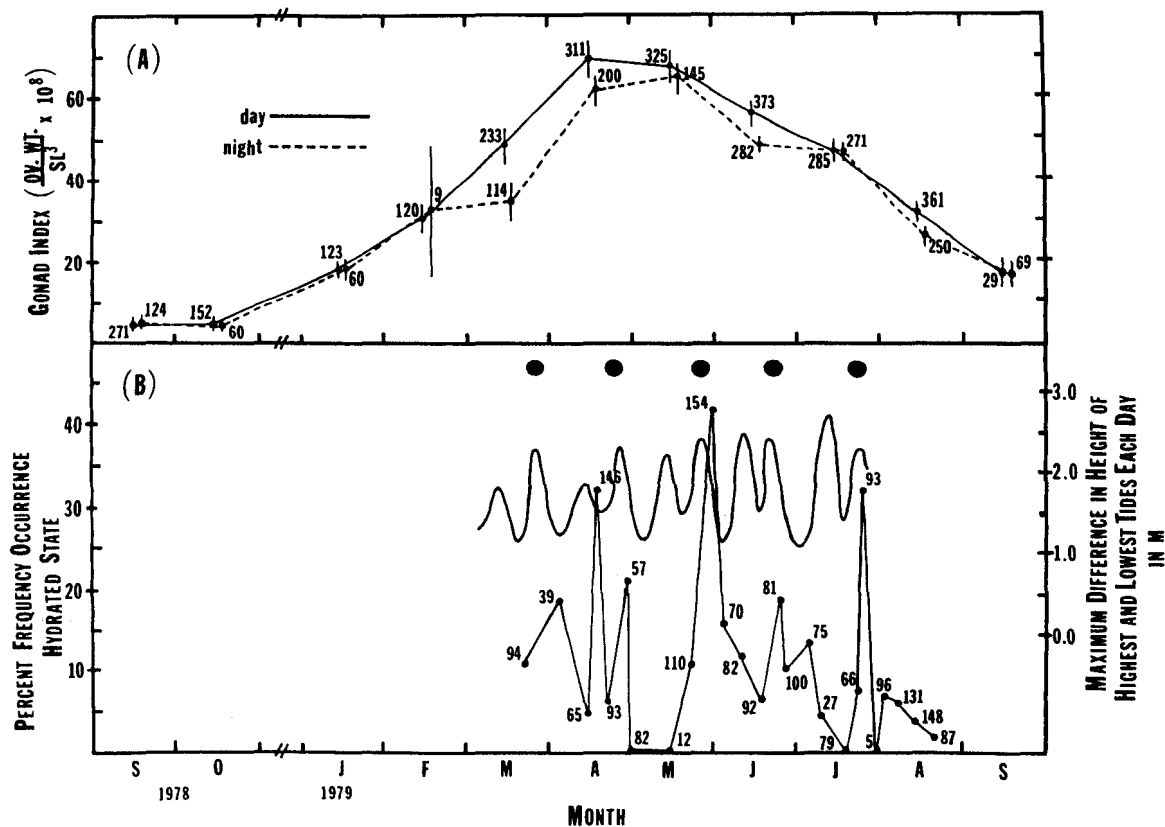

FIGURE 2.—(A) Mean gonad indices of female queenfish (of all body sizes) collected September 1978-September 1979. Indices of day and night sample fish plotted separately. Sample sizes and 95% confidence limits are indicated. (B) Percent frequency occurrence of adult female queenfish with ovaries containing oocytes in hydrated condition during March-August 1979. Fish are from daytime collections at 5-11 m depths. Noted are the numbers of sample fish, dates of new moon, and maximum range in heights of highest and lowest tides each day.
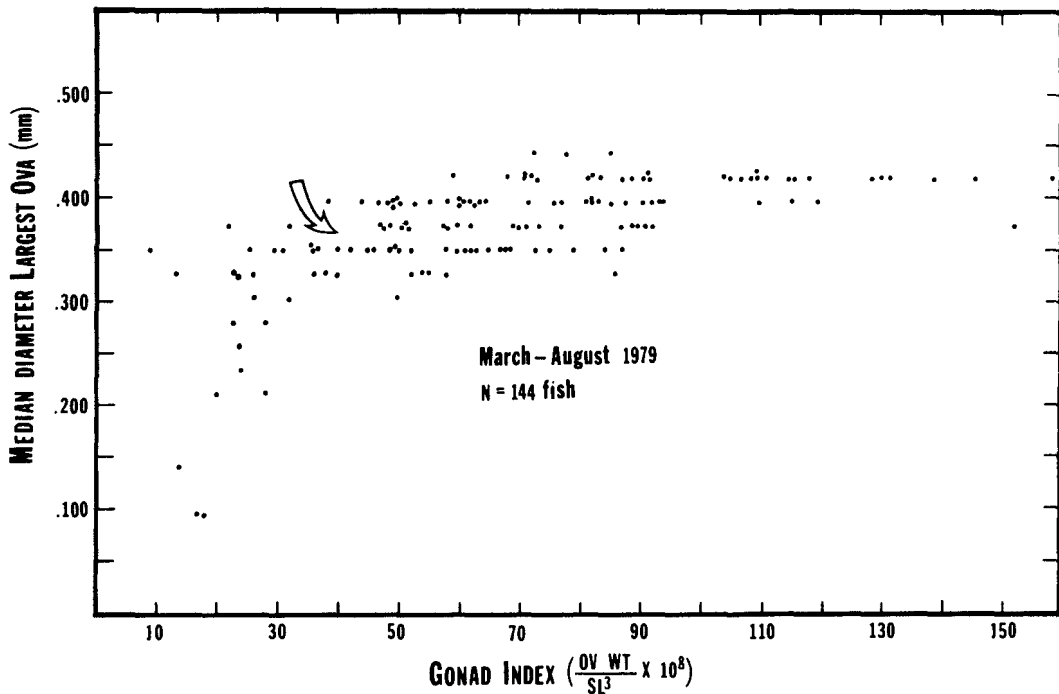
FIGURE 3.—Scattergraph of the median diameter (random axis) of the largest size-frequency mode of oocytes plotted against gonad index of the respective female queenfish. Asymptote (noted by arrow) occurs at an oocyte diameter of about 350 μm, corresponding to a gonad index of about 40.

TABLE 2.—Percent of female queenfish of various length classes[1] that were sexually mature during the 1979 spawning period.

Length class (cm SL)	Percent mature					
	Mar.	Apr.	May	June	July	Aug.
<10.5	0	0	<1	2	3	<1
10.6-11.0	14	63	68	58	22	3
11.1-11.5	18	95	93	92	53	9
11.6-12.0	48	97	100	94	85	12
12.1-12.5	82	98	100	100	96	73
12.6-13.0	90	100	100	98	99	97
13.1-13.5	100	100	100	98	100	100
>13.5	100	100	100	100	>97	>99

[1]An average of 90 female queenfish per length class were examined each month.

spawners to 6 mo in the largest fish. Relatively few females start spawning at age I. Of all sexually active (Stages 2-4, Table 1) females captured during the 1979 spawning season, 6 and 34% were <12 cm and <13.5 cm, respectively.

Ovarian Cycling

Monthly peaks in the proportion of females in ready-to-spawn condition occurred during the moon's first quarter (contingency chi square = 27.7; 3 df; $P < 0.0005$; Siegel 1956). At such times

from 19 to 42% of all the adult females in the day's samples had ovaries containing eggs in a hydrated state (Figure 2B).

Female *S. politus* begin hydrating oocytes after dawn and spawn between late afternoon and evening. No difference existed between the percent frequency occurrence of ready-to-spawn females in samples collected at different times during daylight hours; and no fish caught at any time during the night were ready to spawn (Table 3). These results were reexamined for subsample ovaries, using accepted histological criteria for distinguishing hydrated from non-

TABLE 3.—Frequency occurrence of mature female queenfish whose ovaries contained oocytes in a hydrated vs. a nonhydrated state in samples collected during various 6-h intervals on 25-28 June 1979.

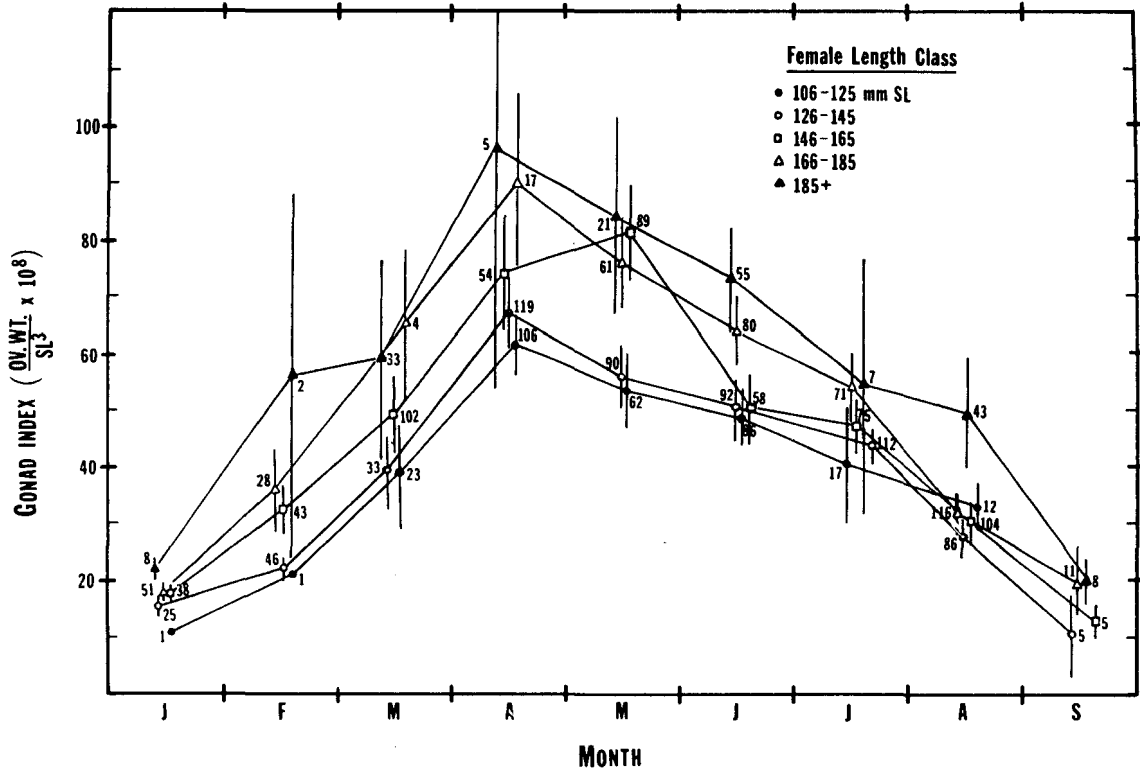| Collection period	No. samples	No. fish containing		No. females examined
		Hydrated oocytes	Nonhydrated oocytes only	
0600-1200	3	10	90	100
1200-1800	4	15	66	81
1800-0000	5	0	81	81
0000-0600	5	0	84	84

FIGURE 4.—Mean gonad indices of adult female queenfish of five length classes collected March-August 1979. Sample sizes and 95% confidence limits of means are indicated.

hydrated oocytes (Yamamoto and Yamazaki 1961; Yamamoto and Yoshioka 1964; Macer 1974; Htun-Han 1978), as illustrated in Figure 5. Histological results verified our conclusions based on the external appearance of ovaries (Table 4).

Spawning frequency thus can be inferred from the proportion of daytime sample fish whose ovarian eggs are in a hydrated state. Throughout the 1979 spawning season, an average of 13.6% of the females (of all sizes) present in daytime samples were in a ready-to-spawn condition (Table 5); thus females spawn on average every 7.4 d. Spawning frequency was similar for females of all body sizes (Table 5). Confidence intervals of these percent frequency occurrence data are necessarily asymmetrical, since female spawners are contagiously distributed among sample fish and, like hydrated-state females of the northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980), their sampling frequency is best described by the normal-log negative binomial distribution.

Sex Ratio

The breeding adult sex ratio of *S. politus* was 1.04 males to 1.00 females. The mean percentage of females among 16,794 adults was 49% with a 95% confidence interval of ±0.8%. The sex ratio was more skewed in favor of males in samples of fish containing one or more females in ready-to-spawn condition (Table 6).

Batch Fecundity

The number of eggs liable to be produced per spawning, i.e., the potential batch fecundity, was estimated for fish collected throughout the 1979 spawning season. The Gilson's fluid-fixed ovaries of daytime sample fish of a complete range of body sizes were used. Potential fecundity varied as the cube of standard length, and was proportional to body size in a consistent manner throughout the season (Figure 6). Bimonthly regressions of
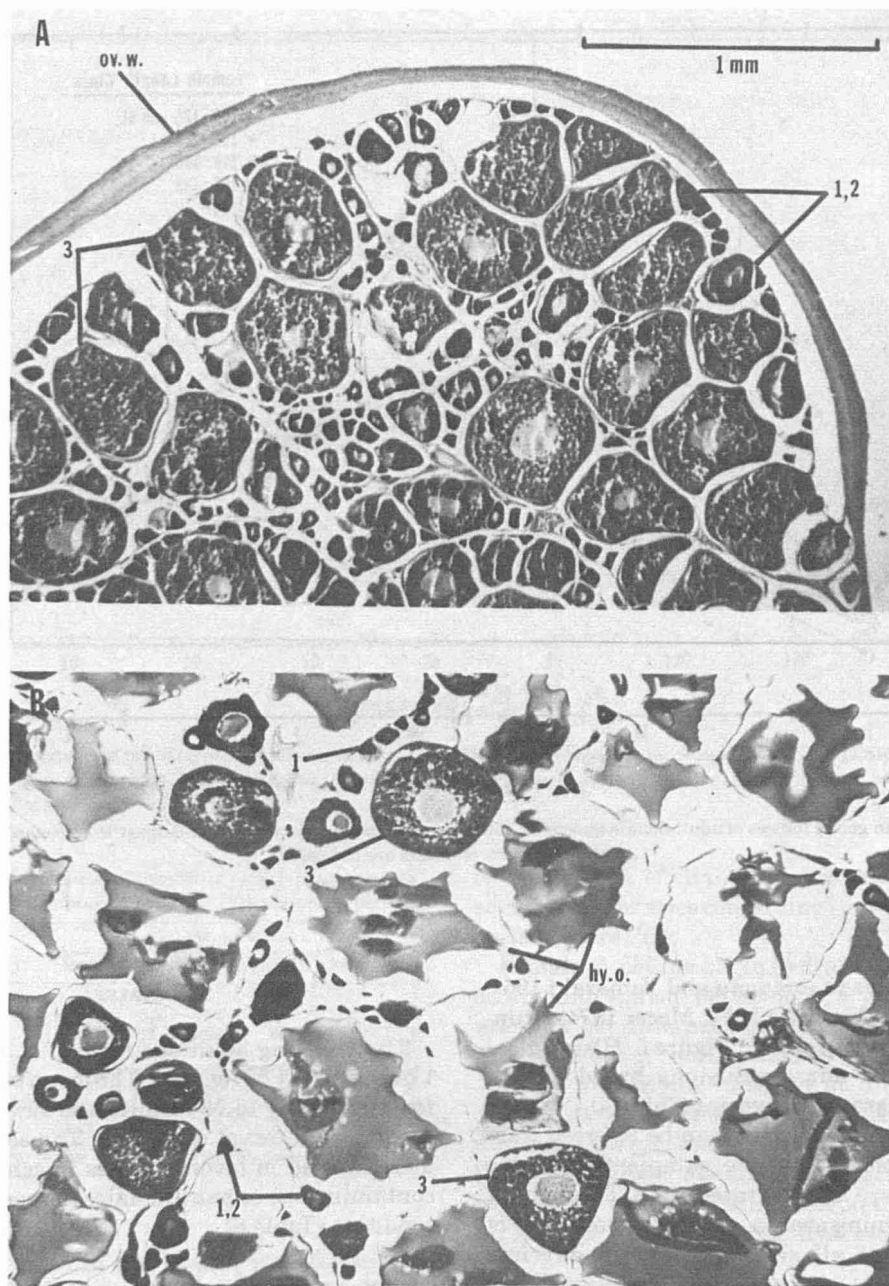
FIGURE 5.—Photomicrographs of transverse sections of (A) Stage 2 and (B) Stage 3 mature queenfish ovaries. Hyaline (hydrated) oocytes are still in their follicles in (B). Key for plate: hy.o. - hyaline oocyte; 1, 2 - Type 1 or Type 2 developing oocyte; 3 - Type 3 developing oocyte; ov.w. - ovarian wall. [See Goldberg (1976) for definitions and histological criteria distinguishing the stages of oocyte development in queenfish.]

TABLE 4.—Agreement between queenfish ovaries classified as hydrated or nonhydrated using external (gross) appearance and histological (microscopic) techniques.[1]

		Microscopic basis	
		Hydrated	Nonhydrated
Gross basis	Hydrated	49	2
	Nonhydrated	2	60

[1]n = 113 ovary pairs scored as (non)hydrated prior to fixation, staining, sectioning, and microscopic examination.

TABLE 5.— Frequency occurrence of queenfish ovaries in hydrated condition[1] as percent of all ovaries from adult sample fish[2] collected March-August 1979. The 95% confidence intervals on the percentage of hydrated females are indicated in parentheses.

Size group (cm SL)	No. sample fish	No. nonhydrated	No. hydrated	Mean[3] percent hydrated
10.5-12.5	342	294	48	14.0 (6.8, 28.8)
12.6-14.5	608	525	83	13.6 (7.9, 23.5)
14.6-16.5	519	462	57	11.0 (7.5, 16.1)
16.6-18.5	450	384	66	14.7 (6.8, 31.9)
>18.5	156	128	28	17.9 (9.0, 35.4)
All sizes	2,075	1,793	282	13.6 (8.2, 22.7)

[1]Classified based on gross characteristics of ovaries.
[2]Four net haul samples (daytime, 5-11 m) collected on 1 d cruise each week during 22 March-20 August 1979.
[3]Calculations based on normal-log negative binomial distribution (Zweifel and Smith in press).

fecundity on body size neither varied in slope ($F = 1.49$; 2,136 df; $P > 0.25$) nor in intercept ($F = 0.50$; 2,138 df; $P > 0.75$). Data were thus pooled over the entire 6-mo season and the general fecundity-length relation described by the best fit ($R^2 = 0.664$, $n = 142$, $P < 0.01$) equation

$$\log_{10} F = 3.3809 \log_{10} SL - 3.1455$$

where F = batch fecundity
SL = standard length in millimeters.

Fecundity was better correlated ($R^2 = 0.816$, $n = 42$) with body weight (Figure 7) than with length of female (Figure 6), as described by the equation

$$\log_{10} F = 1.302 \log_{10} W + 1.968$$
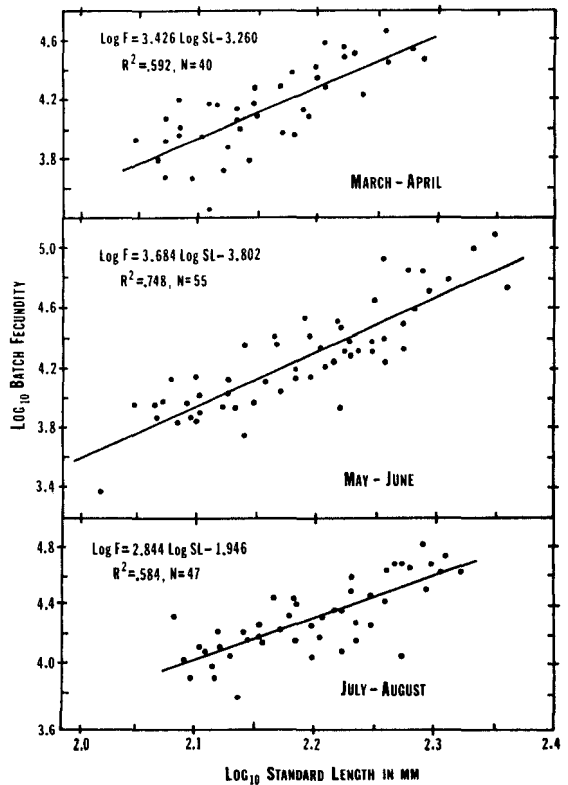
where W = ovary-free weight in grams.

FIGURE 6.— Relation between the common logarithms of batch fecundity (as the number of hydrating oocytes) and length of queenfish collected during the first, middle, and latter third of the 1979 spawning season. Regression equations are least squares best fit.

The length-weight relation was tightly correlated ($R^2 = 0.986$, $n = 175$) according to the equation

$$\log_{10} W = 3.1105 \log_{10} SL - 5.0560.$$

The average-sized (14 cm, 42 g) female had a potential batch fecundity during 1979 of 12,000-13,000 eggs. Batch fecundities ranged from about 5,000 eggs in a 10.5 cm female to about 90,000 eggs in a 25 cm fish.

TABLE 6.—Relation between adult sex ratio (females/total adults) of samples and percent frequency occurrence of female queenfish containing hydrated[1] eggs.

Sex ratio class	Class mean	No. samples[2]	Percent of females containing		No. adult females examined
			Hydrated[1] eggs	Nonhydrated[1] eggs only	
0.22-0.50	0.37	46	15.2	84.8	1,003
.51- .74	0.61	19	13.4	86.6	649
.75- .98	0.84	13	10.9	89.1	384

[1]Classified based on external characteristics of ovaries.
[2]From four to six net haul samples (daytime, 5-11 m) examined each week during 22 March-20 August 1979.
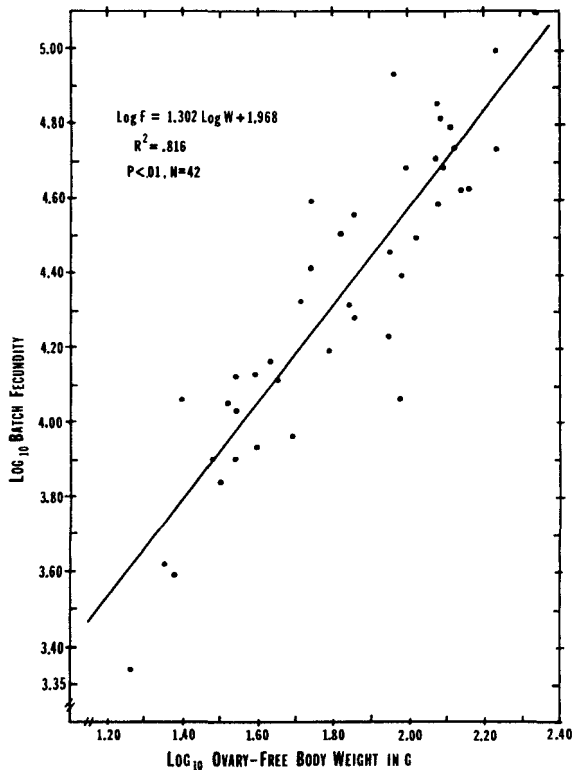
FIGURE 7.—Relation between the common logarithms of batch fecundity and ovary-free body weight of queenfish collected March-August 1979. Regression is the least squares best fit.

Residual Ova

Since not all of the eggs that are ripened and ovulated might be shed, we estimated the numbers of residual, ovulated eggs present in the ovaries of recently spawned, night sample fish. Numbers of residual ova were trivial (Table 7), indicating that females ovulate and shed virtually all of the eggs that undergo hydration.

Annual Egg Production

The spawning season of *S. politus* near San

TABLE 7.—Numbers of residual (ovulated but unspawned) eggs[1] present in spent (Stage 5) ovaries of queenfish. Numbers of residual eggs also expressed as percent of batch fecundity (estimated from standard length).

| Item | No. residual ova | Batch fecundity | |
		Estimated	Percent
Mean	25	25,500	0.1
Range	2-101	8,100-67,100	0.005-.6

[1] Based on examination of 16 females ($\bar{X}$ = 16.2 cm SL, range 12.1-22.0 cm) collected March-August 1979.

Diego lasts 3-6 mo, being longer for larger females (Table 2). Since batch fecundity is also proportional to female body size, annual egg production of individual fish ranges greatly. We estimate that a 10.5 cm female, spawning once every 7.4 d during May-July, produces about 60,000 eggs, whereas a 25 cm fish that spawns once every 7.4 d over a 6-mo period (March-August) produces nearly 2.3 million eggs. The relatively huge egg production by large *S. politus* thus reflects both greater numbers of spawnings over a longer season and larger batch fecundities.

Relative Fecundity

The numbers of eggs produced per unit of body weight, i.e., "relative fecundity" (Nikolskii 1969), is an increasing function of body size in *S. politus* (Figures 4, 8). On a per spawning basis, larger females allocate relatively more energy to egg
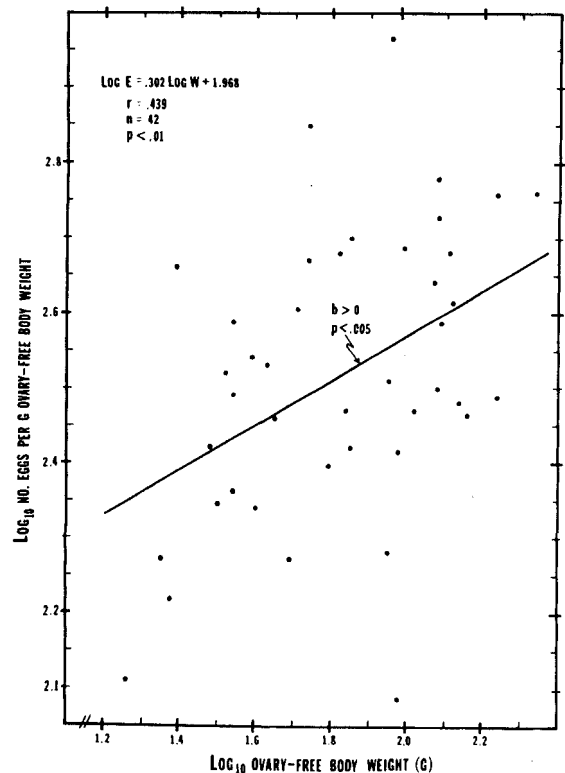

FIGURE 8.—Relation between relative fecundity (as the batch numbers of eggs per gram ovary-free body weight) and ovary-free body weight of queenfish collected March-August 1979. Transformation of raw data to common logarithms provided a tighter correlation (greater R^2) than untransformed data.

production than smaller females. The average 42 g fish produces 287 eggs/g of ovary-free body weight. Values range from an average 218 eggs/g to 494 eggs/g respectively (Figure 8) in a 10.5 cm and a 25 cm fish. Ripening (Stage 2, Table 1) ovaries compose 3.8% (for small fish <13.5 cm) and 4.2% (large fish >13.5 cm) of body weight. Ripe ovaries containing hydrated (Stage 3) oocytes made up an average 7.1% and 8.0% of the body weight of small and large *S. politus*, respectively. The average female produces about 4,570 eggs/g of Stage 3 ovary.

Egg Size

The Gilson's fluid-fixed, hydrated and non-hydrated oocytes of *S. politus* average 540 μm and 400 μm in diameter, respectively, and egg
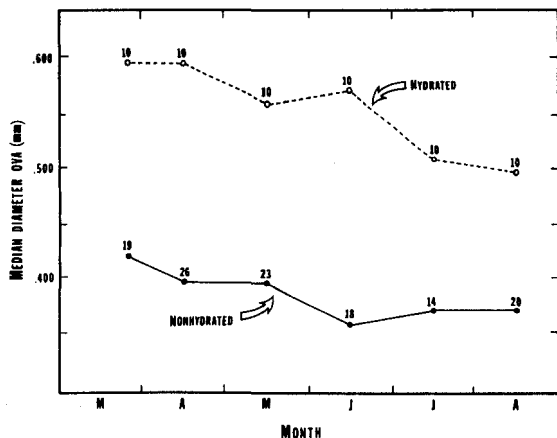

FIGURE 9.—Median diameters (random axis, Gilson's fixed) of the largest size-frequency class of oocytes present in subsampled queenfish of all body sizes collected March-August 1979. Data for fish with Stage 2 and Stage 3 ovaries are plotted separately. Numbers of sample fish are indicated.

TABLE 8.—Results of two-way analysis of variance of the effects of month and female size on the median diameter of the largest oocytes in ripening (Stage 2) ovaries of queenfish. Sample size = 417 fish.

Source of variation	df	F	P
Main effects	9	7.526	0.001
Month[1]	5	9.783	0.001
Female size[2]	4	3.833	0.005
Two-way interaction:			
Month × size	20	1.597	0.05
Explained	29	3.437	0.001
Residual	387	—	—
Total	416	—	—

[1]Spawning season partitioned into 6 mo: March, April, May, June, July, August 1979.
[2]Females divided into five length classes: 10.6-12.5, 12.6-14.5, 14.6-16.5, 16.6-18.5, >18.5 cm SL.

size in general declines as the spawning season progresses (Figure 9). Eggs fixed in Gilson's fluid are 85% the diameter of fresh eggs; thus actual egg size declined from about 685 to 580 μm between March and August 1979. Egg size also varied among different-sized females (Table 8). Throughout the season larger females generally produced larger eggs than did smaller females.

DISCUSSION

Size at Sexual Maturity

The smallest *S. politus* that contained ripe (Stage 3) eggs were 10.0-10.5 cm SL. At this size females are in their first spring or second summer following birth and average about 13 mo old (DeMartini et al. footnote 4). The onset of egg production by recruit spawners is variable, however; on average only 38% of the females this small contained mature eggs throughout the season, and >10% were generally immature at all lengths <13.5 cm (Table 2). A variable body size at first sexual maturity is a common feature of serial spawners and fishes in general (Nikolskii 1969).

Goldberg (1976) found no histological evidence of sexual maturity in female *S. politus* <14.8 cm SL among those he examined during November 1974-October 1975 from Santa Monica Bay, Calif., about 110 km upcoast of our study area. This might be due to geographic or annual variation in size at maturity, but more likely reflects chance error as only two fish <14.8 cm SL were among those examined (Goldberg[5]).

Body Size and Length of Spawning Season

Duration of the spawning season of repeat-spawning *S. politus* is in general about twice as long as the season for recruit spawners (Table 2). An earlier onset and later cessation of spawning by larger, older individuals is known for other serial spawning fishes of southern California, including northern anchovy (perhaps: see Hunter and Macewicz 1980); Pacific sardine, *Sardinops sagax caeruleus* (Clark 1934); jack mackerel, *Trachurus symmetricus* (Wine and Knaggs 1975); Pacific mackerel, *Scomber japonicus* (Knaggs and Parrish 1973); and California grunion, *Leuresthes*

[5]Stephen R. Goldberg, Department of Biology, Whittier College, Whittier, Calif., pers. commun. August 1978.

555

tenuis (Clark 1925). A protracted spawning season is generally characteristic of repeat spawners (Nikolskii 1969).

Temporal Patterns of Spawning

The peaks in spawning synchrony among female *S. politus* during the moon's first quarter are likely adaptive for several reasons. Spawning at dusk while the night sky is still fairly dark probably helps conceal adults and planktonic eggs from visual predators. Furthermore, tidal exchanges are minimal during the moon's first quarter (Figure 2B) and the conservation of planktonic eggs and larvae in nearshore areas may be facilitated. Juvenile and adult queenfish inhabit depths < 20 m during most of the year (DeMartini and Larson[6]), and most queenfish larvae are found in water < 30 m within 4-5 km of shore (Barnett et al.[7]).

Little data exist on the subseasonal spawning patterns of other temperate marine fishes. The data of Clark (1934) suggested monthly spawning peaks for Pacific sardine around times of the full moon. Farris (1963) later showed that no lunar spawning periodicity exists for Pacific sardine and jack mackerel off southern California, although diel and seasonal patterns occur in both species. Northern anchovies spawn between 2200 and 0400 h (Smith 1978, cited in Hunter and Goldberg 1980). A number of north Atlantic fishes have diel spawning periodicities (Simpson 1971). Lunar spawning intervals are known for several littoral fishes that spawn demersal eggs (e.g., California grunion, Clark 1925; mummichog, *Fundulus heteroclitus*, Taylor et al. 1979, Taylor and DiMichele 1980).

Sex Ratio of Spawning Fish

Although the overall adult sex ratio of *S. politus* was only slightly male biased, the male:female sex ratio averaged about 2:1 in groups of fish in which the highest proportion of ready-to-spawn females

were present. Hunter and Goldberg (1980) noted the same phenomenon in spawning schools of the northern anchovy and other pelagic spawners. The skewed sex ratio in spawning schools of the queenfish, however, should not bias our estimates of female spawning frequency either for or against spawning females, as may be the case with northern anchovy (Hunter and Goldberg 1980; Hunter and Macewicz 1980), since queenfish were sampled within the entire water column over the total daytime onshore-offshore distribution of the species.

Egg Production and Fish Body Size

The batch fecundity of *S. politus* is proportional to length cubed and is better correlated with weight than with body length, both being general phenomena in fishes (Nikolskii 1969).

The low standing crop ovary weights (2-4% body weight) of *S. politus*, and of multiple-spawning fishes in general (e.g., 6% in the northern anchovy, Smith and Lasker 1978; 4.1-9.0% in the scaled sardine, *Harengula jaguana*, Martinez and Houde 1975), greatly underrepresent total egg production by serial spawners. We estimate that a 25 cm (253 g) *S. politus* with an annual egg production of about 2.2 million eggs (24 batches averaging 90,000 eggs, each egg an average 0.635 mm diameter and 0.134 mg fresh weight) expends the equivalent of 114% of its body weight in eggs in a year. This is not unexpectedly high, since, for example, females of one species of silverside, *Menidia audens*, produce about 6-8 times their body weight in eggs per year (Hubbs 1976). This is, however, considerably more than the seemingly great egg investments made by fishes in which females are single clutched and spawn large, benthic, adhesive eggs (e.g., 20% in the fourhorn sculpin, *Myoxocephalus quadricornis*, Westin 1968; 30% in the red Irish lord, *Hemilepidotus hemilepidotus*, DeMartini and Patten 1979; 34% in the plainfin midshipman, *Porichthys notatus*, DeMartini[8]). Doubtless the poorer survival of small, planktonic eggs and larvae (Ware 1975) necessitates the production of greater numbers of eggs. Partial overlap in the ripening of eggs in successive batches allows greater numbers of eggs of a given size to be produced per unit time, as

[6] E. E. DeMartini and R. J. Larson, Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106, unpubl. data.
[7] Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. Long term average spatial patterns of ichthyoplankton off San Onofre and their relationship to the position of the SONGS cooling system. A study submitted to the Marine Review Committee of the California Coastal Commission, July 22, 1980. Unpubl. rep., 32 p. Marine Ecological Consultants of Southern California, 533 Stevens Avenue, Suite D-57, Solana Beach, CA 92075.

[8] DeMartini, E. E. Variations in fecundity and growth among geographic populations of the plainfin midshipman, *Porichthys notatus*. Manuscr. in prep. Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106.

space within the female's body cavity must set an upper limit to the numbers of eggs of a given size that can be simultaneously ripened and shed.

Egg production in *S. politus* is not directly proportional to weight, as it is in many marine fishes (Bagenal 1967), but is instead an increasing function of body weight (Figure 8). Relative fecundity thus increases with body size in queenfish, as is also the case for northern anchovy (Hunter and Macewicz 1980) and two other offshore Pacific species, jack mackerel and the gonostomatid *Vinciguerria lucetia* (MacGregor 1976).

Spawning Frequency and Annual Fecundity

The 7-d ovarian cycling frequency of *S. politus* is similar to that of *Engraulis mordax* off southern California, the only other species for which analogous data now exists (Hunter and Goldberg 1980). Having first determined the degeneration rate of ovarian postovulatory follicles in laboratory fish, Hunter and Goldberg (1980) used data on the percent frequency occurrence of 1-d-old ovarian follicles in field sample fish to estimate that *E. mordax* spawns on average once every 6-8 d. Estimates of average spawning interval (5.3 d) based on relative incidence of northern anchovy females bearing hydrated oocytes and new postovulatory follicles were indistinguishable from estimates based on frequency occurrence of day 1 postovulatory follicles (Hunter and Goldberg 1980). Spawning frequency is unrelated to female body size in queenfish and the northern anchovy (Hunter and Macewicz 1980). Incidence of hydration provides accurate estimates of spawning frequency when, as with *E. mordax* and queenfish, an identifiable time of spawning exists, all ripe eggs are shed at this time, and sample fish can be collected accordingly.

Annual egg production is largely dependent on spawning frequency in multiple-spawning fishes. The 6- to 8-d spawning interval of *E. mordax* extrapolated over its 5-mo (January-May) peak spawning season (Lasker and Smith 1977), indicates that an individual northern anchovy ripens and sheds about 20 batches of eggs per year (Hunter and Macewicz 1980). At an average relative fecundity of 421 eggs/g (Hunter and Macewicz 1980), estimated annual egg production of the northern anchovy is over 8,000 eggs/g, or about 14 times greater than previous estimates of annual egg production inferred from standing crop fecundities (606 eggs/g, MacGregor 1968; 556 eggs/g,

Norberg[9]). Similarly, our estimates of the annual egg production of *S. politus* range from 12 to 24 times the batch fecundity of recruit spawners (90-d season) and of the largest repeat spawners (180-d season), respectively. These data on the ovarian cycling frequencies of the queenfish and the northern anchovy indicate that prior studies of egg production in multiple-spawning marine fishes have in general underestimated annual egg production by at least an order of magnitude. This seems generally true whether the egg production estimate was based on standing crop fecundity (e.g., Simpson 1951; MacGregor 1957) or standing crop fecundity multiplied by the number of spawnings as inferred from the number of size classes of yolked eggs (e.g., Hickling and Rutenberg 1936; DeSilva 1973; but see Shackley and King 1977). Our queenfish data and Hunter and Goldberg's (1980) data for the northern anchovy illustrate that the spawning frequency (hence annual egg production) of serial-spawning fishes cannot usually be inferred from the number of size-frequency modes of ovarian eggs. It follows that many past estimates of the standing stocks of serial spawners that have inferred female abundance based on egg-larval abundances and female fecundities have greatly overestimated stock sizes.

Production Cycles, Timing of Reproduction, and Egg Size

The seasonality of phyto- and zooplankton production strongly influences the timing of reproduction of temperate marine fishes; in general spawning seasons in the temperate zone are timed so that planktonic offspring are exposed to peak food densities (Cushing 1975). The spawning season of the northern anchovy, a species with many reproductive attributes similar to those of queenfish, coincides with phytoplankton production at the start of the production cycle, yet precedes the disruption of prey patches that occurs due to subsequent upwelling (Lasker 1975, 1978). Queenfish larvae prey on copepodites and adult zooplankters (Barnett et al.[10]), and thus it would

---

[9]Norberg, R. H. 1975. Investigations on the fecundity of northern anchovy, jack mackerel, and Pacific mackerel. Unpubl. manuscr., 23 p. Calif. Dep. Fish Game, 350 Golden Shore, Long Beach, CA 90802.

[10]Barnett, A. M., P. D. Sertic, and R. Davis. 1980. Data summary of larval fish stomach analysis. A study submitted to the Marine Review Committee of the California Coastal Commission, September 7, 1980. Unpubl. rep., 22 p. Marine Ecological Consultants of Southern California, 533 Stevens Avenue, Suite D-57, Solana Beach, CA 92075.

seem that queenfish reproduction is timed to coincide with peak zooplankton densities later in the production cycle.

Further evidence for the controlling influence of planktonic production on the timing of reproduction by many fishes, including queenfish, comes from subseasonal variations in egg size. Blaxter and Hempel (1963) demonstrated that larval survival is related to hatchling size, which in turn is proportional to egg volume. The egg (hence larval) size of temperate spring-summer spawning species in general declines over the spawning season, whereas size of eggs of autumn-winter spawning species increases over the season (Ware 1975). These changes in egg size coincide with the planktonic production cycle as it affects the kinds, sizes, and quantities of zooplankton prey available for fish larvae. Larval growth and mortality rates (influenced by seasonally changing predator densities and water temperatures as well as densities of planktonic prey) may also elicit adaptive changes in egg size (Ware 1975). A scenario for spring-summer spawners like queenfish might be as follows: At low water temperatures in early spring, growth of fish larvae is slow, relatively few large (adult) zooplankton are available as food for larval fish, and larger hatchlings are better able to temporarily withstand starvation and to capture and ingest large zooplankton. Also, since survival is related to size of larvae (Ware 1975), larger fish larvae have a lower probability of being eaten. As spring becomes summer, water temperatures rise, larvae can grow faster as more zooplankton of a greater array of sizes become available, and it is then adaptive to spawn greater numbers of smaller eggs that subsequently hatch as smaller larvae (Ware 1975). A large number of spring-summer spawners in the temperate zone track the production cycle in this manner (Bagenal 1971). Serial spawning in regions of upwelling appears to be a tropical adaptation to a temperate production cycle of high amplitude that is highly variable in timing (Cushing 1975). Fishes like queenfish spawn on numerous occasions, perhaps so as to "hedge their bet" against unpredictable, and often poor, subseasonal conditions for planktonic propagules. Of course, serial spawning may also be influenced by the fecundity demands necessitated by small adult body size and high adult mortality rates.

We estimate that the spawned eggs of S. politus declined from about 685 to 580 μm in diameter over the interval from March to August 1979. This 15% decrease in diameter corresponds to a 39% decrease in volume, or 65% of the difference expressed as a percentage of the smaller volume. This is a reasonable value; for marine fishes with planktonic eggs, the median percentage difference in intraspecific egg volume is just over 100%, with a range from 4.5 to 403% (Bagenal 1971). Assuming that the chemical composition of yolk in queenfish eggs remains constant during the spawning season, the calorific value of individual eggs declined by about 39%. Since the relation between batch fecundity and female body size is constant throughout the spawning season (Figure 6), queenfish appear to allocate less energy to egg production later in the season by producing smaller eggs. Engraulis mordax likewise produces smaller (Smith and Lasker 1978) and perhaps fewer (Hunter[11]) eggs later in its spawning season. The availability of food for adults as well as larvae appears to determine the timing and intensity of spawning by northern anchovy (Hunter and Goldberg 1980) as well as queenfish and perhaps also influences egg size in these fishes.

SUMMARY

The queenfish is a serial spawner with a protracted spawning season. Spawning frequency, although generally asynchronous among females, can be estimated from the incidence of fish with hydrated eggs and averages about once per week for females of all adult sizes. Duration of the spawning season, however, is proportional to female body size, ranging from 3 mo (April-June) in recruit spawners (10.0-10.5 cm SL) to 6 mo (March-August) in repeat spawners (>13.5 cm). Larger females begin spawning earlier in the year and continue spawning after the smallest fish have ceased. Recruit spawners and the largest repeat spawners thus produce about 12 to 24 batches of eggs during their respective spawning seasons.

Batch fecundity is proportional to female body size and is better correlated with weight than with length of female. Batch fecundity ranges from about 5,000 eggs in 10.5 cm SL recruit spawners to about 90,000 eggs in the largest (25 cm) repeat spawners. The average (14 cm) fish produces about 12,000-13,000 eggs per batch. Almost all hydrated eggs are liberated at the time of spawning, which

occurs at dusk and has monthly peaks in intensity during the week of the moon's first quarter.

Annual egg production ranges from about 60,000 eggs to over 2.2 million eggs in the smallest recruit spawner and the largest repeat spawner, respectively. The average female produces about 300,000 eggs in a year. These estimates of annual egg production are an order of magnitude greater than usually would be inferred based on oocyte size class frequencies.

Relative fecundity of the queenfish is an increasing function of body size. Larger females produce larger eggs, and females of all adult sizes produce larger eggs earlier in the season.

As reflected by the general nature of its protracted, serial spawning activities and by the timing of subseasonal variations in its egg size and in the female size-to-egg size and egg number relationships, the queenfish closely resembles many or most small, planktonic spawners of warm temperate regions. We suggest that the reproductive dynamics of the queenfish typify the suite of reproductive adaptations characteristic of small, short-lived fishes that must cope with irregular (unpredictable) subseasonal variations in planktonic productivity.

ACKNOWLEDGMENTS

LITERATURE CITED

BAGENAL, T. B.
    1967. A short review of fish fecundity. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 89-111. Blackwell Sci. Publ., Oxf., Engl.
    1971. The interrelation of the size of fish eggs, the date of spawning and the production cycle. J. Fish Biol. 3:207-219.

BAGENAL, T. B., AND E. BRAUM.
    1971. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 166-198. IBP (Int. Biol. Programme) Handb. 3.

BLAXTER, J. H. S., AND G. HEMPEL.
    1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. 28:211-240.

CLARK, F. N.
    1925. The life history of *Leuresthes tenuis*, an atherine fish with tide controlled spawning habits. Calif. Dep. Fish Game, Fish Bull. 10, 51 p.
    1930. Size at first maturity of the white sea bass (*Cynoscion nobilis*). Calif. Fish Game 16:319-323.
    1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. Calif. Dep. Fish Game, Fish Bull. 42, 49 p.

CONOVER, W. J.
    1971. Practical nonparametric statistics. Wiley, N.Y., 462 p.

CUSHING, D. H.
    1975. Marine ecology and fisheries. Camb. Univ. Press, N.Y., 278 p.

DeMARTINI, E. E., AND B. G. PATTEN.
    1979. Egg guarding and reproductive biology of the red Irish lord, *Hemilepidotus hemilepidotus* (Tilesius). Syesis 12:41-55.

DeSILVA, S. S.
    1973. Aspects of the reproductive biology of the sprat, *Sprattus sprattus* (L.) in inshore waters of the west coast of Scotland. J. Fish Biol. 5:689-705.

FARRIS, D. A.
    1963. Reproductive periodicity in the sardine (*Sardinops caerulea*) and the jack mackerel (*Trachurus symmetricus*) on the Pacific coast of North America. Copeia 1963: 182-184.

FEDER, H. M., C. L. TURNER, AND C. LIMBAUGH.
    1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

FITCH, J. E., AND R. J. LAVENBERG.
    1971. Marine food and game fishes of California. Univ. Calif. Press, Berkeley, 179 p.
    1975. Tidepool and nearshore fishes of California. Univ. Calif. Press, Berkeley, 156 p.

FREY, H. W.
    1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, Mar. Res. Agency, 148 p.

GOLDBERG, S. R.
    1976. Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*. Fish. Bull., U.S. 74:983-984.

HICKLING, C. F., AND E. RUTENBERG.
    1936. The ovary as an indicator of the spawning period in fishes. J. Mar. Biol. Assoc. U.K. 21:311-316.

HIGHAM, J. R., AND W. R. NICHOLSON.
    1964. Sexual maturation and spawning of Atlantic menhaden. Fish. Bull., U.S. 63:255-271.

HTUN-HAN, M.
    1978. The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: seasonal changes in the ovary. J. Fish Biol. 13:351-359.

HUBBS, C.
    1976. The diel reproductive pattern and fecundity of *Menidia audens*. Copeia 1976:386-388.

HUNTER, J. R., AND S. R. GOLDBERG.
    1980. Spawning incidence and batch fecundity in north-
        ern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:
        641-652.
HUNTER, J. R., AND B. J. MACEWICZ.
    1980. Sexual maturity, batch fecundity, spawning fre-
        quency, and temporal pattern of spawning for the
        northern anchovy, *Engraulis mordax*, during the 1979
        spawning season. Calif. Coop. Oceanic Fish. Invest.
        Rep. 21:139-149.
KNAGGS, E. H., AND R. H. PARRISH.
    1973. Maturation and growth of Pacific mackerel *Scomber
        japonicus* Houttuyn. Calif. Dep. Fish Game, Mar. Res.
        Tech. Rep. 3, 19 p.
LASKER, R.
    1975. Field criteria for survival of anchovy larvae: The
        relation between inshore chlorophyll maximum layers
        and successful first feeding. Fish. Bull., U.S. 73:453-462.
    1978. The relation between oceanographic conditions and
        larval anchovy food in the California Current: identifica-
        tion of factors contributing to recruitment failure. Rapp.
        P.-V. Réun. Cons. Int. Explor. Mer 173:212-230.
LASKER, R., AND P. E. SMITH.
    1977. Estimation of the effects of environmental variations
        on the eggs and larvae of the northern anchovy. Calif.
        Coop. Oceanic Fish. Invest. Rep. 19:128-137.
LIMBAUGH, C.
    1961. Life history and ecologic notes on the black croaker.
        Calif. Fish Game 47:163-174.
MACER, C. T.
    1974. The reproductive biology of the horse mackerel
        Trachurus trachurus (L.) in the North Sea and English
        Channel. J. Fish Biol. 6:415-438.
MACGREGOR, J. S.
    1957. Fecundity of Pacific sardine (*Sardinops caerulea*).
        U.S. Fish Wildl. Serv., Fish. Bull. 57:427-449.
    1968. Fecundity of the northern anchovy, *Engraulis mor-
        dax* Girard. Calif. Fish Game 54:281-288.
    1976. Ovarian development and fecundity of five species
        of California current fishes. Calif. Coop. Oceanic Fish.
        Invest. Rep. 18:181-188.
MARTINEZ, S., AND E. D. HOUDE.
    1975. Fecundity, sexual maturation, and spawning of
        scaled sardine (*Harengula jaguana* Poey). Bull. Mar.
        Sci. 25:35-45.
MILLER, D. J., AND R. N. LEA.
    1972. Guide to the coastal marine fishes of California.
        Calif. Dep. Fish Game, Fish Bull. 157, 235 p.
MOSER, H. G.
    1967. Reproduction and development of *Sebastodes pauci-
        spinis* and comparison with other rockfishes off southern
        California. Copeia 1967:773-797.
NIKOLSKII, G. V.
    1969. Theory of fish population dynamics as the biological
        background for rational exploitation and management
        of fishery resources. Oliver & Boyd, Edinb., 323 p.

SHACKLEY, S. E., AND P. E. KING.
    1977. The reproductive cycle and its control; frequency of
        spawning and fecundity in *Blennius pholis* L. J. Exp.
        Mar. Biol. Ecol. 30:73-83.
SIEGEL, S.
    1956. Nonparametric statistics for the behavioral sciences.
        McGraw-Hill, N.Y., 312 p.
SIMPSON, A. C.
    1951. The fecundity of the plaice. Fish. Invest. Minist.
        Agric. Fish. Food (G.B.) Lond., Ser. II, 17(5), 27 p.
    1971. Diel spawning behaviour in populations of plaice,
        dab, sprat and pilchard. J. Cons. 34:58-64.
SKOGSBERG, T.
    1939. The fishes of the family Sciaenidae (croakers) of
        California. Calif. Div. Fish Game, Fish Bull. 54:1-62.
SMITH, P. E., AND R. LASKER.
    1978. Position of larval fish in an ecosystem. Rapp.
        P.-V. Réun. Cons. Int. Explor. Mer 173:77-84.
TAYLOR, M. H., AND L. DiMICHELE.
    1980. Ovarian changes during the lunar spawning cycle
        of *Fundulus heteroclitus*. Copeia 1980:118-125.
TAYLOR, M. H., G. J. LEACH, L. DiMICHELE, W. M. LEVITAN,
    AND W. F. JACOB.
    1979. Lunar spawning cycle in the mummichog, *Fundulus
        heteroclitus* (Pisces: Cyprinodontidae). Copeia 1979:
        291-297.
WARE, D. M.
    1975. Relation between egg size, growth, and natural
        mortality of larval fish. J. Fish. Res. Board Can. 32:
        2503-2512.
WESTIN, L.
    1968. The fertility of fourhorn sculpin, *Myoxocephalus
        quadricornis* (L). Inst. Freshwater Res. Drottningholm
        Rep. 48:67-70.
WINE, V. L., AND E. H. KNAGGS.
    1975. Maturation and growth of jack mackerel, *Trachurus
        symmetricus*. Calif. Dep. Fish Game, Mar. Res. Tech.
        Rep. 32:1-25.
YAMAMOTO, K., AND F. YAMAZAKI.
    1961. Rhythm of development in the oocyte of the gold-fish,
        Carassius auratus. Bull. Fac. Fish. Hokkaido Univ.
        12:93-110.
YAMAMOTO, K., AND H. YOSHIOKA.
    1964. Rhythm of development in the oocyte of the medaka,
        Oryzias latipes. Bull. Fac. Fish. Hokkaido Univ. 15:5-19.
YOUNG, P. H.
    1963. The kelp bass (*Paralabrax clathratus*) and its fish-
        ery, 1947-1958. Calif. Dep. Fish Game, Fish Bull. 122,
        67 p.
ZWEIFEL, J. R., AND P. E. SMITH.
    In press. A time series of anchovy embryonic and larval
        mortality estimates with method for confidence limits on
        the estimates of abundance of all sizes and on the mortal-
        ity rate. *In* R. Lasker and K. Sherman (editors), The
        early life history of fish. Rapp. P.-V. Réun. Cons. Int.
        Explor. Mer 177.