REPRODUCTIVE BIOLOGY OF THREE CALIFORNIA SPECIES OF *PARALABRAX* (PISCES: SERRANIDAE)

DEBRA L. ODA, ROBERT J. LAVENBERG, AND JAMES M. ROUNDS
Natural History Museum of Los Angeles County
Section of Fishes
900 Exposition Boulevard
Los Angeles, California 90007

ABSTRACT

Paralabrax clathratus, P. maculatofasciatus, and *P. nebulifer,* common off California, spawn in the warm summer months. All three species are capable of daily spawning, but our data indicate that the mean interval between spawning events is about two days. In general, *P. clathratus* and *P. maculatofasciatus* appear to spawn most frequently in the late afternoon and evening hours; *P. nebulifer* may spawn most often at midday. Our data indicate that batch fecundity (*BF*, number of eggs) is approximately related to the ovary-free body weight (*OFW*, grams) of *P. clathratus*, according to the equation $\log_{10} BF = 0.91^{*}\log_{10} OFW + 5.26$ ($n = 25$). Preliminary data are provided that relate batch fecundity to ovary-free body weight in *P. maculatofasciatus* and *P. nebulifer*. Evidence of hermaphroditism occurs in each species: *P. maculatofasciatus* is a protogynous hermaphrodite; the reproductive patterns of the other two species remain unclear.

RESUMEN

Paralabrax clathratus, P. maculatofasciatus y *P. nebulifer,* comunes frente a California, desovan en los meses cálidos de verano. Las tres especies son capaces de desovar diariamente; sin embargo, nuestros datos indican que el intervalo promedio entre eventos de desove es de alrededor dos días. En general, pareciera que el desove de *P. clathratus* y *P. maculatofasciatus* es más frecuente en horas avanzadas de la tarde y al anochecer, mientras que el desove de *P. nebulifer* pareciera ocurrir a menudo al mediodía. Nuestros datos indican que la fecundidad de cada puesta (*BF*, en número de huevos) en *P. clathratus* se relaciona aproximadamente con el peso corporal libre de ovarios (*OFW*, en gramos) de acuerdo a la ecuación $LOG_{10}BF = 0.91^{*}\log_{10}OFW + 5.26$ ($n = 25$). Se proveen datos preliminares que relacionan la fecundidad por puesta con el peso corporal libre de ovarios en *P. maculatofasciatus* y *P. nebulifer*. Se observa evidencia de hermafroditismo en las tres especies: *P. maculatofasciatus* es un hermafrodita protogínico; los patrones reproductivos de las otras dos especies son poco claros.

INTRODUCTION

Three species of *Paralabrax* are common in the waters off southern California: *P. clathratus* (kelp bass) and *P. nebulifer* (sand bass) in nearshore coastal waters, and *P. maculatofasciatus* (spotted sand bass) in harbors and bays. *Paralabrax nebulifer* and *P. clathratus* have been recognized as important game fish in southern California since 1916 (Collyer 1949). They remain one of the most frequent catches for sportfishers, ranking second and third, respectively, in number of fish taken in the state in 1989 (Oliphant 1990).

Aspects of spawning and reproduction in the species of *Paralabrax* have been variously reported. All three species spawn in the warm summer months (Clark 1933; Limbaugh 1955; Smith and Young 1966). *Paralabrax clathratus* (typically solitary) and *P. nebulifer* are known to gather in large schools during spawning (Limbaugh 1955). All three species are multiple spawners, although this has not always been clearly stated in previous literature. Quast (1968) suggested that *P. clathratus* may spawn more than once a season and that sex products are not completely released at spawning. Smaller *P. clathratus* were thought to spawn less frequently—only once each season—and to mature later than the multiply spawning larger individuals (Frey 1971). DeMartini (1987) reported that *P. clathratus* and *P. nebulifer* are multiple spawners, and estimated batch fecundity for specimens of both species collected between 1982 and 1985. Hastings (1989) has established that *P. maculatofasciatus*, from the northern Gulf of California, is a protogynous hermaphrodite. Most other members of the family Serranidae are hermaphroditic. Hermaphroditic characters were found in *P. clathratus*, but because of a lack of transitional individuals, the species was identified as a secondary gonochorist—i.e., having separate sexes but derived from a hermaphroditic ancestor (Smith and Young 1966).

For the past decade the reproductive biology of multiply spawning marine fishes has come under

[Manuscript received February 1, 1993.]

scrutiny. Techniques have been established to estimate spawning frequency and batch fecundity. Spawning frequency is estimated from the percentage of mature female fish with postovulatory follicles of a known age, or from the percentage of mature females with a full complement of hydrated oocytes (Hunter and Macewicz 1985). Eggs of the most advanced stage—typically hydrated oocytes—from an ovary sample of known weight are counted to estimate the number of ova that will be spawned in a single batch (Hunter et al. 1985). Our objectives were to estimate the spawning frequency and batch fecundity of *P. clathratus, P. nebulifer*, and *P. maculatofasciatus* using these techniques, and to determine at what time of day and in which season they spawn. Preliminary evidence for hermaphroditism is examined for each species.

MATERIALS AND METHODS

Adult and juvenile *Paralabrax* were collected between Ventura and Mission Bay, California, in spring and summer 1988. Fish were taken by hook and line, trawls, and entrainment during the initial phase of a heat treatment at the Los Angeles County Scattergood Generating Station, Playa del Rey, California. Most fish were sacrificed to obtain field data (*P. clathratus* n = 84, *P. maculatofasciatus* n = 79, *P. nebulifer* n = 81); some fish were transported live to the R & D Laboratory at the Southern California Edison Redondo Beach Generating Station. Time of collection, standard length (SL, mm), and weight (grams) were recorded for all field-collected specimens. Gonads were removed from sacrificed fishes, weighed, and preserved in 10% buffered Formalin.

Transported fish were allowed to acclimate to ambient conditions in 1,100-liter outdoor tanks equipped with flow-through seawater systems. Water temperature varied between 14.7° and 19.9°C during the *P. maculatofasciatus* experimental time period, between 15.3° and 20.9°C for *P. clathratus*, and between 16.9° and 19.9°C for *P. nebulifer*. On June 12–13, 1989, each fish was catheterized to determine spawning status, and tagged with a colored, numbered "spaghetti tag." All *P. clathratus* females, 97% of the *P. maculatofasciatus* females, and 26% of the *P. nebulifer* females were reproductively active (largest oocytes at least 0.4–0.5 mm). *Paralabrax nebulifer* females were reexamined on July 12; 73% were active. Each tank contained about equal numbers of mature specimens of each sex. Reproductively active females were injected with the hormone LHRHa (des-Gly^{10}-[d-Ala^{6}]-LHRH) to induce the maturation of oocytes (*P. clathratus* n = 17, *P. maculatofasciatus* n = 29, *P. nebulifer* n = 20). A dosage of 50 μg LHRHa per kg of fish weight was injected into the dorsal muscle tissue between the pectoral fin and anus. All tanks were visually and quantitatively inspected at least every hour for the presence of running ripe individuals or freshly spawned eggs. The time at which each female spawned was noted, and the fish were then sacrificed at predetermined time intervals. Each was weighed and measured (SL) before sacrifice, and ovaries were removed, weighed (wet weight), and preserved in 10% Formalin.

Samples of the preserved ovaries were embedded in Paraplast, sectioned (ca. 6 μm) and counterstained with hematoxylin-eosin for histological examination (Hunter and Macewicz 1985).

The appearances of postovulatory follicles in the specimens for the timed sacrificial series were used as a standard upon which to estimate spawning times in field-collected material. A general histological classification of the ovaries for all three species is as follows:

Hydrated: Hydrated or migratory-nucleus-stage oocytes in the ovary, and no new postovulatory follicles (figure 1A–C).

Day 0 (age ≤4-hour-old postovulatory follicles): New postovulatory follicles, typically convoluted with a well-defined lumen, ranging in size to ca. 300 μm. The granulosa epithelial cell and thecal connective cell layers may be separate; little or no degeneration of the cells is apparent (figure 1D and E).

Day 1 (age >4- to ≤24-hour-old postovulatory follicles): Postovulatory follicles reduced in size, generally 150–300 μm, zero to few folds in the granulosa cell and thecal cell layers, and small lumen. Granulosa cells often with pycnotic nuclei, vacuoles, and degenerating cytoplasm (figure 2A–C).

Nonspawning (mature): Ovaries with many yolked oocytes, no postovulatory follicles, and no hydrating oocytes (figure 2D and E).

The degeneration of postovulatory follicles in *Paralabrax* is generally similar to that found in most other multiply spawning marine fishes that have been investigated (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Goldberg et al. 1984; Hunter et al. 1986; Schaefer 1987). But we could confidently identify only postovulatory follicles that were ≤24 hours old.

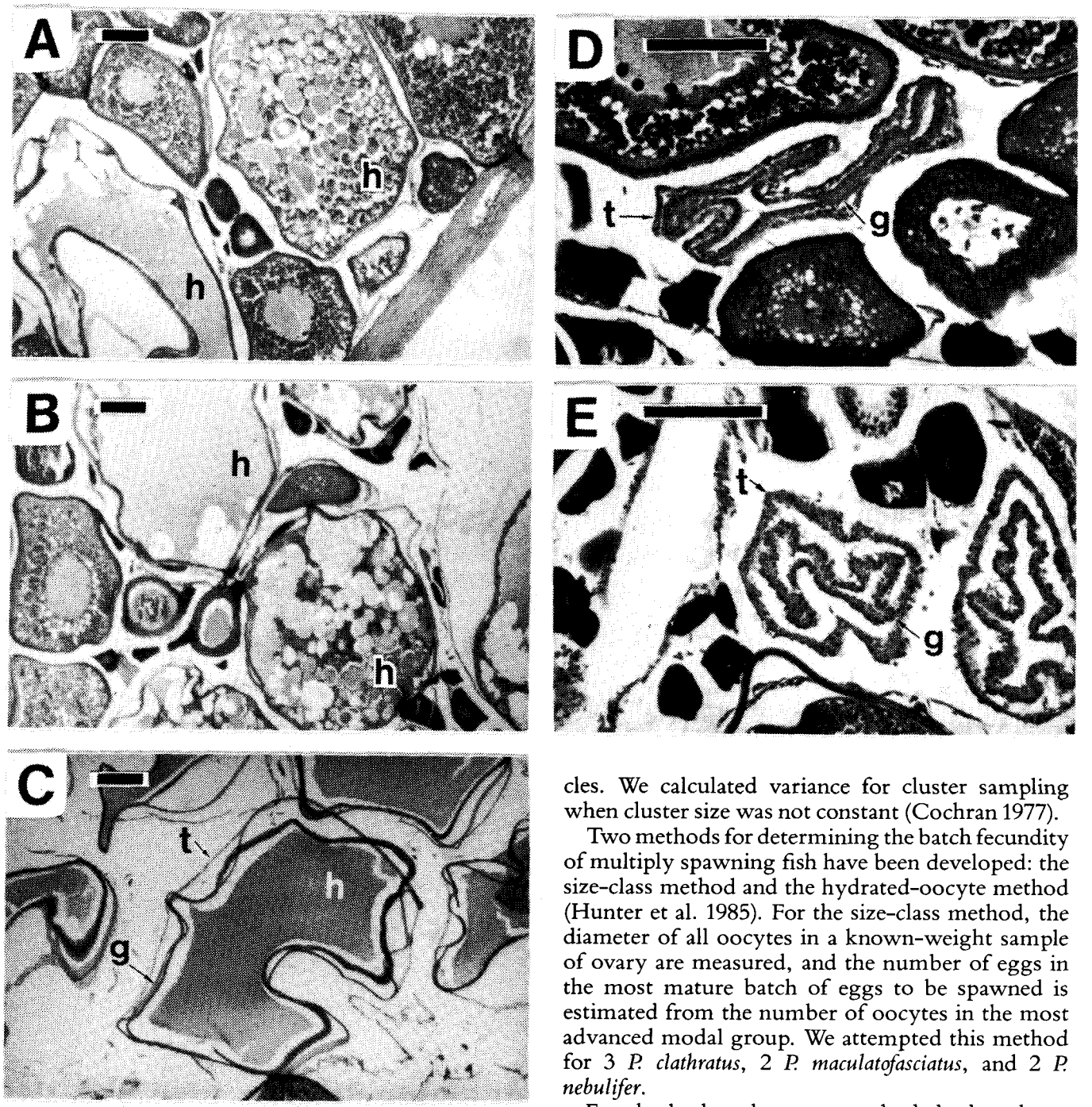

Figure 1. Hydrating oocytes: *A, Paralabrax maculatofasciatus*; *B, P. clathratus*; *C, P. nebulifer*. Postovulatory follicles, age day 0 (≤4 hrs old): *D, P. clathratus*; *E, P. nebulifer*. *h* = hydrating oocytes; *g* = granulosa epithelial cell layer; *t* = thecal connective cell layer. *Bar* = 0.1 mm.

Following the methodology of Hunter et al. (1986), we considered the data from our field collections of *Paralabrax* gonads as statistical clusters of samples from the population. We estimated spawning frequency on the basis of the number of females whose ovaries contained day-1 postovulatory follicles. We calculated variance for cluster sampling when cluster size was not constant (Cochran 1977).

Two methods for determining the batch fecundity of multiply spawning fish have been developed: the size-class method and the hydrated-oocyte method (Hunter et al. 1985). For the size-class method, the diameter of all oocytes in a known-weight sample of ovary are measured, and the number of eggs in the most mature batch of eggs to be spawned is estimated from the number of oocytes in the most advanced modal group. We attempted this method for 3 *P. clathratus*, 2 *P. maculatofasciatus*, and 2 *P. nebulifer*.

For the hydrated oocyte method, hydrated oocytes in a weighed sample of ovarian tissue are counted, and the ratio of hydrated oocytes to grams of ovary is extrapolated to total ovary weight in order to estimate the number of eggs in the most mature batch to be spawned. Specimens used in this method must have ovaries with oocytes that have sufficiently begun hydration, and show no evidence of ovulation of the batch. Initially, we used samples from 12 *P. clathratus*, 9 *P. maculatofasciatus*, and 4 *P. nebulifer* to test whether the location of tissue sam-

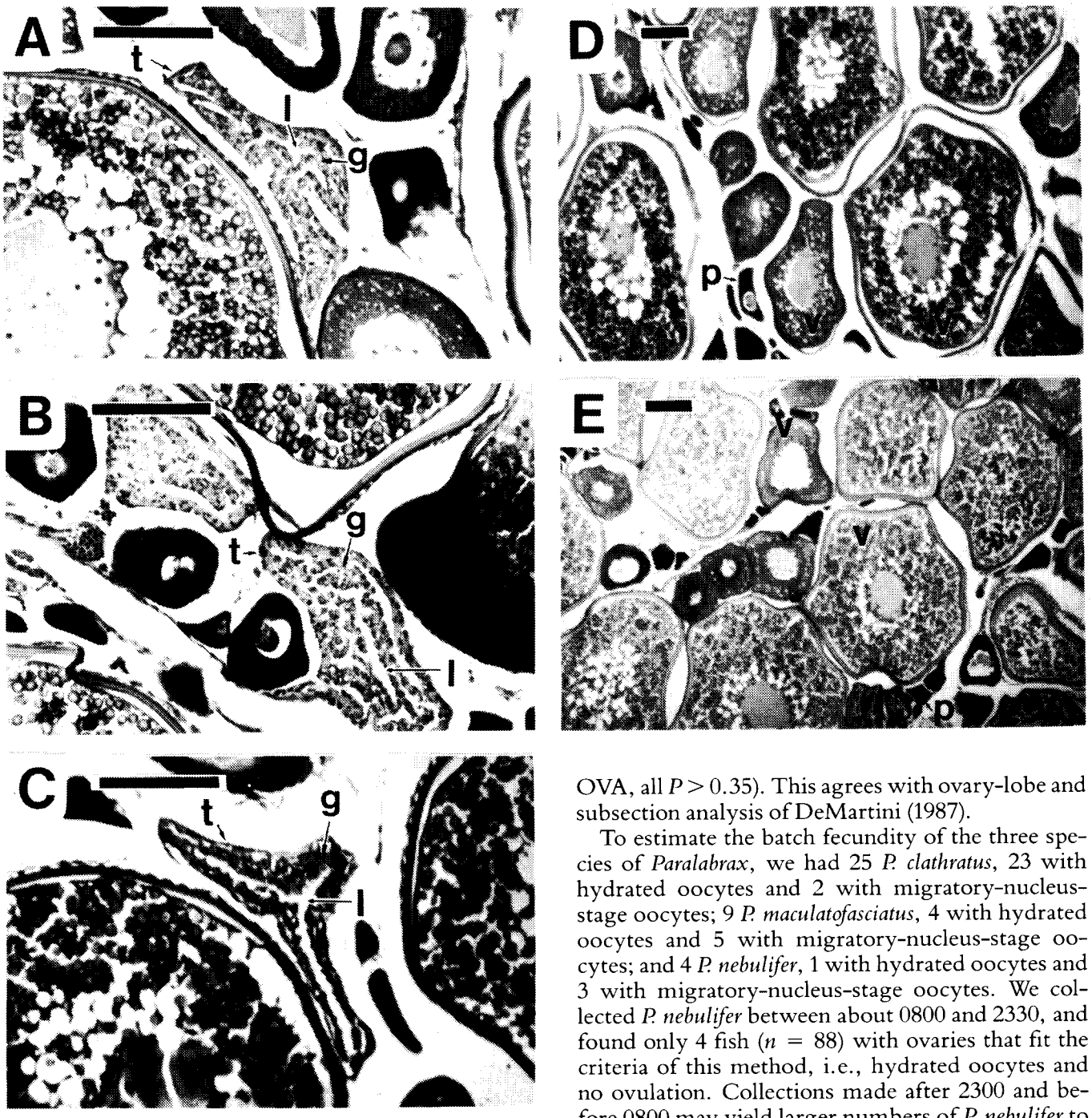

Figure 2. Postovulatory follicles, age day 1: *A*, *Paralabrax clathratus* (12–18 hrs old); *B*, *P. maculatofasciatus* (ca. 18 hrs old); *C*, *P. nebulifer* (12–18 hrs old). Nonspawning (mature) ovaries: *D*, *P. clathratus*; *E*, *P. maculatofasciatus*. *g* = granulosa epithelial cell layer; *l* = lumen; *p* = primary oocytes; *t* = thecal connective cell layer; *v* = vitellogenic oocytes. *Bar* = 0.1 mm.

ples (right or left ovarian lobe, position of the sample on the ovary lobe) would affect the estimate of batch fecundity in these species (Hunter et al. 1985). We found no statistically significant location difference in the number of mature oocytes (two-way ANOVA, all $P > 0.35$). This agrees with ovary-lobe and subsection analysis of DeMartini (1987).

To estimate the batch fecundity of the three species of *Paralabrax*, we had 25 *P. clathratus*, 23 with hydrated oocytes and 2 with migratory-nucleus-stage oocytes; 9 *P. maculatofasciatus*, 4 with hydrated oocytes and 5 with migratory-nucleus-stage oocytes; and 4 *P. nebulifer*, 1 with hydrated oocytes and 3 with migratory-nucleus-stage oocytes. We collected *P. nebulifer* between about 0800 and 2330, and found only 4 fish ($n = 88$) with ovaries that fit the criteria of this method, i.e., hydrated oocytes and no ovulation. Collections made after 2300 and before 0800 may yield larger numbers of *P. nebulifer* to use for estimating batch fecundity.

Our data provide two estimates of diel spawning period. We histologically examined ovaries of field-collected fish and categorized them according to the developmental stage of the most advanced oocytes. We followed oocyte development temporally to estimate a probable spawning time for each species. We estimated the age of postovulatory follicles by comparing them with our laboratory series, and back-calculated the time of spawning from capture time.

RESULTS AND DISCUSSION

Annual Spawning Period

Paralabrax are recognized as summer spawners off southern California. Clark (1933) reported a June-through-August spawning period for rock bass (*P. clathratus* and *P. nebulifer*), which was substantiated by Collyer and Young (1953) and Limbaugh (1955). Limbaugh (1955) also found that *P. maculatofasciatus* were ripe in July. Yearlong, monthly examinations of the gonads of *P. clathratus* by Smith and Young (1966) indicate that oocytes mature from May through September and that spermatocytes develop between April and September (no samples from October). Quast (1968) reported that the relative gonadal weight of *P. clathratus* increased in April and decreased in November, and spawning rate peaked from May to July.

Larval *Paralabrax* occur in ichthyoplankton samples collected in the nearshore Southern California Bight in early summer (Lavenberg et al. 1986). From 1978 to 1984, larval abundance peaked inshore of the 36-m contour between June and September, coinciding with reported peak spawning times. Generally, spawning occurs in the warm summer months when water temperatures typically exceed 16°C. When summer water temperatures drop, oocyte maturation or embryonic development may be affected. In July 1980, when sea temperatures were below 16°C, significantly fewer *Paralabrax* larvae were collected (Lavenberg et al. 1986; Petersen et al. 1986).

Diel Spawning Period

Estimated spawning times from both temporal oocyte development and postovulatory follicle ageing are generally comparable for each species. Spawning in *P. clathratus* probably begins in the late afternoon: migratory-nucleus-stage oocytes begin to develop in the morning; hydration and ovulation occur throughout the day; and individuals with new (0 to 4 hrs old) postovulatory follicles were collected in the evening (figure 3A). Age classification of postovulatory follicles (figure 3B) supports this estimate: our peak spawning estimates are from the late afternoon into the evening. During our limited collection periods for *P. maculatofasciatus*, we observed no spawning. We found hydrated oocytes throughout the day, and a few ovulating females in the afternoon (figure 3C). Spawning probably occurs late in the day: studies of postovulatory follicles indicate peak spawning in the afternoon and night (figure 3D). Evidence exists for prolonged day-long spawning in *P. nebulifer*: we collected ovulating females throughout the day, from 0800 to 1100, 1330 to 1500, and 1900 to 2300 (figure 3E). Age classification of postovulatory follicles also suggests prolonged daily spawning for *P. nebulifer*, with a noticeable peak at midday (noon–1400, figure 3F).

Our data support DeMartini's (1987) suggestion that the prolonged presence of hydrated oocytes in *P. nebulifer* resulted from a lengthy process of hydration. Oocyte maturation may be as long as 15 hours in *P. clathratus*. The earliest migratory-nucleus stages develop by ca. 0600 (females whose ovaries contained migratory-nucleus-stage oocytes, not at the earliest stage, were collected beginning at 0830), and spawning appears to peak at 2100 (figure 3B). Evidence of the length of time involved in oocyte maturation is less clear in *P. nebulifer* and *P. maculatofasciatus*.

Spawning Frequency

All three species — *P. clathratus*, *P. maculatofasciatus*, and *P. nebulifer* — are capable of daily spawning. Histological examination of ovaries of each species revealed individuals with both migratory-nucleus-stage or hydrating oocytes and postovulatory follicles that indicated ovulation had occurred 8 to 24 hours prior to collection (table 1, figure 4). These fish had all spawned before being collected (within 24 hours) and were hydrating a new batch of eggs to spawn, presumably within 15 hours. Two *P. nebulifer* had ovaries that contained early migratory-nucleus-stage oocytes, postovulatory follicles that were less than 4 hours old, and postovulatory follicles that were 18 to 24 hours old. These fish had recently spawned (<4 hours before capture), spawned the day before collection, and were maturing a new batch of oocytes that would have been spawned on the day after capture. Not all fish captured demonstrated evidence of daily spawning: 32% of the *P. clathratus* females (n = 84), 20% of the *P. maculatofasciatus* females (n = 79), and 31% of the *P. nebulifer*

TABLE 1
Evidence of Daily Spawning in Three Species of *Paralabrax**

Stages present in ovary	Numbers of female *Paralabrax*		
	P. clathratus	*P. maculatofasciatus*	*P. nebulifer*
POF_1 + MN	0	13	10
POF_1 + H	17	2	3
POF_1 + O	6	0	0
POF_1 + POF_0	1	0	16

*Each *Paralabrax* female had day-1 postovulatory follicles (8 to 24 hours old, POF_1) and either migratory-nucleus-stage oocytes (MN); hydrated oocytes (H); initial stages of ovulation (hydrated oocytes and new postovulatory follicles, O); or new (≤4 hours old) postovulatory follicles (POF_0).

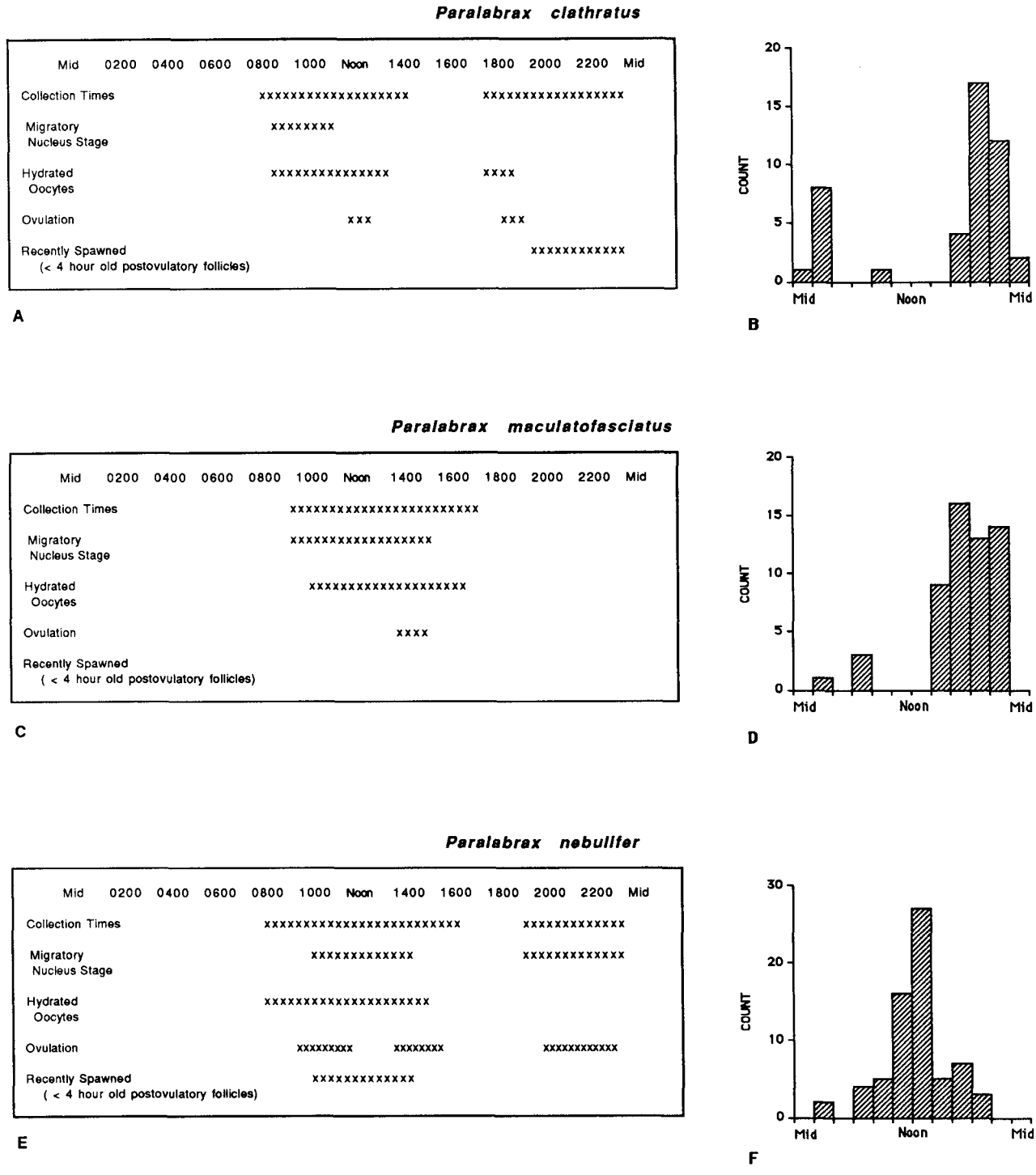

Figure 3. Time periods at which fish in various developmental stages were collected (*A*, *C*, *E*) and frequency distribution of estimated spawning times based on ages of postovulatory follicles (*B*, *D*, *F*).

females (n = 81) showed evidence of spawning on two consecutive days. There was no statistically significant difference in the average size of specimens that exhibited evidence of daily spawning, compared to those that had spawned the day before collection (but showed no evidence of maturing a new batch to be spawned the next day), those with hydrated oocytes in the ovary, or nonspawners (one-

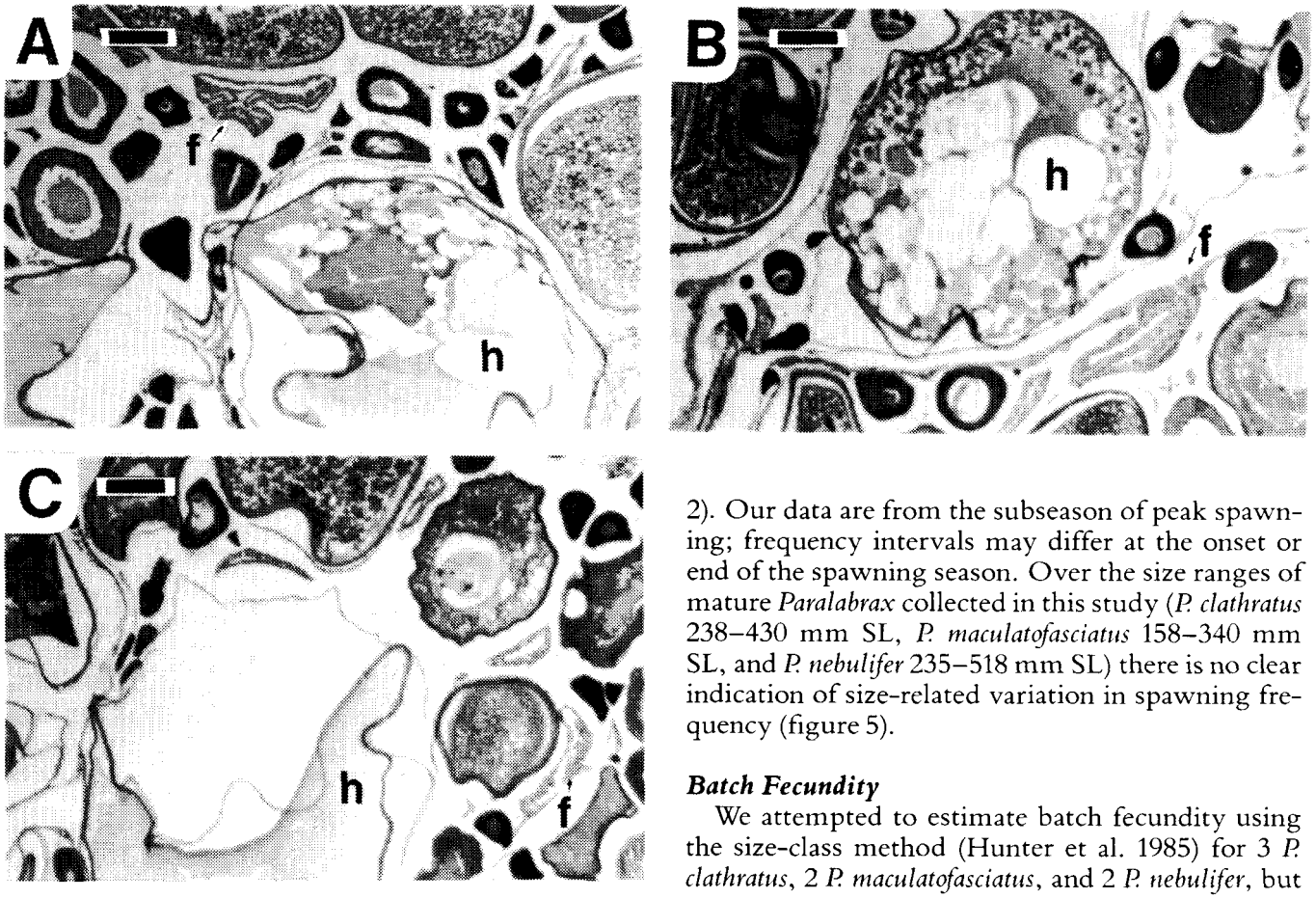

Figure 4. Evidence of daily spawning: presence of both day-1 postovulatory follicles and hydrating oocytes. *A*, *Paralabrax clathratus*; *B*, *P. maculatofasciatus*; and *C*, *P. nebulifer*. *h* = hydrating oocytes, *f* = day-1 postovulatory follicle. *Bar* = 0.1 mm.

way ANOVA, *P. clathratus*, $P = 0.221$, $n = 80$; *P. maculatofasciatus*, $P = 0.959$, $n = 79$; and *P. nebulifer*, $P = 0.554$, $n = 74$).

The proportion of females with day-1 postovulatory follicles was calculated as the total number of day-1 females divided by the total number of mature females. Spawning frequency is estimated by assuming that the proportion of females with day-1 ovaries is the proportion of fish that will spawn each day. The fraction of mature female *Paralabrax clathratus* collected with day-1 postovulatory follicles was 0.42 (standard deviation = 0.04; table 2), indicating an average of 2.4 days between each spawning event. An interval of 1.5 days between spawns was estimated for *P. maculatofasciatus* because the fraction of mature females collected with day-1 postovulatory follicles was 0.68 (standard deviation = 0.19; table 2). The average interval between spawning for *P. nebulifer* was estimated at 1.6 days; the fraction of mature females collected with day-1 postovulatory follicles was 0.63 (standard deviation = 0.19; table 2). Our data are from the subseason of peak spawning; frequency intervals may differ at the onset or end of the spawning season. Over the size ranges of mature *Paralabrax* collected in this study (*P. clathratus* 238–430 mm SL, *P. maculatofasciatus* 158–340 mm SL, and *P. nebulifer* 235–518 mm SL) there is no clear indication of size-related variation in spawning frequency (figure 5).

Batch Fecundity

We attempted to estimate batch fecundity using the size-class method (Hunter et al. 1985) for 3 *P. clathratus*, 2 *P. maculatofasciatus*, and 2 *P. nebulifer*, but

TABLE 2
Numbers of *Paralabrax* Females Collected in Various Spawning States

	Day 0				
Collection	Hydrated	≤4 Hours	Day 1	Nonspawning	Total
Paralabrax clathratus					
19 July	0	1	1	0	2
27 July	3	5	7	5	20
28 July	12	0	19	18	49
17 Aug.	1	0	8	4	13
Total	16	6	35	27	84
Paralabrax maculatofasciatus					
2 Aug.	0	0	37	3	40
3 Aug.	1	0	5	3	9
4 Aug.	4	0	11	13	28
8 Sep.	1	0	1	0	2
Total	6	0	54	19	79
Paralabrax nebulifer					
19 July	1	0	21	1	23
21 July	0	0	22	1	23
26 July	6	0	5	5	16
27 July	1	0	0	1	2
28 July	2	2	3	10	17
Total	10	2	51	18	81

Day 0 females had hydrated oocytes in the ovary (hydrated) or postovulatory follicles ≤4 hours old. Day-1 females had postovulatory follicles >4 and ≤24 hours old. The ovaries of nonspawning females contained yolked oocytes, but no hydrating oocytes or postovulatory follicles.

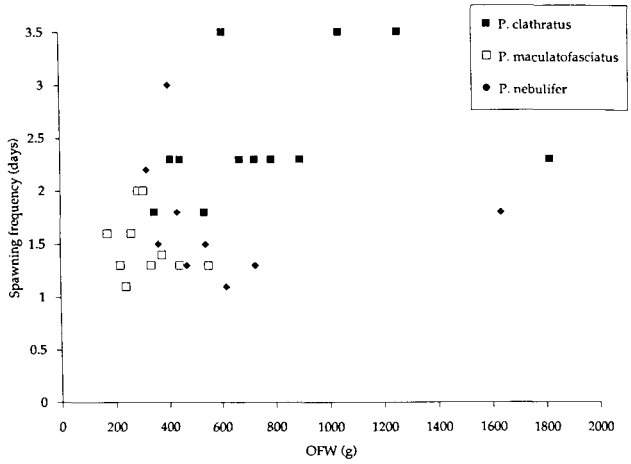

Figure 5. Relation between spawning frequency and size (ovary-free weight) of *Paralabrax clathratus*, *P. maculatofasciatus*, and *P. nebulifer*. Collections of each species were ranked by size (*OFW*) and partitioned into groups of equal numbers (*P. clathratus*, 12 groups, $n = 7$; *P. maculatofasciatus*, 10 groups, $n = 8$; and *P. nebulifer*, 9 groups, $n = 9$) represented on the graph by the mean *OFW*.

were unable to consistently determine a most-advanced mode; in cases where a most-advanced mode was identifiable, the estimates ranged from 3 to 8 times the estimates determined with the hydrated-oocyte method. Size ranges for the developing oocytes of these *Paralabrax* spp. were determined (table 3, which also includes chorion diameters of field-collected *Paralabrax* eggs from the ichthyoplankton collection of the Natural History Museum of Los Angeles County).

In our collections only 25 specimens of *P. clathratus* (collected in the Ventura/Port Hueneme area), 9 of *P. maculatofasciatus* (from Mission Bay), and 4 of *P. nebulifer* (collected at the Huntington Flats, off Seal Beach) fit the criteria required to use the hydrated-oocyte method for determining batch fecundity. Log transformation of the data improved the fit of the batch fecundity to ovary-free weight, and of the batch fecundity to standard-length linear relationships of *P. clathratus*, as it did for DeMartini (1987).

TABLE 3

Oocyte Size Ranges at Developmental Stages for *Paralabrax* Spp. (*P. clathratus*, *P. maculatofasciatus*, and *P. nebulifer*, $n = 200$)

Primary oocytes	to 0.16 mm
Partially yolked oocytes	0.14–0.31 mm
Fully yolked oocytes	0.24–0.58 mm
Migratory-nucleus-stage oocytes	0.55–0.82 mm
Hydrated oocytes	0.72–0.84 mm
Water-hardened eggs (5% Formalin)	0.86–0.90 mm
Water-hardened eggs (70% ethanol)	0.79–0.90 mm

Table also includes chorion diameter ranges for field-collected *Paralabrax* eggs, preserved in 5% buffered Formalin and 70% ethanol (from the Natural History Museum of Los Angeles County ichthyoplankton collection).

TABLE 4

Linear Regression Parameters for Log_{10}-Transformed Batch Fecundity (*BF*)–Ovary-Free Weight (*OFW*), and Log_{10}-Transformed *BF*–Standard Length (SL) Relationships of Female *Paralabrax*

	P. clathratus	*P. maculatofasciatus*	*P. nebulifer*
$\log_{10} BF = a + b*\log_{10} OFW$			
N	25	9	4
Intercept (a)	5.26	7.19	3.40
Coefficient (b)	0.91	0.56	1.25
Standard error	0.445	0.227	0.328
R^2	0.454	0.257	0.737
P	<0.001	0.163	0.141
$\log_{10} BF = a + b*\log_{10} SL$			
N	25	9	4
Intercept (a)	−5.57	−1.41	−6.78
Coefficient (b)	2.93	2.17	3.17
Standard error	0.430	0.217	0.342
R^2	0.491	0.325	0.714
P	<0.001	0.109	0.155

The number of samples available for *P. maculatofasciatus* and *P. nebulifer* are quite low and are included only as preliminary information (table 4, figure 6); linear regression analyses for these two taxa indicate no statistically significant relationship between size and batch fecundity at these low n values. The log-transformed linear relationship of ovary-free weight to batch fecundity in *P. clathratus* is statistically significant, $P = <0.001$ (table 4, figure 6). A standard-weight female (ca. 700 g *OFW* and 300 mm SL for this collection) would average 81,000 eggs per batch applying this regression equation. The average batch size per spawning by a standard-weight female varied by a factor of 2 in seven years of estimates for *Engraulis mordax* (Hunter et al. 1985). Because of this interannual variation, Hunter et al. (1985) recommended that when the egg production method is used to estimate biomass for *E. mordax*, batch fecundity must be recalculated for each biomass estimation. Our estimations of batch fecundity for *Paralabrax* are higher than those reported by DeMartini (1987) and may indicate the variability possible in these species of *Paralabrax*. Batch fecundity estimates calculated for *Seriphus politus* (Sciaenidae) from southern California did not vary like those for *Engraulis mordax* (DeMartini 1991). DeMartini concluded that batch fecundity estimates for *S. politus* were relatively invariant over four years (1979, 1980, 1985, and 1986) but significantly lower in 1984, during a major El Niño event. In 1987, DeMartini estimated batch fecundity for *Paralabrax* that were collected, in part, during the same El Niño event. Estimates of the batch fecundity of *Paralabrax* should be calculated over several years to determine whether fecundity is relatively invariant as in *S. politus*, or fluctuates among years as in *E. mordax*.

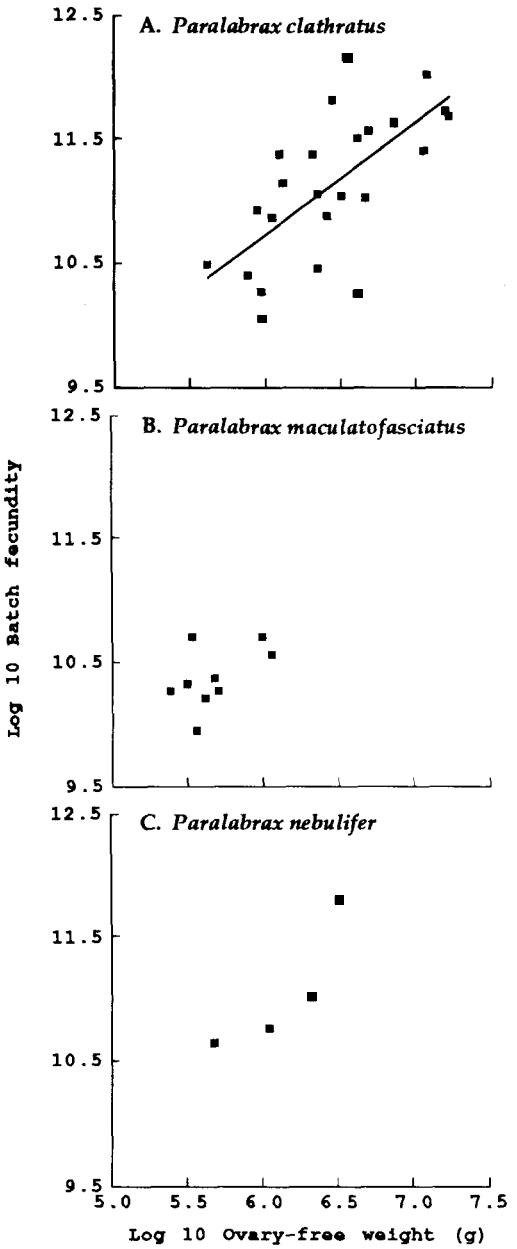

Figure 6. Relations between $\log_{10}$-transformed batch fecundity and ovary-free weight for our collections of *Paralabrax clathratus*, *P. maculatofasciatus*, and *P. nebulifer*.

The relative fecundity (batch fecundity/ovary-free weight) of *Paralabrax clathratus* does not seem to be influenced by body size (ovary-free weight; figure 7), and the average relative fecundity of *P. clathratus* that would have spawned on consecutive nights did not differ significantly from that of fish which had not spawned the night before collection (independent t test, df = 16, p = 0.475).

Hermaphroditism

Smith (1965) indicated that many serranids are specialized in their "reproductive mechanisms":

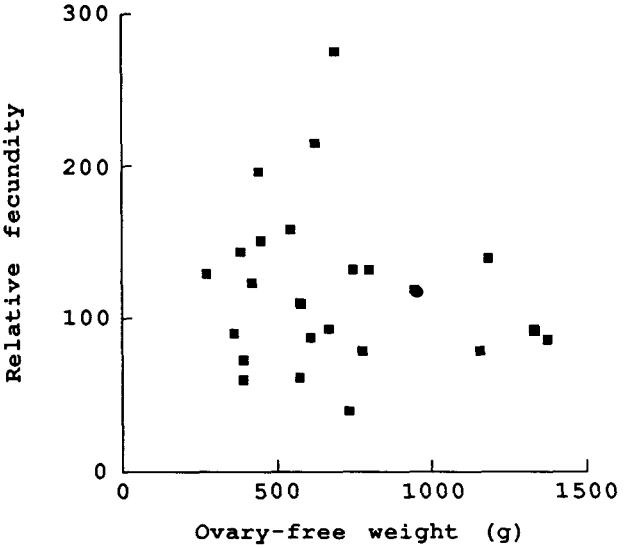

Figure 7. Relative fecundity (number of hydrated oocytes per gram of ovary-free weight) versus ovary-free weight (g) of *Paralabrax clathratus*.

some are gonochoristic, some are synchronous hermaphrodites, and others are protogynous hermaphrodites. Sadovy and Shapiro (1987) list five features of fishes that clearly indicate protogynous hermaphroditism: a membrane-lined central cavity in the testes; sperm sinuses in the gonadal wall; transitional individuals; stage 1, 2, or 3 atretic oocytes in the testes; and experimentally induced sex change. In our studies we found that these three species of *Paralabrax* share two characters: a central membrane-lined cavity in the testes, and sperm sinuses in the gonadal wall.

Gonads of six specimens of *P. nebulifer* contained both testicular and ovarian tissue. Of these, four were active males with primary oocytes in the testes (figure 8A). Proliferating testicular tissue, in the area corresponding to the testicular islet (Hastings 1989), was present in two specimens: one was immature (121 mm SL) and had only primary oocytes in the ovarian tissue (figure 8B), the other (278 mm SL; figure 8C) had vitellogenic oocytes. This suggests the possibility of protogynous hermaphroditism in *P. nebulifer*, which would mean that *P. nebulifer* is capable of both prematurational and postmaturational sex change. No signs of oocyte degeneration were detected in any of the six fish; therefore we believe that, on the basis of the criteria of Sadovy and Shapiro (1987), insufficient evidence exists to call *P. nebulifer* a protogynous hermaphrodite, although other evidence is certainly suggestive.

None of the *P. clathratus* specimens that were collected had both tissue types in the gonad. Smith and Young (1966) examined the gonads of *P. clathratus* and labeled them as secondary gonochores based on

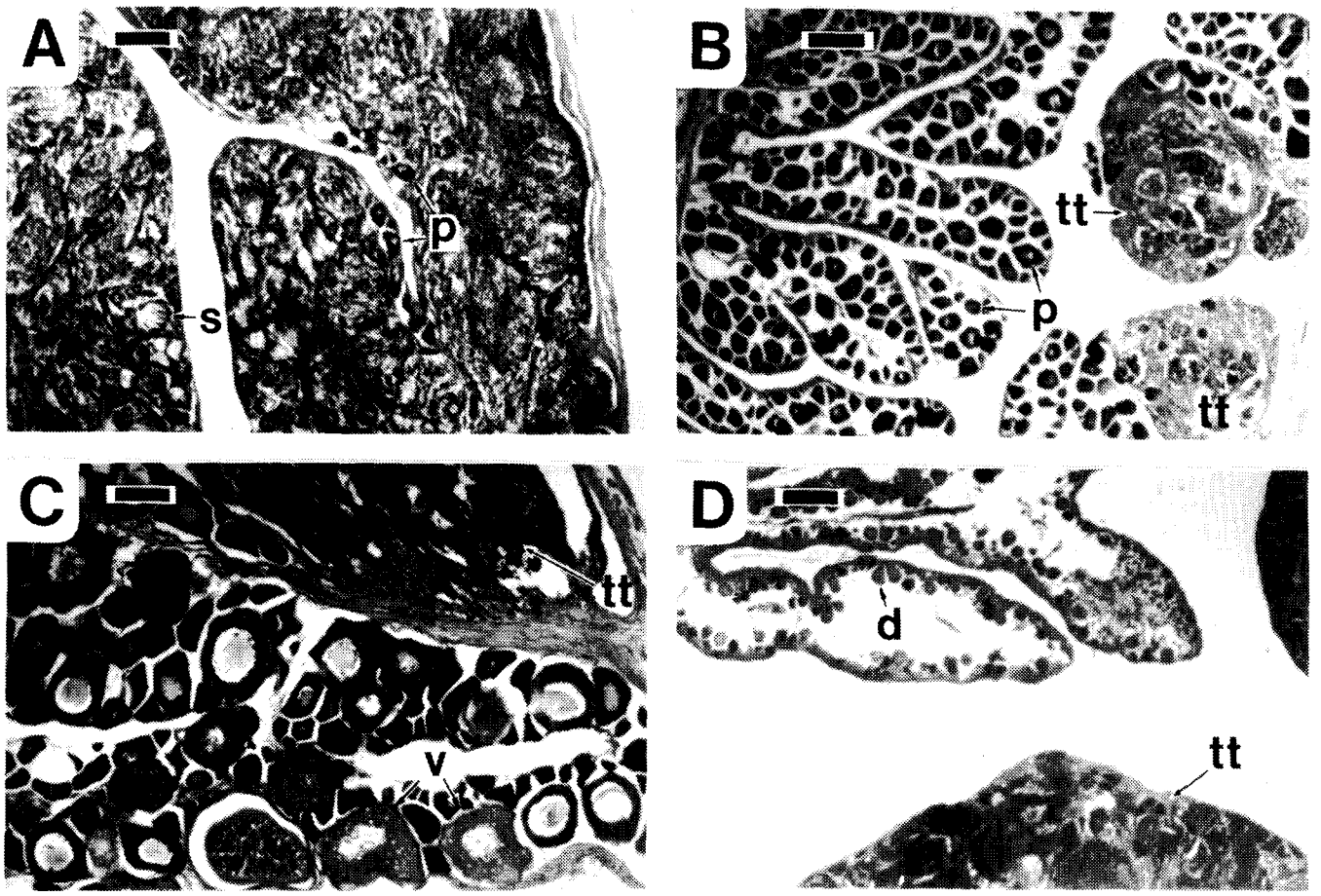

Figure 8. *Paralabrax nebulifer* (*A–C*) and *P. maculatofasciatus* (*D*) gonads with simultaneously occurring testicular and ovarian tissues: *d* = degenerating oocytes; *p* = primary oocytes; *s* = sperm crypts; *tt* = testicular tissue; *v* = vitellogenic oocytes. *Bar* = 0.1 mm.

the presence of a membrane-lined central cavity in the testes, sperm sinuses in the gonadal wall, a lack of transitional individuals, and no observed differences in the size ranges of males and females. Transitional individuals may be more prevalent at times different from those of our collections; sex change is seasonal in some species, occurring primarily at the end of the spawning season (Sadovy and Shapiro 1987).

One *P. maculatofasciatus*, which had been maintained at the King Harbor Laboratory for one year, was catheterized (cellular material not clearly male or female) and injected with LHRHa on June 30, 1989, at 0810 and sacrificed on July 3, 1989, at 0800. Active testicular tissue occupied 80%–85% of the gonad, but was enclosed in lobes that attached to about 25% of the gonadal wall (columnar nature of the epithelial lining was not evident). Attached to the remaining 75% of the gonadal wall were regressing ovarian lobes lined with columnar epithelium and containing degenerating primary oocytes (figure 8D). These characters support Hastings's (1989) identification of *P. maculatofasciatus* as a protogynous hermaphrodite.

ACKNOWLEDGMENTS

We thank Chris Donoho, Peter Dottin, David Griffith, and Sharon Kramer (Hubbs-Sea World Group), JoEllen Hose, Laura Targgart (VanTuna Research Group, Occidental College), the Department of Water and Power (Scattergood Facility), and the local sportfishing operators and their passengers for assistance with collections; Stephen R. Goldberg and Beverly Macewicz for sharing their knowledge of the histology of the gonads of multiply spawning fishes; and Stephen R. Goldberg, Gerald McGowen, James H. Petersen, and anonymous reviewers for their help in strengthening this manuscript. We thank the California Department of Fish and Game for financial support.

LITERATURE CITED

Clark, F. N. 1933. Rock bass (*Paralabrax*) in the California commercial fishery. Calif. Fish Game 19(1):25–35.

Cochran, W. G. 1977. Sampling techniques. Third edition, chapter 3: Sampling procedures and proportions. New York: John Wiley and Sons, pp. 50–68.

Collyer, R. D. 1949. Rock bass. Calif. Dep. Fish Game Fish Bull. 74: 113–115.

Collyer, R. D., and P. H. Young. 1953. Progress report on a study of the kelp bass, *Paralabrax clathratus*. Calif. Fish Game 39(2):191–208.

DeMartini, E. E. 1987. Tests of ovary subsampling options and preliminary estimates of batch fecundity for two *Paralabrax* species. Calif. Coop. Oceanic Fish. Invest. Rep. 28:168–170.

———. 1991. Annual variations in fecundity, egg size, and the gonadal and somatic conditions of Queenfish *Seriphus politus* (Sciaenidae). Fish. Bull., U.S. 89(1):9–18.

Frey, H. W., ed. 1971. California's living marine resources and their utilization. Sacramento: Calif. Fish Game, 148 pp.

Goldberg, S. R., V. H. Alarcon, and J. Alheit. 1984. Postovulatory follicle histology of the Pacific sardine, *Sardinops sagax*, from Peru. Fish. Bull., U.S. 82(2):443–445.

Hastings, P. A. 1989. Protogynous hermaphroditism in *Paralabrax maculatofasciatus* (Pisces: Serranidae). Copeia 1989(1):184–188.

Hunter, J. R., and S. R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish Bull., U.S. 77(3):641–652.

Hunter, J. R., and B. J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139–149.

———. 1985. Measurement of spawning frequency in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. R. Lasker, ed. U.S. Dept. Commerce, NOAA Tech. Rep. NMFS 36, pp. 79–94.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. R. Lasker, ed. U.S. Dept. Commerce, NOAA Tech. Rep. NMFS 36, pp. 67–78.

Hunter, J. R., B. J. Macewicz, and J. R. Sibert. 1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific. Fish. Bull., U.S. 84:895–903.

Lavenberg, R. J., G. E. McGowen, A. E. Jahn, J. H. Petersen, and T. C. Sciarrotta. 1986. Abundance of southern California nearshore ichthyoplankton. Calif. Coop. Oceanic Fish. Invest. Rep. 27:53–64.

Limbaugh, C. 1955. Fish life in the kelp beds and the effects of kelp harvesting. Calif. Inst. Mar. Res., IMR Ref. 55-9.

Oliphant, M. 1990. Recreational fishery. *In* Review of some California fisheries for 1989. Calif. Coop. Oceanic Fish. Invest. Rep. 31:9–21.

Petersen, J. H., A. E. Jahn, R. J. Lavenberg, G. E. McGowen, and R. S. Grove. 1986. Physical-chemical characteristics and zooplankton biomass on the continental shelf off southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:36–52.

Quast, J. C. 1968. Observations on the food and biology of the kelp bass, *Paralabrax clathratus*, with notes on its sportfishery at San Diego, California. Calif. Fish Game Fish Bull. 139:81–108.

Sadovy, Y., and D. Y. Shapiro. 1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia 1987(1):136–156.

Schaefer, K. M. 1987. Reproductive biology of the black skipjack, *Euthynnus lineatus*, an eastern Pacific tuna. Inter-American Trop. Tuna Comm. 19(2):169–260.

Smith, C. L. 1965. The patterns of sexuality and the classification of serranid fishes. Amer. Mus. Novit. 2207, 20 pp.

Smith, C. L., and P. H. Young. 1966. Gonad structure and the reproductive cycle of the kelp bass, *Paralabrax clathratus* (Girard), with comments on the relationships of the serranid genus *Paralabrax*. Calif. Fish Game 52(4):283–292.