Annual reproductive cycle of oocytes and embryos of yellowtail rockfish *Sebastes flavidus* (Family Scorpaenidae)

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Abstract. – Female yellowtail rockfish *Sebastes flavidus*, a viviparous species employing intralumenal gestation following fertilization of ovulated eggs, were caught from Cordell Bank (seamount 20 miles west of Pt. Reyes, central California) on a monthly basis from May 1985 through April 1986 to determine their annual reproductive cycle. Since histological methods provide precise and detailed information, this method was employed to (1) examine oocytes and embryos to describe developmental stages, and (2) provide temporal assessment of the annual reproductive cycle. The description and staging scheme developed provide a basis to compare reproductive developmental patterns between cycles and populations.

Oogonia (Stage I) and early perinucleolus (Stage II) oocytes were present in samples from all months. Progressive growth of oocytes from early- to late perinucleolus (Stage III) was evident in spent and recovering ovaries, indicating the end of a reproductive year and the beginning of a new reproductive cycle. Initial yolk accumulation (Stage IV) occurred in July, and final yolk accumulation (Stage V) was predominant from September through January. In February, the majority of samples displayed fertilized ova in early-celled stages of embryonic development. Gestation continued for about 30 days with parturition occurring between January and March. Mature oocytes were also collected in March, suggesting the Cordell Bank yellowtail population has a prolonged reproductive season extending into April.

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Sixty species of rockfish (genus *Sebastes*) have been recorded in waters off the California coast; twenty species are utilized by commercial and recreational fisheries (Lenarz 1986). Rockfishes display a wide variety of life history patterns with respect to their habitat and seasonality of reproduction (Wyllie Echeverria 1987). The majority of investigations on rockfish reproduction have focused on the development, occurrence, and identification of larvae and juveniles. Evaluating annual reproductive success as a direct consequence of variations in oocyte viability has received less attention.

The *Sebastes* complex contributed approximately 37,806 mt to west coast fisheries in 1985 (PFMC 1990) and management of this resource is heavily dependent upon predictions of strong and weak year-classes. Since no single trait accurately represents reproductive capacities of fish populations (Eldridge et al. 1991), fisheries management is based on a variety of information. Year-class strength estimates may be enhanced by understanding factors influencing annual fluctuations in reproduction. Reproduction within this genus is characterized by intralumenal gestation, following fertilization of ovulated, mature eggs. This process is somewhat unique among teleosts occurring only in scorpaenids and zoarcids (Wourms et al. 1988). The investigation described here focuses on the development and temporal occurrence of oocytes and embryos within the ovary of yellowtail rockfish *Sebastes flavidus*. Characterization of oocyte growth and embryonic development provides a basis for assessing reproductive performance. This study is part of a larger effort to acquire information on the reproductive biology of yellowtail rockfish to ultimately determine factors that influence reproductive success.

Although characteristics of oocyte growth are generally similar among teleosts (Wallace and Selman 1981), numerous ovary maturity scales and oocyte classification schemes exist (Yamamoto 1956, Htun-Han 1978, Robb 1982, Howell 1983). These classification schemes are useful for determining reproductive strategies (synchronous, group-synchronous, or asynchronous) and evaluating aspects of reproductive trends. Each oocyte staging system is, however, less likely to be adapted for teleosts outside the genus of original study due to the variety of reproductive strategies. An oocyte classification scheme to assess the reproductive status of the marine, viviparous genus Sebastes in the Eastern Pacific has not been reported. Taking these factors under consideration, the objectives of the study reported here were two-fold: (1) to describe oocyte and embryonic development in *Sebastes flavidus* through one complete reproductive cycle, and (2) establish a staging

classification as a basis for the comparison of oocyte and embryonic development between populations, reproductive years, and other species of Sebastes. Such data may be used to monitor reproductive development during a particular year. In addition, descriptions of oocyte and embryonic development provide a basis to compare the impacts of environmental fluctuations and physiological responses with the production of viable offspring. An understanding of environmental and physiological interactions influencing reproductive success could provide valuable contributions to the understanding of recruitment dynamics and allow for more efficient resource management.

Materials and methods

Specimens were collected from Cordell Bank (38°00'N, 123°25'W), a seamount 20 miles west of Pt. Reyes, at monthly intervals. Adult female yellowtail rockfish were captured by hook-and-line at depths of 50–150 m, from May 1985 through April 1986. No samples were obtained in June 1985 due to inclement weather. Mean age and size of samples for each month are shown in Table 1.

Fish were held on ice and transported to the laboratory where pieces of ovaries (~4×4×6 mm) were dissected and fixed in 10% neutral buffered formalin. Routine paraffin embedding followed the guidelines of Humason (1967). Samples were sectioned at 6 μ thickness with a rotary microtome. Mounted sections were stained in hematoxylin and counterstained in eosin (H&E).

Cell measurements were made using a video coordinate digitizer (Model 582 AVCD, H.E. Inc., Las Vegas, NV) on cells sectioned through the nucleus. Oocytes were measured and staged randomly. Mean cell diameters were determined from a subsample of 10–20 cells for each stage. All cell diameters reported are from fixed tissues.

In each monthly sample, the first 200–400 cells encountered were counted and staged. Percent frequency distributions of the various oocyte stages were calculated by dividing the total number of a particular stage by the total number of oocytes observed, expressed as a percentage. Because the probability of an individual oocyte being sectioned is proportional to its size as well as its abundance, larger oocytes tend to be overestimated and smaller oocytes underestimated (Howell 1983). Nonetheless, frequency distributions do indicate seasonal changes within the ovary. Because of the wide range of cell diameters, overlapping sizes among oocyte stages, and shrinkage due to fixation, criteria for staging oocytes was based on histological appearances and cell structure.

Table 1

Monthly means and standard errors for age, standard length (SL), and weight (Wt) of *Sebastes flavidus* collected off central California, May 1985–April 1986, used for histological analysis.

Month	Age (yr)	SL (cm)	Wt (g)	*n*
May	14.7±2.0	37.4±1.0	1434±115	6
June	—	—	—	0
July	17.9±2.3	39.5±1.5	1600±146	9
Aug.	13.2±2.0	36.8±1.8	1387±181	4
Sept.	30.0±2.6	44.4±0.6	2349±111	6
Oct.	26.2±4.0	42.6±1.2	2017±157	7
Nov.	21.1±2.2	40.9±0.6	1780± 97	6
Dec.	18.7±2.1	39.3±1.1	1830±122	10
Jan.	15.4±1.8	36.1±1.1	1272±107	10
Feb.	14.6±1.8	36.1±1.1	1315± 83	10
Mar.	19.3±1.8	37.5±1.2	1489±102	10
Apr.	23.4±2.2	38.3±0.6	1387± 52	10

Although ovaries in varying stages of postfertilization development were observed, monthly collection of ovaries was inadequate for a detailed study of rapid embryonic development. Therefore, additional samples of embryonic stages were collected by catheterization from female yellowtail rockfish held in captivity. Ten adult female yellowtail rockfish captured after copulation were catheterized weekly for 6 weeks while being maintained in a flow-through, sand-filtered (to 10 μ) seawater system. Photoperiod was ambient. The mean temperature and salinity (10.4°C and 34.7‰) for the 2-month holding period (January and February) were well within the range of parameters at the sampling site.

Abbreviations used in figures

BC	blastodermal cap	MU	muscle
BR	brain	NC	notochord
C	capillary	NU	nucleoli
CH	chorion	N	nucleus
EB	embryonic body	OG	oil globule
EF	empty follicle	ON	oogonial nest
ER	erythrocyte	OP	optic vesicle
EY	eye	OV	oil vacuole
FOL	follicle	POF	postovulatory follicle
G	granulosa	RE	retina
GR	germ ring	SO	somite
HG	hind gut	T	theca
LC	lampbrush chromosome	VM	vitelline membrane
LN	lens	YG	yolk globule
LT	liver tissue	YM	yolk mass
MN	migratory nucleus		

Table 2

Classification and temporal occurrence of oocytes from *Sebastes flavidus* collected off central California, based on histological appearance. See text for additional histological descriptions.

Stage		Major histological characteristics	Temporal occurrence
I	Oogonia	Small cells (5–25 μ) found in clumps or "nests." Cytoplasm pale to clear. Basophilic nucleus occupying most of cell volume.	All year
II	Early perinucleolus	Wide range of cell diameters (20–100 μ). Intense basophilic cytoplasm. One or two large nucleoli in nucleus.	All year
III	Late perinucleolus	Diameters 50–140 μ. Small, clear vesicles present in cytoplasm. Cytoplasm pale-blue to light-gray. Several small nucleoli around inner margins of nuclear membrane.	Feb.–Oct.
IV	Initial yolk accumulation	Cell diameters 120–210 μ. Small spherical, eosinophilic yolk granules in a distinct cortical zone in cytoplasm. Cytoplasm vesicular and light-gray. Well-developed follicle surrounds a developing vitelline membrane. Several small nucleoli around the inner margins of nuclear membrane.	July–Oct.
V	Final yolk accumulation	Large cells (200–600 μ). Cell volume one-half to entirely full of yolk spheres. Lampbrush chromosomes visible in nucleoplasm. Lipid vacuoles appear larger as they coalesce.	Sept.–March
VI	Migratory nucleus	Cell diameters 600–750 μ. A single, large lipid vacuole present. Nuclear membrane indistinct or absent. Nuclear material irregularly shaped and no longer centrally located. Follicle may be distorted and irregularly shaped.	Dec.–March
VII	Ovulation & Fertilization	Mature oocyte free from follicle. The yolk mass is a single, large homogeneous mass, staining deep-purple. In fresh (unfixed) ovaries, ova appear clear or translucent.	Dec.–March

Results

Oocyte development

Major histological characteristics distinguishing stages for *S. flavidus* are listed in Table 2. All cells could be categorized into one of the seven stages. Terminology and nomenclature follow Moser (1967a) and Howell (1983).

Stage I: Oogonia These small cells were 5–25 μ in diameter and were found in clumps or "nests" along the lamellar branches (Figs. 1A, 4E). Larger oogonia in the 20 μ range possessed a deeply-stained chromatin network attached to a single, large basophilic nucleolus.

Stage II: Early perinucleolus These oocytes were 20–100 μ in cell diameter. While still closely associated with neighboring oogonia, there was noticeable movement away from oogonial nests. The most obvious feature of this cell was the intensely basophilic cytoplasm (Figs. 1B, 4E).

Stage III: Late perinucleolus Diameters were 50–140 μ. Clear vacuoles appeared in the cytoplasm of oocytes as small as 50 μ. Initially these vacuoles were distributed as a poorly organized ring surrounding the nucleus, but were seen randomly scattered throughout the cytoplasm of larger oocytes (Figs. 1B, 4E). As growth continued, they increased in size and number.

Stage IV: Initial yolk accumulation The earliest signs of yolk accumulation were seen in oocytes of 120–210 μ in diameter. Small, spherical globules of yolk were seen in a distinct cortical zone in the cytoplasm (Fig. 1C,D). The follicle enclosing the oocyte is more complex and composed of several identifiable structures (see below).

Stage V: Final yolk accumulation To simplify the staging of yolked oocytes, cells with approximately one-half their volume filled with yolk spheres, and cells whose volumes were entirely filled with yolk, were placed in Stage V. Yolk spheres increased in number and size. By the end of this stage, the cell diameter increased to about 650 μ. The cytoplasm was entirely filled with yolk spheres of various sizes (Fig. 2A). The vacuoles which were distributed throughout the cytoplasm began to coalesce, forming larger vacuoles.

An eosinophilic nucleoplasm with lampbrush chromosomes was visible (Fig. 2B). In the late Stage-V cell, the nucleus became irregularly shaped and the nuclear membrane was often indistinct (Fig. 2A).

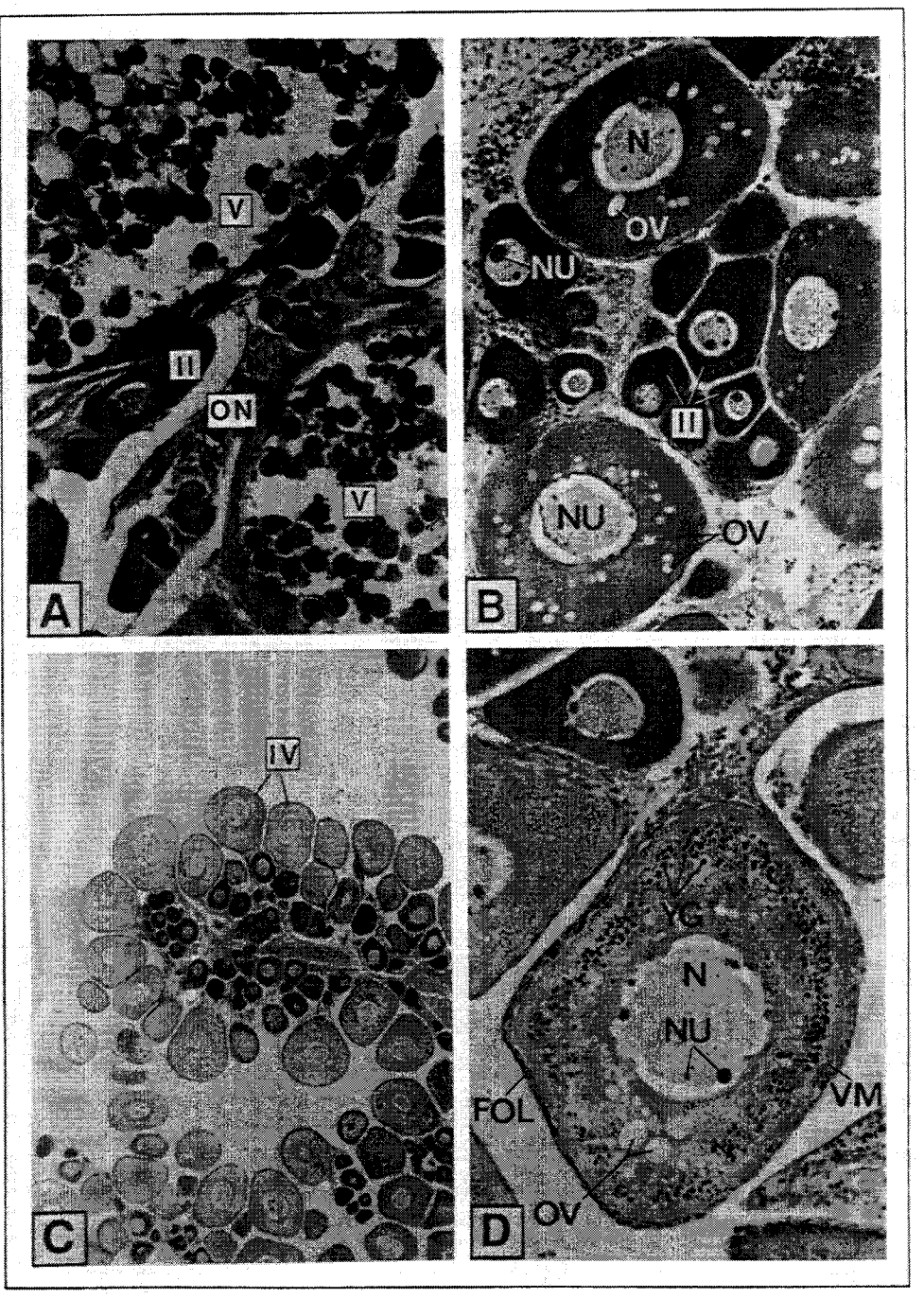
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Figure 1 (left page)
(A) Oogonial nest (Stage-I oocyte) from *Sebastes flavidus*, containing several primary oocytes collected Dec. 1985, 400×. (B) Section of oocytes in ovary of *S. flavidus* collected May 1985, 250×. Basophilic properties of cytoplasm in Stage-II cells and their large nucleoli are shown. Distribution of vacuoles are seen in the larger Stage-III cells. (C) Cross-section of an ovary collected Aug. 1985 showing arrangement of Stage-IV oocytes in grape-like clusters on outer margins of a lamellar branch, 63×. (D) Typical Stage-IV (initial yolk accumulation) oocyte showing the first indications of yolk, 250×.

The cellular composition of the mature follicle was best observed in Stage-IV or Stage-V oocytes (Fig. 2D). A bilaminar vitelline membrane about 1 μ in thickness was next to the plasma membrane of the oocyte. Outside the vitelline membrane was a single inner epithelial layer, the granulosa. Encapsulating the granulosa was an intricate capillary network filled with erythrocytes. The theca, a single epithelial layer consisting of squamous cells with large nuclei, surrounded the profuse capillary system.

Stage VI: Migratory nucleus Cell diameters ranged from 600 to ~750 μ. Lipid material had coalesced to form a single, large vacuole, usually centrally located. Nuclear material was ameboid in appearance and no longer occupied a centralized position in the cell (Fig. 2C). Nucleoli were small, indistinct, or entirely absent.

Stage VII: Ovulation/Fertilization Histological evidence of ovulation was verified by observing the integrity of the surrounding follicle. Follicles appeared either as irregularly shaped and shrunken away from the oocyte or displayed a loss of continuity. Postovulatory follicles appeared throughout the sectioned ovary (Fig. 2C).

Because fertilization of the mature oocyte occurs rapidly after ovulation, distinction between ovulated oocytes and recently-fertilized oocytes was unnecessary. Therefore, fertilization was considered an event rather than a stage of histological distinction, and is included in Stage VII to maintain logical continuity of the developmental process. Following fertilization, however, the yolk material became a single homogeneous mass staining bright-purple in histological preparations, appearing clear or translucent in unfixed samples (Fig. 3A, B). This distinguishes fertilized from recently ovulated ova.

Embryonic development

A complete series of sequential embryonic developmental stages was not obtained from field collections due to the sampling interval and rapid development of embryos. Embryos from field collections were, however, satisfactorily placed into one of three broad categories: (1) early-celled, (2) embryonic body, or (3) eyed-larvae (where retinal pigmentation was visible).

Early-celled The early celled stage of embryonic development observed from field collections of yellowtail rockfish ovaries corresponded to stage 9 of Oppenheimer's classification for *Fundulus heteroclitus* (Oppenheimer 1937). The early-celled stage was seen as an undifferentiated mass of cells (blastodermal cap) on top of a large yolk mass (Fig. 3A). This stage was first collected in January, most frequently seen in February, and last occurred in March.

Embryos in a more advanced state (i.e., flattening or expansion of the blastula) occasionally occurred within an ovary primarily containing early-celled embryos. This suggests rapid cellular divisions and growth.

Embryonic body The appearance of an embryonic body was first seen in an ovary collected in February and last seen in March. This embryonic stage closely corresponds to Oppenheimer's stages 14 or 15 (Oppenheimer 1937). At the beginning of this stage, an undifferentiated mass of cells (taking on the appearance of tissue rather than individual cells) was located in a high ridge lying over the yolk mass. The oil globule was evident at the opposite pole (Fig. 3B). With further development, embryos displayed optic vesicles originating from lateral buds, distinguishing the cephalic region (Fig. 3C). By the end of this growth phase, somites along the trunk were visible along with lengthening of the tail. The head had further developed to include lens formation (Fig. 3D).

Figure 2 (overleaf, left page)
(A) Cross-section of ovary from *Sebastes flavidus* with clutch of oocytes in late Stage V, 63×. (B) Cross-section through nucleus of a Stage-V oocyte showing distribution of nucleoli and lampbrush chromosomes in the nucleoplasm, 400×. (C) Section through two nearly-mature oocytes in Stage VI (migratory nucleus), 63×. (D) Tangential section of Stage-V oocyte showing components of the follicle outside of vitelline membrane, 400×.

Figure 3 (overleaf, right page)
(A) Early-celled embryos from *Sebastes flavidus* ovary collected Feb. 1986, 63×. (B) First appearance of embryonic body, showing cellular differentiation. Whole embryo, formalin-fixed, 40×. (C) Section through developing embryo (embryonic body, late stage) showing optic vesicle formation originating from lateral expansions in cephalic region, 63×. (D) Embryonic body stage further developed than in Fig. 3C, with better definition of brain, retina, and lens formation, 63×.

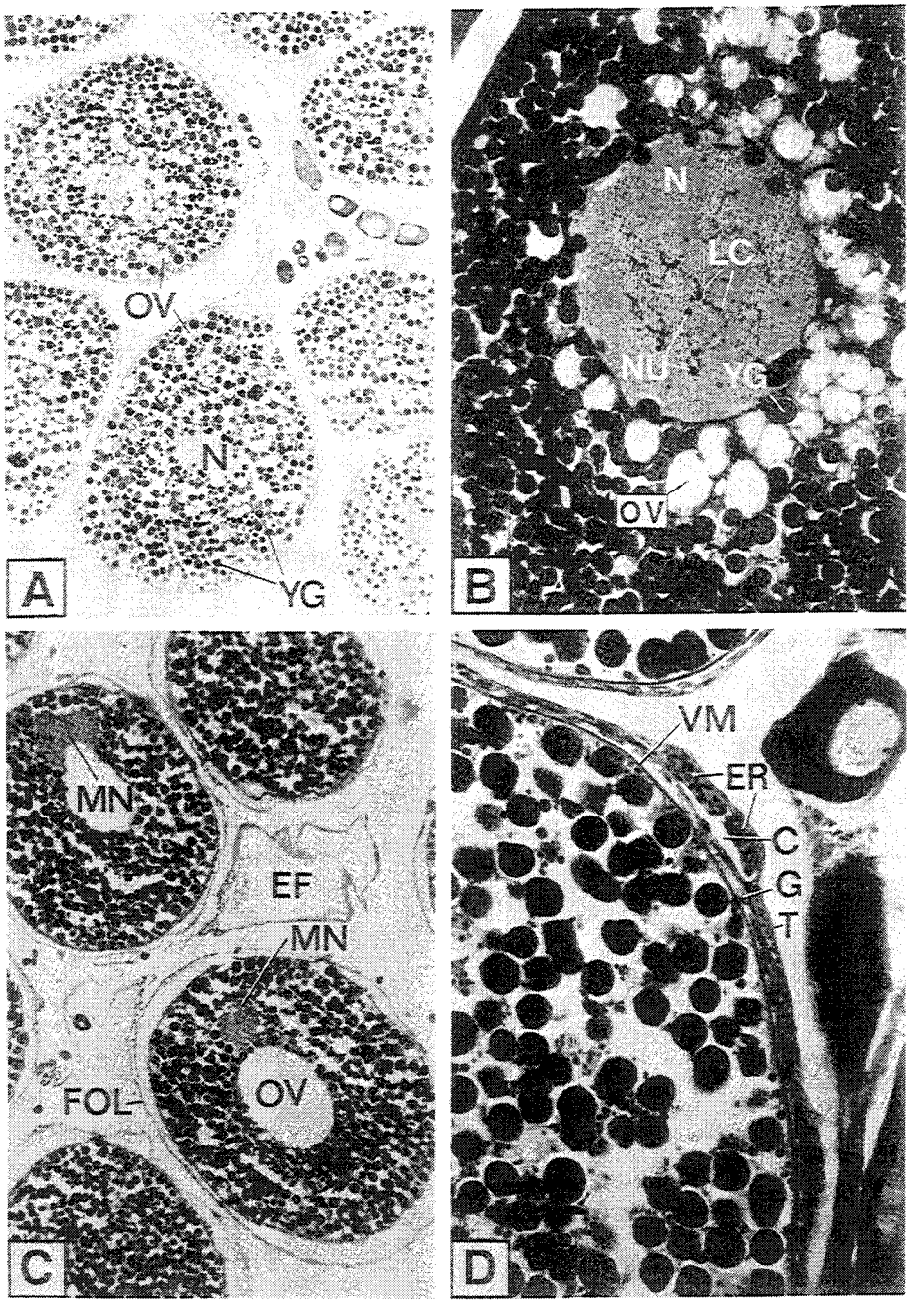

Figure 2

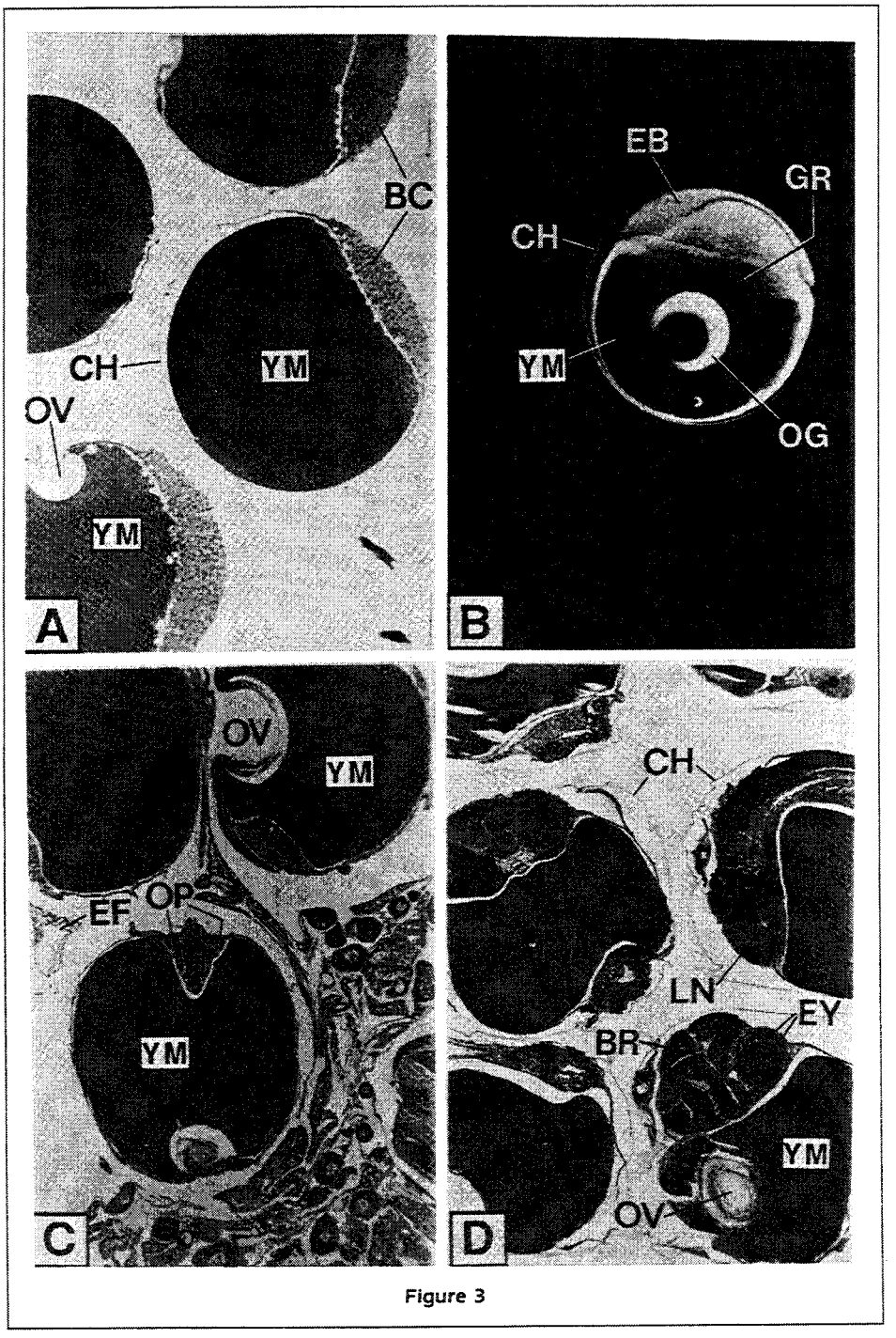

Figure 3

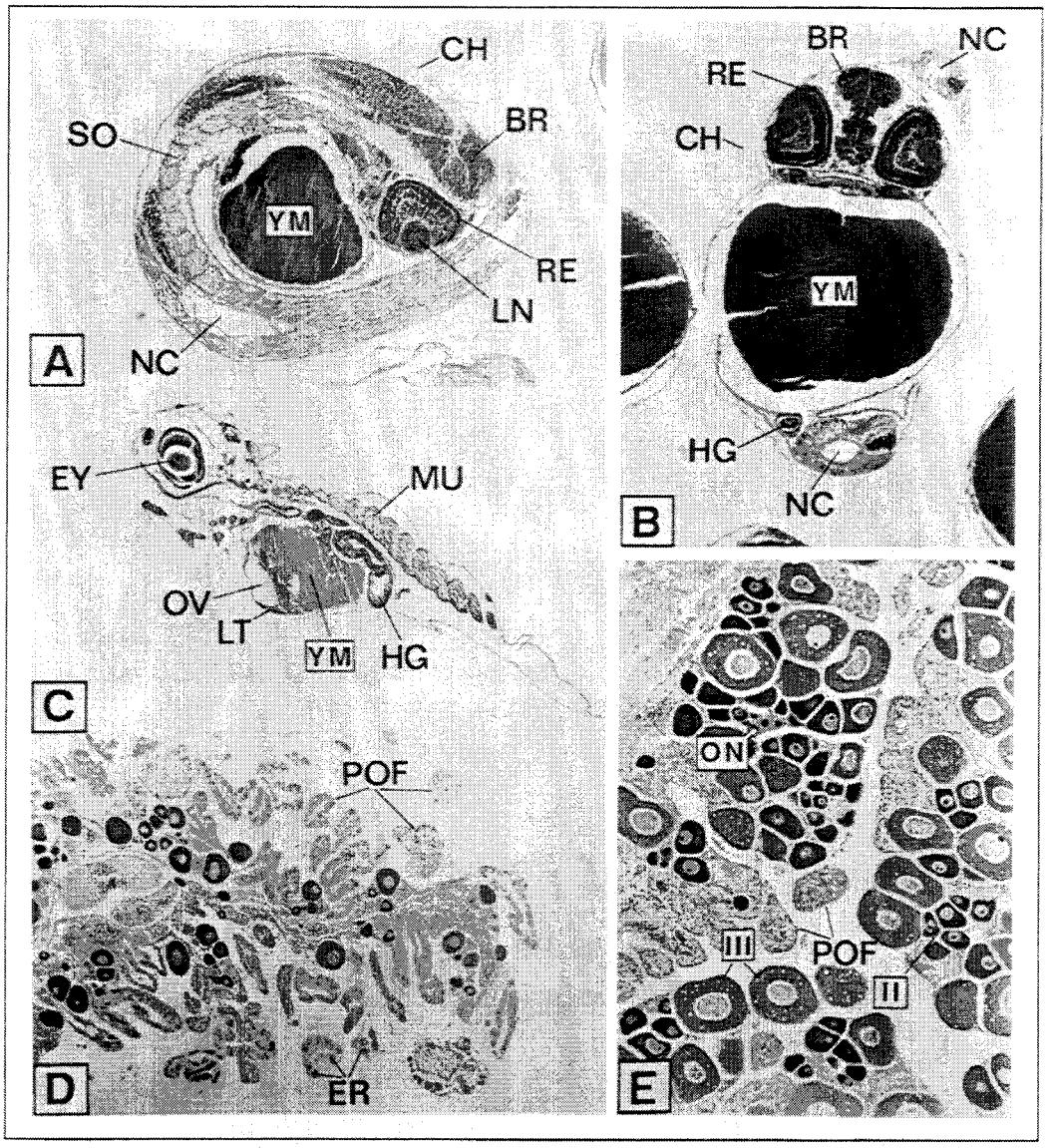

Figure 4 (above)
(A) Unhatched prolarvae of *Sebastes flavidus* collected Feb. 1986. Pigmentation of retina is apparent, as are well-formed somites, 63×. (B) Tangential section of unhatched prolarvae with completed pigmentation of the retina. Tail continues to lengthen and is seen to pass the head slightly, 63×. (C) Newly-hatched larva of *S. flavidus* showing close association of liver with oil vacuole, developing jaw and well-developed gut, 40×. (D) Cross-section of a recently-spent ovary of *S. flavidus* collected March 1986. Many empty and collapsed follicles are being resorbed, 40×. (E) Recovering and early developing ovary collected April 1986 showing reorganization of ovarian stroma as resorption nears completion, 63×.

Eyed-larvae Retinal pigmentation began as a black deposit outlining the periphery of the retina. Concurrently, somites were well formed in the thoracic and tail regions (Fig. 4A). Mature embryos (prehatching larvae) exhibited complete pigmentation of the eyes and a well-developed musculature system along the entire length of the tail (Fig. 4B). Embryos in this broad developmental category were in field samples collected in January and February. Had ovaries containing

hatched embryos (larvae) been collected in the field, they would have been included in this stage. Larvae were, however, taken from females held in the laboratory. These larvae were 4–6 mm in length and had open mouths with functional jaws. The yolk mass appeared to be reduced, and liver tissue was associated with a persistent oil globule (Fig. 4C).

Seasonal oocyte cycle Oogonial nests were observed in all samples, with about 25% frequency of occurrence throughout the entire reproductive cycle (Fig. 5). These Stage-I cells were most conspicuous early in the reproductive season and in ovaries of spent females.

Stage II or early-perinucleolus oocytes were also noted year-round and accounted for about one-third of all oocyte types observed (Fig. 5). The large nucleoli and dark cytoplasm were features that easily distinguish this stage. Mid- to late Stage-II cells were observed either singly or in groups around oocytes of later maturational stages (Stages III–VII) and were considered the 'resting' stage oocytes of other investigators (Bowers and Holliday 1961, Howell 1983).

In early spring, a broader range of Stage-II cell diameters was evident, indicating continued oocyte growth. Stage-III cells rapidly increased during March and April to a maximum frequency of 40% in April, and decreased in frequency by August as this clutch of oocytes developed (Fig. 5).

Copulation of yellowtail rockfish typically occurs over three months beginning in August and ending in October (Eldridge et al. 1991). The incidence and frequency of sperm in yellowtail rockfish ovaries were not evaluated in this study. However, small clumps or 'packages' of sperm were occasionally seen closely associated with the stroma or in spaces between developing (yolked) oocytes.

Initial yolk accumulation (Stage IV) was first documented in females collected in July, with all specimens collected in August showing this stage. In August, 34% of oocytes were Stage IV. Oocytes of Stage IV appeared as grape-like clusters on the outer margins of the lamellar branches, developing in a group-synchronous manner (Fig. 1C). The occurrence of Stage-IV oocytes sharply declined from August to November when no Stage-IV oocytes were observed (Fig. 5). As yolk accumulation continued, yolk spheres increased in size and number, filling the cytoplasm to about one-half its volume. At this point, oocytes were categorized as Stage V. Stage V was the most advanced oocyte observed from its first appearance in September until December when the frequency declined (Fig. 5). Oocytes in this developmental stage were most prevalent in November when they accounted for a mean of 48% of all oocytes. Stage-VI (Migratory nucleus) oocytes were first observed in December.

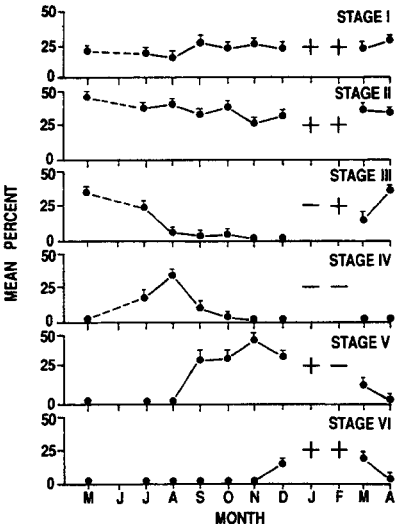

Figure 5
Mean monthly frequency distributions of oocyte Stages I–VI in ovaries of *Sebastes flavidus* during 1985–86. Error bars represent 1 SE. Plus signs = present, minus = not present. Monthly sample size same as in Table 1.

Ovaries with an advanced mode of Stage-VI oocytes continued to be collected over the next 3 months (January–March). This stage appeared to have a short duration, as ovaries containing Stage VII were also collected in some of the same months as Stage VI (December–February).

Ovary maturation was determined by using the most advanced oocyte or embryonic stage present in each monthly sample, and their frequency of occurrence was expressed as percent(s) (Fig. 6). Temporal ovarian development is illustrated and reflects a prolonged reproductive season.

While accurate frequency distributions on Stage-VII oocytes were not possible, the peak month of ovulation and fertilization appeared to be February. Sections of samples with Stage-VII oocytes showed eggs free from (e.g., outside) their follicular remnants. While continuity of follicular components (theca and granulosa) was disrupted, the integrity of the capillary network was maintained and there was a close association with the developing embryo.

Ovaries recently spawned (parturition) were seen as early as January and most frequently collected in March (Fig. 6). The ovary was greatly reduced in size,

reddish-blue in color, and very soft in texture. Histologically, the spent ovary displayed increased vascularization, a thickening of the tunica, and postovulatory follicles undergoing various stages of resorption (Fig. 4D). In addition, larvae remaining after parturition and yolked oocytes not reaching maturity are frequently seen in various stages of resorption.

Late-recovering and early-developing ovaries possessed reorganized lamellar branches containing Stages I, II, and early Stage-III oocytes as resorption nears completion (Fig. 4E). All samples collected in April were in this condition (Fig. 6), which marked the end of one reproductive season and the beginning of the next reproductive cycle.

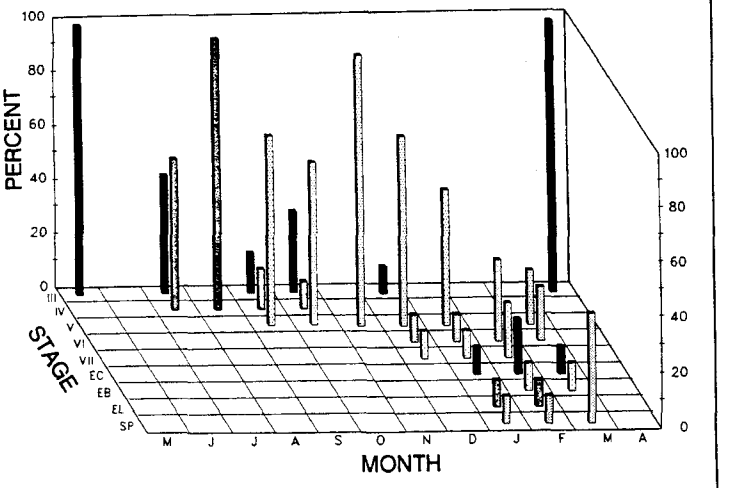

Figure 6

Percent distribution of ovarian maturation stages (derived from the most advanced oocyte or embryonic stage categorized histologically) from monthly collections of *Sebastes flavidus*; *n* is same as presented in Table 1. III = late perinucleolus, IV = early yolk, V = late yolk, VI = migratory nucleus, VII = ovulation/fertilization, EC = early-celled embryo, EB = embryonic body, EL = eyed-larvae, SP = spent.

Discussion

In the present study, I established an oocyte/embryonic classification that allows rapid determination of a rockfish population's status in the annual reproductive cycle. The use of this staging system allows one to establish oocyte frequency distributions and categorize ovaries as to their seasonal development, both temporally and spatially. This information, in turn, not only permits interannual and interpopulational comparisons, but may help reveal variations related to environmental factors.

Developmental events that occur in the oocytes of *Sebastes flavidus* are similar to those described for other teleosts with group-synchronous development (see review by Wallace and Selman 1981). Embryogenesis and the basic reproductive patterns follow observations reported for other members of the genus *Sebastes* (Moser 1967a, Wyllie Echeverria 1987). Temporal occurrence of reproductive events and seasonal variations of these events differ within the genus (Wyllie Echeverria 1987).

In the present work, oocyte development in *S. flavidus* has been categorized by separating oocyte growth into seven distinct stages. Oogonia and early-perinucleolus stages (Stages I and II, respectively) are found in the ovaries throughout the year. These stages appear to grow continuously, develop asynchronously, and, particularly in Stage-II cells, display a wide range of cell diameters. Development of unyolked oocytes in *S. flavidus* is similar to that described for *S. paucispinus* (Moser 1967a,b). However, seasonal occurrence of Stage-III oocytes differs between the two species. Stage-III oocytes in *S. flavidus* decline rapidly in number as yolk accumulation (Stage IV) is initiated. They are not observed again in the ovaries until after parturition and the beginning of the reorganization of the lamellar branches. While Moser (1967a) did not suggest a staging classification scheme, his descriptions for *S. paucispinus* included oocytes corresponding to Stage III (in the present study). In contrast to *S. flavidus*, these oocytes occurred in ovaries of *S. paucispinus* throughout the year (Moser 1967a). The temporal difference in occurrence of Stage-III oocytes between these two species is most likely a reflection of the number of broods produced annually. Viviparous species producing more than one brood annually require a reserve of Stage-III oocytes. In rockfish where two or more broods of young are produced in one reproductive season, a second clutch of yolked oocytes develops concurrently with the initial brood of gestating embryos. Moser (1967a) reported the second clutch of yolked oocytes to occur in *S. paucispinus* when the initial brood had reached eye-lens formation. A distinct seasonal absence of Stage-III oocytes, or a

clutch of yolked oocytes during embryonic gestation, distinguishes single from multiple spawners.

There were approximately 30–40 days between the appearance of fertilized ova and well-developed larvae or recently-spawned females. Therefore, gestation appears to be 30–40 days in *S. flavidus*. Moser (1967b) estimated 1–2 months gestation for the multiple-spawner *S. paucispinus*, and Boehlert and Yoklavich (1984) noted 37 days for *S. melanops*, a single-season spawner. Similarly, Mizue (1959) compared a multiple-spawner, *S. marmoratus* to a single-season spawner, *S. inermis*. His data suggest approximately 30–45 days for embryonic gestation in both species.

While the basic reproductive pattern among the various Sebastes species is similar, variations exist in reproductive strategy and life history (Boehlert and Yoklavich 1984). Temporal variations in reproductive seasonality of rockfishes are perhaps the most obvious and, therefore, well documented. Releasing larvae over an extended period of time increases the probability that a portion of the reproductive population would encounter favorable environmental conditions for the survival of the progeny. Wyllie Echeverria (1987) listed the peak parturition months for 34 species of *Sebastes* and reported that larval extrusion occurs for up to 9 months in some species. In her study, from samples collected over a 7-year period, the principal month of parturition for yellowtail rockfish was February. In the present study, and in more recent work (unpubl. data), March was the peak month of parturition; however, the samples were from a smaller geographical area. Phillips (1964), who sampled northern, central, and southern California rockfish populations, determined *S. flavidus* to be a "winter" spawner (November–March). Wyllie Echeverria (1987) reported parturition for yellowtail rockfish from north-central California to occur from January to July. In the present study, a shorter parturition time was observed for the Cordell Bank yellowtail population (January–March). This temporal variance may reflect a clinal reproductive variation in yellowtail rockfish populations. Care must be taken, however, when interpreting and comparing results where macroscopic characteristics are used. While field assessments by microscopic staging of whole oocytes or macroscopic examinations are less time-consuming, validation by histological methods is required for precise and detailed information (West 1990). Furthermore, studies on the impact of atresia and postovulatory follicles are relevant to understanding functional relationships between yellowtail rockfish reproduction and their environment. West (1990) suggests histology as the appropriate method of use for these types of studies.

A prolonged reproductive season is characteristic of the genus *Sebastes*, but the factors regulating such a mechanism are not clear. While temperature and photoperiod appear to effect later spawning in higher-latitude populations (Wooton 1984), inherent factors may also play a key role in the prolonged seasonality displayed by rockfishes. There is some evidence that age, at least in yellowtail rockfish, may account for some variation in parturition time within a season (M.J. Bowers, unpubl. data; Eldridge et al. 1991). In addition, Boehlert and Yoklavich (1984) estimated 5 days between hatching and birth in *S. melanops*, while parturition has been reported to occur immediately after hatching in the ovary in the subgenus *Sebasticus* (Tsukahara 1962). In this study, it could not be determined if hatched larvae remained in the ovaries of yellowtail rockfish. Further investigations are necessary to determine the occurrence, significance, and regulatory mechansims of larval retention.

Rockfish are an important economic resource to the Washington, Oregon, and California fisheries. Estimates of total commercial rockfish landings in 1985 were 37,806 mt (PFMC 1990). In the same year, recreational anglers landed approximately 4000 mt of rockfish in California alone. Yellowtail, blue, and black rockfishes represented 30% of the recreational landings (Lenarz 1986). Fluctuations in year-class strength cause the fishery to be somewhat unpredictable (Lenarz 1986), leaving it difficult for optimal management strategies to protect stock depletion and establish harvest guidelines. The earlier one can predict recruitment success, the more precise management decisions are likely to be. Leaman (1988) discussed the value of directing management models toward biological principles. Responses of yellowtail rockfish ovaries to environmental fluctuations are early indicators of reproductive performance. This study documents the process of oocyte development in yellowtail rockfish and provides a basis for interannual comparisons.

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