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Reproduction of Darkblotched Rockfish off the Oregon Coast

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Abstract.—Seasonal reproductive development, size and age at sexual maturity, and fecundity were described for darkblotched rockfish *Sebastes crameri* collected off the Oregon coast. Altogether, 1,060 fish captured by commercial groundfish and shrimp trawlers between July 1986 and July 1987 were examined. Reproductive events were protracted. Insemination of females occurred from August to December, and fertilization and parturition followed from December through March. Spermatozoa were observed within both vitellogenic and previtellogenic ovaries between July and November. Reproductive events in smaller males and females were delayed relative to those in larger individuals. Females attained 50% maturity at a greater size (36.5 cm total length) and age (8.4 years) than males (29.6 cm total length; 5.1 years). The unimodal development of eggs and larvae indicated one parturition per year. Most age-6, age-7, and age-8 females possessed ovaries in an intermediate "maturing" condition. Histological analysis revealed that most of these females were immature; ovaries showed no evidence of previous spawning, oocytes never developed beyond an early vitellogenic stage, and during months of parturition, many of these females were resorbing their advancing oocytes. Total fecundities ranged from 19,815 to 489,064 oocytes per ovary pair and increased exponentially with increasing fish length, linearly with fish weight, and asymptotically with fish age (6 to 66 years).

Darkblotched rockfish *Sebastes crameri* are viviparous, as are other species of the genus *Sebastes* (Boehlert and Yoklavich 1984; Wourms 1991). Darkblotched rockfish larvae are pelagic when released during winter, and juveniles likely shift to a benthic habitat upon attaining a standard length of 40–60 mm (Richardson and Laroche 1979). Although previous investigators have provided some demographic information on darkblotched rockfish (Phillips 1964; Westrheim 1975; Wyllie Echeverria 1987; Barss 1989), none have examined the reproductive biology of this species in detail.

Darkblotched rockfish have been an important component of the Oregon commercial groundfish trawl fishery (Niska 1976; Fraidenburg et al. 1977). Previous investigators have expressed concern that the slow growth, low natural mortality, and variable recruitment associated with species of the genus *Sebastes* make them extremely vulnerable to overfishing (Gunderson 1977; Leaman and Beamish 1984; Francis 1986; Leaman 1991). Knowledge of the reproductive biology of many of these rockfish species, including darkblotched rockfish, is essential for the establishment of biologically sound management programs.

This paper describes an annual reproductive cycle (based on gross and cellular examination of ovary and testis morphology), size and age at sexual maturity, and fecundity of darkblotched rockfish off the coast of Oregon.

Methods

Data collection.—Seven hundred thirty-five specimens were collected between July 1986 and July 1987 during research surveys (Pikitch et al. 1988) conducted off the Oregon coast (43°10′N to 45°50′N latitude) aboard commercial groundfish and shrimp trawlers (Table 1). An additional 325 filleted darkblotched rockfish were collected from December 1986 to June 1987 at fish processing plants in Newport, Oregon. Fish were weighed (nearest gram; whole fish only) and measured for total length (TL) and fork length to the nearest millimeter. Sagittal otoliths were removed and stored in 50% ethanol for subsequent age determination. Gonads were removed and weighed to

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TABLE 1.—Summary of darkblotched rockfish collections and allocation of gonadal tissue for use in histology and fecundity estimation. Numbers in parentheses indicate number of specimens used for histological examination.

Date of capture	Source[a]	Number of samples: Males	Females	Fecundity	Total specimens
11 Jul 1986	A	32 (12)	29 (11)		61
12 Jul 1986	A	2 (2)	5 (2)		7
28 Jul 1986	B	30 (0)	24 (0)		54
19 Aug 1986	A	22 (10)	25 (3)		47
20 Aug 1986	A	5 (5)	14 (6)	4	19
25 Aug 1986	A	11 (2)	23 (4)	1	34
18 Sep 1986	A	20 (12)	13 (5)	1	33
19 Sep 1986	A	21 (3)	22 (1)	1	43
22 Sep 1986	A	7 (4)	38 (2)		45
2 Nov 1986	A	35 (17)	21 (3)	2	56
8 Nov 1986	A	40 (10)	41 (7)		81
14 Dec 1986	C	50 (35)	54 (7)	15	104
16 Dec 1986	C	7 (5)	14 (1)	9	21
16 Jan 1987	D	10 (10)	9 (6)	3	19
19 Jan 1987	C	28 (22)	28 (15)	3	56
18 Feb 1987	A	34 (25)	14 (9)	1	48
28 Mar 1987	C	18 (17)	14 (10)		32
29 Mar 1987	C	17 (16)	35 (26)		52
21 Apr 1987	A	27 (26)	12 (11)		39
9 May 1987	B	7 (0)	5 (0)		12
10 May 1987	B	2 (0)	3 (0)		5
13 May 1987	B	7 (0)	9 (0)		16
9 Jun 1987	B	25 (1)	34 (0)		59
10 Jun 1987	B	23 (0)	42 (3)		65
10 Jun 1987	C	16 (14)	25 (17)		41
17 Jul 1987	B	5 (1)	6 (1)		11
Total		501 (249)	559 (150)	40	1,060

[a] A = collected aboard a commercial groundfish trawler; B = collected aboard a commercial shrimp trawler; C = collected at a fish processing plant, filleted fish carcasses; D = collected at a fish processing plant, whole fish.

the nearest 0.01 g. Based on macroscopic observations, gonadal maturity stages were assigned to each gonad pair according to criteria of Wyllie Echeverria (1987). Gonad color, size, and morphology were recorded for each specimen. Additional macroscopic observations were made for the presence of milt and swelling of the sperm duct in testes and the presence of fertilized eggs, eyed larvae, and residual larvae in ovaries. Gonads were preserved in 10% phosphate-buffered formalin for later histological analysis and fecundity estimations.

Sections of the left otolith of each fish were prepared for age reading as described by Boehlert (1985). Ages were determined for all collected specimens according to criteria established by Chilton and Beamish (1982).

Histological preparation.—A representation subsample for histological analysis was selected on the basis of macroscopic gonad condition and fish size. Some samples frozen prior to formalin storage, and those collected in May (all small, obviously immature fish), were excluded from histological analysis. Histological cross sections from the middle portion of 249 testes and 150 ovaries were examined (Table 1). Testicular and ovarian tissues were embedded in paraffin and then sectioned at 7 μm and 8 μm, respectively. Sections were stained with Myer's hematoxylin and counterstained with eosin.

Histological and macroscopic evaluations.—Brief microscopic descriptions of each gonad section were recorded. Criteria to describe testicular sections included the presence of germ cells, primary spermatogonia, secondary spermatogonial cysts, primary or secondary spermatocyte cysts, spermatid cysts, and spermatozoa. The presence of spermatozoa in the testis lumen and signs of spermatozoa resorption were also recorded. For ovarian sections we noted the presence of vesicles, yolk globules, developed follicles, eyed larvae, atretic oocytes, and stored spermatozoa.

Maximum oocyte diameters were measured with an ocular micrometer. Randomly selected ovarian histological sections (one per ovary) were scanned for the largest spherical nonatretic oocyte in the most advanced oocyte phase. A minimum of five such oocytes was measured for diameter, the largest of which was recorded as the maximum oocyte diameter.

The initial macroscopic criteria for gonadal stages were reevaluated following the microscopic assessments. Microscopic descriptions following terminology of Moser (1967b) and Bowers (1992). Gonadal stages with criteria specific to darkblotched rockfish were described.

Length and age at maturity.—Length and age at 50% maturity were estimated for males and females separately by fitting data to the logistic equation

$$\mathrm{PROP}_x = 1/(1+e^{a x - b});$$

PROP_x is the proportion mature at length (cm) or age x and a and b are constants. Parameters were estimated by nonlinear least-squares regression (SAS Institute 1987). Length and age at 50% maturity (L_{50} and A_{50}) were determined by substituting 0.5 for PROP_x in the equation above, yielding

$$x = -b/a.$$

Standard errors (SE) for L_{50} and A_{50} were ap-

proximated by the delta method (Seber 1982). This analysis was performed with data from all months of collection and also with data limited to collections made in months of near spawning or spawning (copulation for males and parturition for females), when determination of maturity state (mature versus immature) should have been most accurate.

Fecundity.—Total fecundity, the number of advanced oocytes per ovary pair, was estimated for 40 ovary pairs. Because ovaries were stored in formalin, we employed a gravimetric subsampling method similar to that used by Phillips (1964) and MacGregor (1970). Unlike them, however, we recognized that *Sebastes* ovaries lack homogeneity between oocytes and intraovarian tissue due to a central dense string of stromal connective tissue that extends from the ovary hilum (see Moser 1967a). Our subsampling method attempted to account for this.

Ovaries were blotted dry and weighed to the nearest 0.1 mg. Subsamples, averaging 82.8 mg and 304 oocytes, were taken from the anterior, medial, and posterior regions of the left or right ovary and then weighed to the nearest 0.1 mg. After removing the ovarian sacs, ovary pairs were broken apart and the central concentrated stromal connective tissue was removed. Ovigerous tissue was teased away from the central stromal connective tissue. Connective tissue was washed with water to remove any remaining ovigerous tissue, then blotted dry. Ovarian sacs and central stromal connective tissue were weighed to the nearest 0.1 mg and subtracted from the total paired ovary weight.

Each subsample was placed on a slide with 3 or 4 drops of 33% glycerin (Hunter et al. 1985; Yoklavich and Pikitch 1989). Oocytes were teased apart and then transferred to a Plexiglas grid; vitellogenic oocytes were counted with the aid of a dissecting microscope. All ovaries used for fecundity estimations were in the latter stages of vitellogenesis. Previtellogenic and atretic oocytes were excluded from the counts.

Oocyte densities (oocytes per gram subsample) were calculated for each sample region (anterior, middle, and posterior). Final total fecundity estimates for each fish were derived by multiplying the paired ovary weight (less the ovarian sac and central connective tissue) by the oocyte density averaged across the three ovary subsample regions. We assumed for these calculations that each region could be given equal weight, but we tested for differences in oocyte densities among the three sample regions with a repeated-measures design analysis, Fisher's least-significant-difference multiple-comparison test (SAS Institute 1987). Replicate counts (two per sample region) were made with five ovary pairs to examine the precision of the subsampling method.

Nonlinear least-squares regression (SAS Institute 1987) was used to relate fecundity to fish length and age. Linear regression was used to relate fecundity to ovary-free fish weight.

Results

Maturity Stage Criteria

Gonadal maturity stages, based on criteria of Wyllie Echeverria (1987), were reclassified (Tables 2, 3) to incorporate differences observed for darkblotched rockfish. Contrary to Wyllie Echeverria (1987), we observed no distinguishing gonad traits (gross or cellular) that could accurately denote that a fish was in its first year of maturity (i.e., spawning for the first time). For males, Wyllie Echeverria's (1987) "first year maturity" stage was deleted; however, an additional mature stage was added. Seventy-seven percent of the mature males collected from April to June had testes in which spermatogenic stages preceding spermatozoa predominated. This maturity stage, absent from Wyllie Echeverria's (1987) classification, was incorporated as stage 2, development of spermatogenic cycles (Table 2). For females, those ovaries corresponding macroscopically to Wyllie Echeverria's (1987) "first year maturity" were reclassified as "maturing" (stage 2; Table 3).

"Maturing" Females

Forty-eight percent of the females, collected throughout the year, possessed "maturing" stage 2 ovaries. These females averaged 34.2 cm TL (SE, 0.12) and 7 years of age (SE, 0.08). Paired ovary weights did not exceed 4.5 g and ovarian sacs were less than 15 mm long. Unlike oocytes in stage 3 ovaries, ovarian stage 2 oocytes never exceeded maximum diameters of 260 μm and never progressed beyond an early vitellogenic stage. Histological examination of these ovaries collected from November through March revealed varying degrees of oocyte atresia; 40% were undergoing mass oocyte resorption. Those stage 2 ovaries collected in December and January and examined histologically contained vast numbers of atretic oocytes (Figure 1). No macroscopic features (coloration, shape, ovarian wall thickness) indicated these ovaries were resorbing their oocytes. Be-

TABLE 2.—Maturity stage criteria for testes of darkblotched rockfish, based on macroscopic and cellular observations. The presence of germ cells (GC), primary spermatogonia (PG), secondary spermatogonial cysts (SGC), primary spermatocyte cysts (PSC), secondary spermatocyte cysts (SSC), spermatid cysts (STC), and spermatozoa (SZ) is noted. Terminology follows Moser (1967b).

Maturity stage	Macroscopic description	Cellular description
1. Immature	Translucent, threadlike, often bloodshot; no milt, sharp edges; paired testis weight, <0.6 g	GC, PG, and SGC are the predominant stages of the spermatogenesis; more advanced stages rare
2. Development of spermatogenic cycles	Dull to milk-white in color; swollen; no milt; color of cross section uniform; sperm duct not swollen	PSC usually predominant; GC, SGC, SSC, STC, and a few SZ cysts also present; no SZ in lumen; residual sperm in lumen rare
3. Maturation	Dull to milk-white in color; swollen; slight to no milt in sperm duct; color of cross section uniform; sperm duct not swollen	SZ predominate; SZ cysts broken open; SZ in efferent ducts and sperm duct; GC, PSC, SSC, and STC also present; spermatogonia rare
4. Spawning (copulation)	Milk-white to white-brown in color; sperm duct swollen with milt; periphery translucent and center white in cross-section	SZ predominate, mostly present in lumen; periphery cleared; germ cell development at testis periphery; resorption at periphery
6. Spent	Light-brown or mottled white in color, translucent; slight milt in sperm duct; periphery translucent	GC predominate; resorption of SZ in sperm duct; no SZ in efferent ducts; PSC, SSC, and STC rare
7. Resting	Brown, tan or brown-grey in color; triangular, sharp edges, firm, short in length; small testes translucent; no milt	GC, PG, and SGC predominate; sperm duct empty; residual sperm present early in this stage

TABLE 3.—Maturity stage criteria for ovaries for darkblotched rockfish, based on macroscopic and cellular observations. The presence of oogonia within nests (ON), early perinucleolus (EP), and late perinucleolus (LP) oocyte stages are noted. Terminology follows Moser (1967b) and Bowers (1992).

Maturity stage	Macroscopic description	Cellular description
1. Immature	Pink and translucent; oocytes not visible; ovarian wall thin, <15 mm long; paired ovary weight, <1 g	Oocytes, <150 μm in diameter; stages of oogenesis include ON, EP, and LP oocytes; in ovaries nearing 15 mm in length, secondary oocyte growth is initiated with the formation of oil vacuoles
2. Maturing	Pink, often bloodshot; oocytes small, pink to cream color; ovarian wall thin, taut, 15–30 mm long; paired ovary weight, 1–4.5 g	Maximum oocyte diameter, 150–260 μm; ON and EP still present but predominantly occupied with oocytes in LP and initial yolk accumulation stages; oil vacuoles in midcortex region increase in size and number from summer to winter; follicular atresia may be common from December to March
3. Vitellogenesis	Cream to cream-pink color; oocytes large, cream color; large ovaries have black pigmentation on ovarian wall	Maximum oocyte diameter, 260–600 μm; yolk globules and oil vacuoles present; spermatozoa sometimes found near or attached to ovigerous lamellae and outer surface of follicles; ON through LP oocytes
4. Fertilized	Ovaries flaccid with delicate ovarian wall and pink cast; embryos spherical, hydrated (clear)	Embryos measure up to 800 μm; yolk globules completely coalesced to a uniform translucent fluid; oil vacuoles coalesced to single vacuole; preblastula to blastula embryo stages; empty follicles fill stroma surrounding embryos; ON through LP oocytes present
5. Eyed larvae	Ovaries translucent grey, fluid-filled, extremely flaccid; free-floating elongate embryos with black pigmented eyes	Embryos with well-developed, pigmented eyes and bodies with well-organized skeletal muscle; collapsed follicles and ON through LP oocytes present
6. Spent	Ovaries reddish to purple-grey; ovarian wall thick and loose from interior; residual larvae present	Presence of collapsed follicles and atretic oocytes throughout (indicating resorption); ON through LP oocytes present
7. Resting	Ovaries grey-pink; thick ovarian wall; some with undefined black dots visible through ovarian wall	Presence of collapsed follicles and atretic oocytes early in this stage; oogonial growth from ON to oocytes with initial yolk accumulation later in this stage

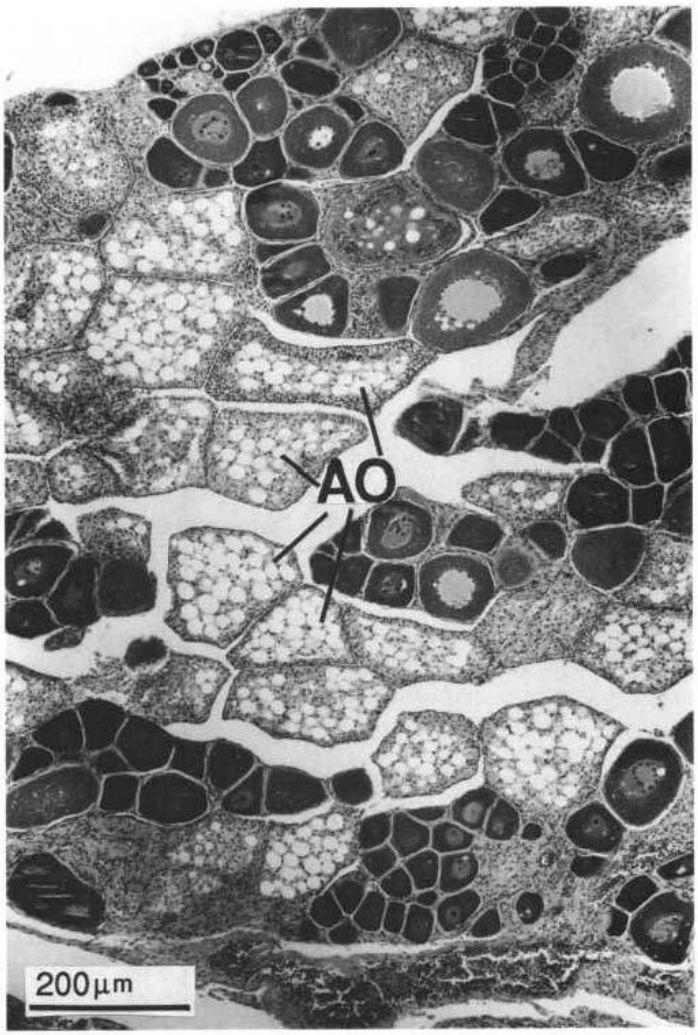

FIGURE 1.—Cross section of a stage 2 "maturing" ovary from a darkblotched rockfish female captured 19 January 1987. Note complete mass atresia of advancing oocytes; AO denotes atretic oocyte.

cause stage 2 ovaries contained no advanced nonatretic oocytes during months when mature females were spawning, it was evident that many of these fish were functionally immature.

We examined the percent occurrence of stage 2 (maturing) females among mature females, by age-group, during spawning (December–March) and nonspawning periods (July–September; Figure 2). This percentage decreased with increasing age. A lower overall percentage of maturing fish were found in spawning than in nonspawning months, suggesting that some recruitment from maturing fish to mature stage 3 females did occur during the sampling year.

Seasonal Development of Testes

Most mature adult males examined were near spawning condition in July, the start of the sampling period (Figure 3A). Spermatozoa were present in the sperm duct and efferent ducts, although sperm ducts were not swollen (stage 3). Most males remained in this condition through August. A few large males collected in August were in spawning condition (stage 4), although testes at this stage were observed more frequently in males collected between September and November (Figure 3A). Most testes were either spent (stage 6) or in a resting condition (stage 7) by the end of December, and most then were in a resting condition through March. Testes began developing new spermatogenic series (stage 2) from April to June.

Seasonal Development of Ovaries

All mature females collected in July exhibited vitellogenic oocytes (stage 3; Figure 3B). Yolk de-

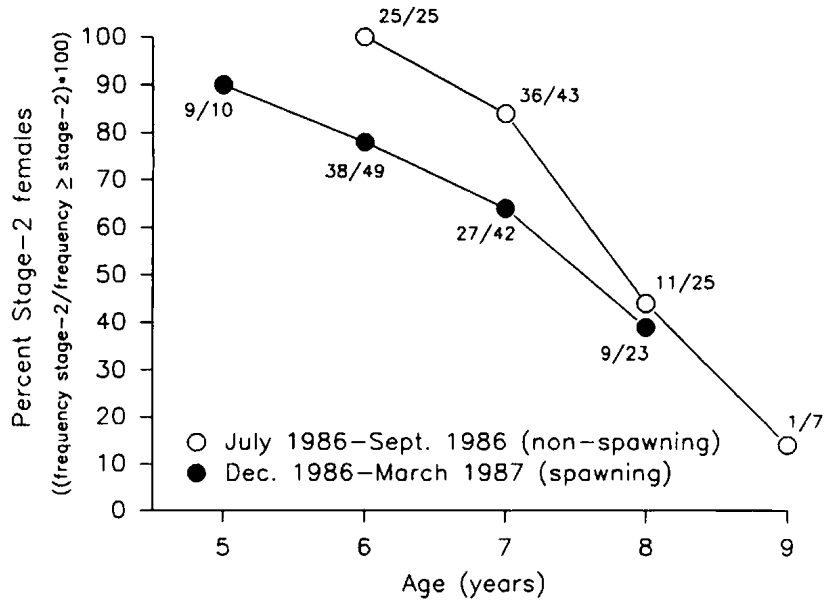

FIGURE 2.—Frequencies of darkblotched rockfish with "maturing" stage 2 ovaries as percentages of mature females during spawning (parturition) and nonspawning months, by cohort-specific age (age of fish during 1986). Ratios indicate the observed frequency of females with stage 2 ovaries over the sum of those at stages 2–7.

position and accumulation continued through November.

Spermatozoa were observed outside vitellogenic oocyte follicle surfaces or within the ovarian stroma in more than 50% of the histologically examined females collected from July to early November (Figure 4). Several maturing stage 2 ovaries collected during these months also contained spermatozoa, but only within the central stroma. The difficulty in detecting spermatozoa (due to their small size) within ovaries and the lack of October samples precluded further analysis of spermatozoa storage.

Fertilized ovaries (stage 4) and ovaries containing eyed larvae (stage 5) were found from December through February. Although no specimens with eyed larvae were observed past February, one specimen collected in March contained fertilized eggs. Therefore, parturition in some individuals probably occurred through March. Based on the observed occurrence of spent females, the principal months of parturition were February and March. Nearly all the mature females were in a postspawning condition (stage 6 or 7) from March through June. The unimodal development of eggs and larvae indicated the spawning of only a single brood per reproductive year.

Size Effect on Gonad Cycles

Males and females both exhibited an annual reproductive cycle in which timing was size dependent. The reproductive cycle in smaller males was delayed relative to the cycle of larger males. Larger males were observed in developmental (stage 2) through resting conditions (stage 7) earlier in the season than smaller males. Larger males also tended to end spawning earlier than smaller ones (Figure 5A). Likewise, the reproductive cycle of small females appeared delayed relative to the cycle of larger females. Larger females were observed with a vitellogenic ovarian condition (stage 3) earlier in the season than smaller females (Figure 5B).

Length and Age at Maturity

Estimates of length and age at 50% maturity were 29.6 cm TL and 5.1 years for males and 36.5 cm TL and 8.4 years for females, based on data from all months of collection (Table 4). Problems associated with classifying fish as mature or immature during nonspawning periods (i.e., classifying stage 2 females as immature in late summer when some had actually spawned the preceding winter or spring) appeared minimal. Estimates of 50% maturity derived from fish collected only during near spawning or spawning months were only slightly higher; 29.8 cm TL and 5.2 years for males; 36.7 cm TL and 8.5 years for females (Table 4).

Fecundity

Significant differences in estimates of fecundity were found among ovarian sampling locations (re-

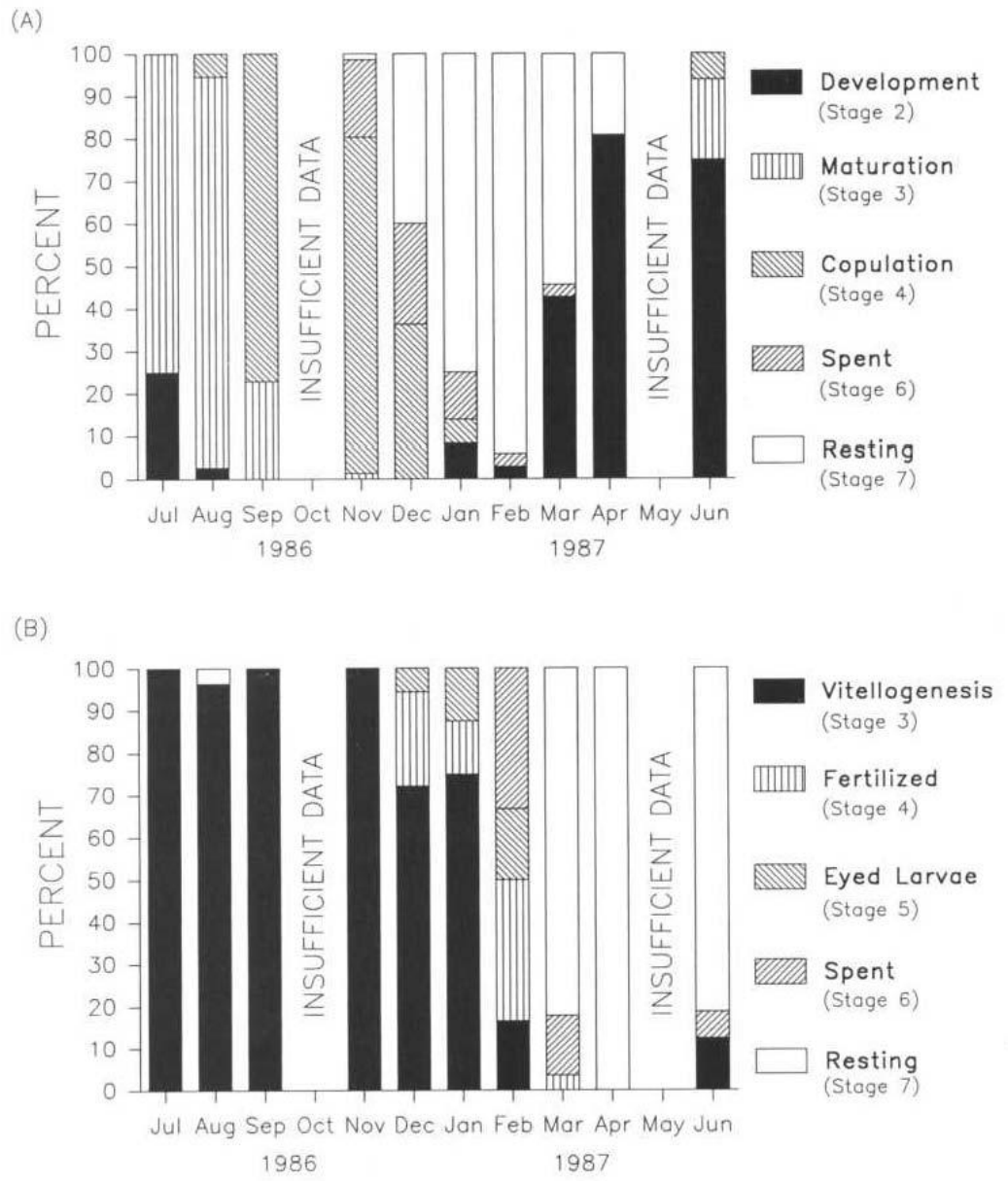

FIGURE 3.—Seasonal changes in gonad condition for **(A)** mature testes and **(B)** mature ovaries of darkblotched rockfish, based on maturity stage criteria. May and October are omitted due to small sample sizes. Gonad stages are described in Tables 2 and 3.

peated-measures design; $F = 6.60$; df = 2, 78; $P = 0.002$). Fisher's least-significant-difference multiple-comparison test ($P < 0.005$) indicated that fecundities estimated from posterior ovary subsampling were significantly lower than those estimated from either anterior or medial subsampling. In addition to the central connective tissue, which was removed prior to subsampling, there remained interstitial connective tissue that appeared more dense in posterior subsamples. Accordingly, the average oocyte density from posterior subsamples (5,887 oocytes/g; SE, 765.94) was lower than both medial (6,236 oocytes/g; SE, 838.20) and anterior (6,281 oocytes/g; SE, 820.69) subsamples. Fecundity estimates from anterior subsampling were not significantly different from those estimated by medial subsampling.

Coefficients of variation (100·SD/mean) for mean oocyte density across subsample replicates (two replicates in each of three regions for five ovaries) ranged from 0.43 to 3.35%, averaging 1.81%.

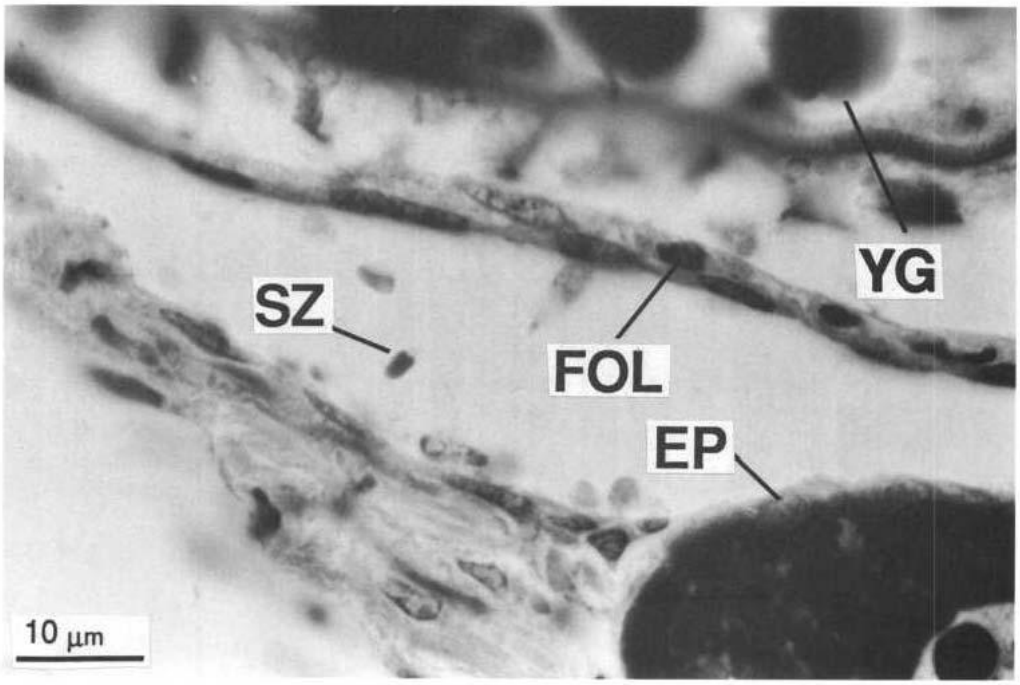

FIGURE 4.—Cross section of a vitellogenic (stage 3) ovary, containing spermatozoa, from a darkblotched rockfish female captured 22 September 1986; *SZ*, spermatozoa; *YG*, yolk globule; *FOL*, follicle; *EP*, early perinucleolus stage oocyte.

Total fecundity estimates ranged from 19,815 to 489,064 oocytes, increasing nonlinearly with fish length and linearly with fish weight (Figure 6A, B). Specimens used in the analysis ranged from 325 to 470 mm TL, 565 to 1,742 g ovary-free fish weight, and 6 to 66 years of age. The length–fecundity relationship was best fit by the power function

$$FEC = (4.3459 \times 10^{-10})L^{5.6049}$$

($r^2 = 0.905$); FEC is fecundity (number of oocytes per female) and L is total length of the fish (mm). The weight–fecundity relationship was

$$FEC = 370.03 \cdot W' - 182{,}381.36$$

($r^2 = 0.974$); W' is ovary-free fish weight (g). Fe-

TABLE 4.—Estimates of size and age of darkblotched rockfish at 50% maturity, derived from logistic equations ($P = 1/1 + e^{a x \cdot b}$) fitted by nonlinear regression to proportions of mature males and females; x = total length (TL, cm) or age (years); N = number of fish used to calculate proportions; SE = standard error of x at 50% maturity.

Sex	x	Data used[a]	Equation constants		r^2	N	50% maturity estimate (TL or years)	SE
			a	b				
Males	TL	All months	−2.47	73.25	>0.99	500	29.6	0.06
		May–Nov	−1.82	54.14	>0.99	309	29.8	0.05
	Age	All months	−3.32	17.08	>0.99	500	5.1	0.02
		May–Nov	−3.14	16.45	>0.99	309	5.2	0.02
Females	TL	All months	−0.65	23.66	0.98	559	36.5	0.17
		Dec–Mar	−0.64	20.57	0.96	168	36.7	0.27
	Age	All months	−0.68	5.70	0.97	559	8.4	0.23
		Dec–Mar	−0.68	5.77	0.97	168	8.5	0.26

[a] Maturity data from all months are compared with data from months of near spawning or spawning, when the determination of maturation state (mature or immature) should be most accurate. Months of near spawning to spawning were May–July 1987 and July–November 1986 for males, and December 1986–March 1987 for females.

cundity increased asymptotically with fish age (Figure 6C) and was described with a von Bertalanffy-type function:

$$FEC = 386{,}668\,[1 - e^{-0.0564(t-2.58)}]$$

($r^2 = 0.903$); t is age in years.

Discussion

Timing of Reproductive Events

Reproductive events for darkblotched rockfish off the Oregon coast overlapped and were protracted (Figure 3A, B). Insemination occurred from August to December, fertilization from December to March, and parturition from December through March. Based on the timing of insemination and fertilization, some females may have stored spermatozoa in their ovaries for up to 3 months.

Differences in timing of reproductive events among fish of different sizes contributed to the overall protraction and overlap of reproductive events. Major reproductive events began and ended earlier in larger individuals (Figure 5A, B). Eldridge et al. (1991) reported a similar trend in size-specific reproduction for yellowtail rockfish *Sebastes flavidus*. Earlier seasonal spawning by larger or older individuals has been documented for fish species such as largemouth bass *Micropterus salmoides* (Miranda and Muncy 1987; Mayer et al. 1990), the freshwater sculpin *Cottus gobio* (Mann and Mills 1979), and summer flounder *Paralichthys dentatus* (Morse 1981). Larson (1991) suggested that delayed reproduction in *Sebastes* may result from reduced food availability, which would disproportionately affect smaller and younger individuals that have greater metabolic demands to support somatic growth and therefore decreased levels of fat reserves.

The flexibility in the timing of reproductive events in *Sebastes* may enhance reproductive success. Lisovenko (1970) suggested that the prolonged copulation period of *Sebastes* may increase the probability that each female will be fertilized. Protracted spawning seasons have been attributed to species employing a "bet-hedging" reproductive strategy in response to unpredictable environments (Lambert 1984; Lambert and Ware 1984; Alheit 1989). Correspondingly, a protracted parturition period increases the probability that larvae will be released when conditions are favorable for their survival.

Length and Age at Maturity

Males matured at a smaller size and younger age than females. Ninety-seven percent of all the males captured with commercial groundfish gear (exclusive of shrimp gear) were mature. In contrast, only 51% of the females captured were mature.

Length at maturity appears to increase with increasing latitude (Table 5). Lengths at 50% maturity (L_{50}) estimated in this study were similar to values presented by Barss (1989), who also ex-

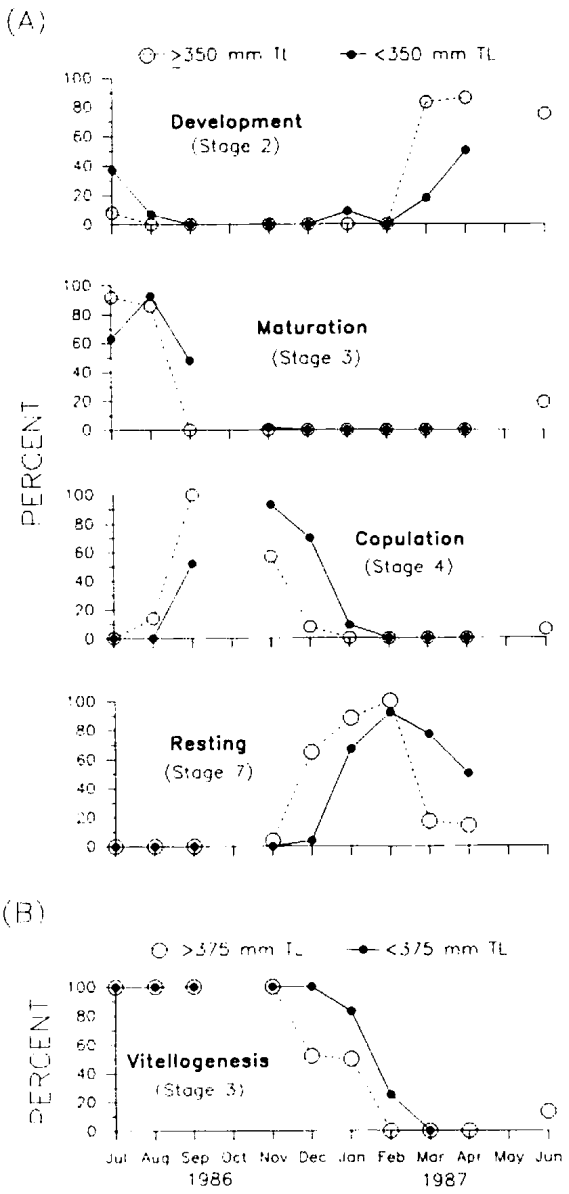

FIGURE 5.—Percentages of gonadal stage occurrence by month for two size-groupings of sexually mature darkblotched rockfish (A) males and (B) females. Omissions of testicular stage 6 and ovarian stages 4–7 are due to insufficient data. Months of May and October are also omitted because of small sample sizes.

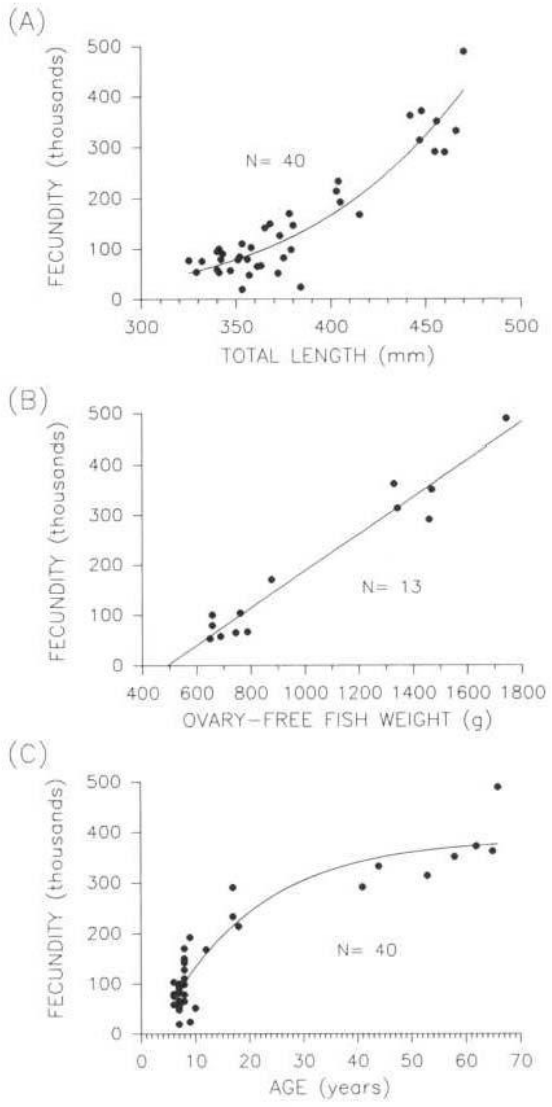

FIGURE 6.—Estimated fecundity of darkblotched rockfish as a function of **(A)** total length, **(B)** ovary-free fish weight, and **(C)** age. Curves represent the fitted equations.

amined fish caught off the central Oregon coast. Westrheim (1975), who examined fish off British Columbia, reported significantly larger values of L_{50} for both males (38.9 cm TL) and females (35.6 cm TL; Table 5). Phillips (1964) presented L_{50} (30.5 cm TL) and age at 50% maturity (6 years) for darkblotched rockfish captured from central to northern California. Although sexes were combined in Phillips' (1964) analysis, it appears that estimates of L_{50} were smaller than those found in the present study (Table 5). Wyllie Echeverria (1987) presented considerably smaller values of L_{50} and age at 50% maturity (A_{50}) for darkblotched rockfish collected off central to northern California for both males and females (Table 5). Interpretation of the various maturity estimates is difficult because the investigations were conducted during different years and the techniques used to assess maturity may not have been consistent.

Uncertainty in defining the size and age at sexual maturity of species in the genus *Sebastes* has been related to the difficulty in determining the reproductive viability of relatively young fish with "maturing" gonads (Westrheim 1975; Gunderson 1977; Wyllie Echeverria 1987; Leaman 1988; Eldridge et al. 1991). Eldridge et al. (1991) questioned whether small, young yellowtail rockfish with "maturing ovaries" actually complete mature gonadal cycling. Evidence from our study of darkblotched rockfish indicates that many "maturing" (stage 2) ovaries undergo an "immature cycling," whereby developing oocytes are resorbed just prior to yolk accumulation. Eldridge et al. (1991) observed a cessation of oocyte development and resorption of oocytes in ovaries of young laboratory-held yellowtail rockfish. Similar reproductive failures in young female rockfish, particularly those that have not yet spawned for the first time, may be common in the field as well. Reproductive failures (mass oocyte resorption) in fishes have been associated with poor physical condition of fish (MacGregor 1966; Wallace and Selman 1981), poor nutrition (Hunter and Macewicz 1985), environmental stress (Ball 1960; Hontela and Stacey 1990), and sex ratio imbalance (Trippel and Harvey 1990). Hunter and Macewicz (1985) noted higher rates of ovarian atresia among smaller females of northern anchovy *Engraulis mordax*. Incidence of mass oocyte atresia in darkblotched rockfish ovaries may also be attributed to constraints associated with energy allocation, particularly because this phenomenon was limited to actively growing females less than 9 years of age. Eight-five percent of stage 2 females were 6, 7, or 8 years of age. Further investigation is needed to determine if the reproductive failures observed among stage 2 darkblotched rockfish females occur annually or if conditions specific to the year of investigation were responsible.

The presence of spermatozoa within stage 2 ovaries indicated that some maturing females mated, even though most did not spawn (undergo parturition). Successful mating, therefore, does not necessarily result in successful spawning. Perhaps under more optimal conditions (greater food

TABLE 5.—Comparison of lengths (L_{50}) and ages (A_{50}) of darkblotched rockfish at 50% maturity estimated by various authors. Lengths are presented in centimeters total length; ages are in years.

Source	Capture location	L_{50}		A_{50}	
		Males	Females	Males	Females
Phillips (1964)[a]	California	30.5		6	
Wyllie Echeverria (1987)	California	27	27	4	4
Barss (1989)[b]	Central Oregon	31.5	36.7		
Present study	Central Oregon	29.6	36.5	5.1	8.4
Westrheim (1975)[bc]	British Columbia	35.6	38.9		

[a] Sexes combined.
[b] Converted from fork length (FL) to total length (TL) by TL = 0.846 + 1.046(FL); N = 1,058, r^2 = 0.99.
[c] Original length data were measured to the nearest lower centimeter, but in analysis data were lumped into even-numbered 2-cm intervals. Values of L_{50}, therefore, are biased low by approximately 0.25 cm.

availability), a greater proportion of maturing fish would have matured and spawned. Given the high percentage of stage 2 females (48% of all females sampled), such an occurrence would significantly affect estimates of both length and age at maturity.

It is difficult to predict when a fish will spawn for the first time or to predict when a stage 2 ovary (maturing) will transform to a mature vitellogenic (stage 3) condition. It is clear, however, that fish with stage 2 ovaries had never previously spawned, and in the context of computing length–maturity and age–maturity relationships, it is correct to consider them immature.

Fecundity

Phillips (1964) estimated fecundities of 36,600–609,800 oocytes per ovary pair using the gravimetric technique with 12 darkblotched rockfish ranging from 335 to 575 mm TL. Testing the null hypothesis that the linear log(fecundity)–log(length) relationship in the present study was not different from that of Phillips (1964) revealed no significant differences in either slopes (analysis of covariance: F = 0.24; df = 1, 48; $P > 0.63$) or intercepts (F = 1.80; df = 1, 49; $P > 0.10$).

The largest, oldest individuals were the most fecund. Thus, available evidence suggests that reproductive senescence does not occur for this species.

Management Implications

Exploitation of long-lived species such as darkblotched rockfish may compromise their reproductive success. Long life spans and repeated spawning (iteroparity) reduce the risk of stock depletion when environmental conditions are unfavorable for extended periods (Leaman and Beamish 1984) or when reproductive success is variable from year to year (Holgate 1967; Murphy 1968; Charnov and Schaffer 1973; Stearns 1976; Mann and Mills 1979; Leaman 1991). As fishing reduces the number of age-groups in a population, the potential for population collapse increases (Gunderson 1977; Borisov 1979; Leaman and Beamish 1984; Francis 1986). The timing of reproductive events for darkblotched rockfish was shown to be related to fish size. In the absence of density-dependent growth, the selective removal of larger individuals through fishing may shift the spawning peak to later in the year (Bye 1990), and may reduce the duration of the spawning season, further reducing the chances for reproductive success.

Although it is difficult to differentiate the relative impacts of fishing mortality and recruitment variability based on only one year of data, the age distribution of darkblotched rockfish, which was highly skewed toward younger ages (Nichol 1990), may indicate that reproductive potential has been reduced relative to the unfished state. We estimate that 49% of the darkblotched rockfish females in Oregon commercial trawl catches had never spawned. Females were fully recruited to the fishery by age 7 (Nichol 1990), yet 50% maturity did not occur until age 8.

Leaman (1991) effectively demonstrated how vulnerable rockfish stocks are to fishing exploitation and how current management policies, developed for shorter-lived species, are inappropriate for rockfishes. These concerns certainly apply to darkblotched rockfish stocks off Oregon, and strategies currently employed to manage this and other *Sebastes* species merit reevaluation.

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