# Reproductive performance of yellowtail rockfish, Sebastes flavidus

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## Synopsis

Field and laboratory studies were conducted for 3 years on the yellowtail rockfish, *Sebastes flavidus*, from Cordell Bank, California, in order to characterize the reproduction of this species whose northern stocks have declined. Research findings included reversal of the sex ratios and male-female ages and sizes at age throughout the annual cycle, heavier and longer females at age than males after sexual maturation, maturation of females at 6 and males at 8 years, long reproductive lifespans, distinct male and female gonadosomatic index patterns over the annual cycle, age- and size-specific fecundity, no difference between potential and realized fecundity and the seasonal changes associated with gonadogenesis. The reproductive profile of the Cordell Bank yellowtail rockfish provided a base for comparison with northern populations that appeared to differ, especially in age and size.

#### Introduction

In this study the reproduction of yellowtail rockfish, Sebastes flavidus, is thought of as a complex of observable, measurable performances. These traits continuously and dynamically change or adapt in time and space at multiple levels of organization from the community to tissue levels in response to environmental conditions, including exploitation. This expands on Lewontin's (1958) concept that populations adapt in two ways: through intergenerational genetic variability and through individual phenotype plasticity. Since no single trait or property can accurately represent the adaptive or reproductive capacities of individual fish, populations or species, we used a multidimensional research approach to understand reproduction and its role in population persistence.

To examine the functional relationships between yellowtail rockfish and their environments, a physi-

ological ecology research program was initiated in 1985. The research goal was to identify, describe and understand the factors that determine yellowtail rockfish condition and reproduction for use in assessing health of the stock and ultimately forecasting recruitment in the population. This paper describes reproductive performance and characterizes a yellowtail rockfish population from a California coastal seamount.

### Materials and methods

Subadult and adult yellowtail rockfish were collected from April 1985 to April 1988 from Cordell Bank, California. Fish that had immature, nonfunctional gonads were classified as subadults. Monthly cruises provided 1418 specimens caught by hook and line; of these 487 (390 females and 97 males) were randomly subsampled for further de-

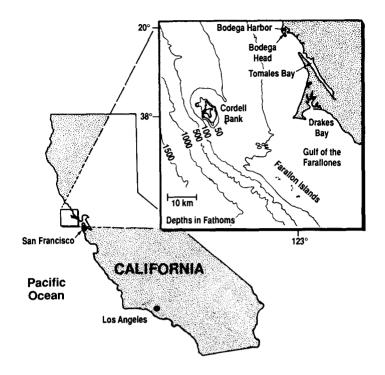


Fig. 1. Cordell Bank, California, site of study on reproduction of yellowtail rockfish.

tailed analysis. All fish collected during these monthly cruises were identified and enumerated. An additional total of 168 trawl-caught yellowtail rockfish females were sampled from the commercial catch from November to March of each year for studies relating to maturity and fecundity. Cordell Bank is the northernmost seamount (38°01'N, 123°25'W) of the California continental shelf (Fig. 1). The bank lies approximately 372 km west of the California coast and covers 62 km of seafloor within the 91 m depth contour. The highest elevation on the bank is 35 m below the sea surface. A total of 22 adult yellowtail rockfish were captured on the bank in November and December of each year and transported, after air bladder deflation, to 22001 tanks in the laboratory. Fish were held in the laboratory throughout the normal maturation period and allowed to complete parturition, being maintained under ambient photoperiod and water conditions and fed fresh fish ad libitum. All fish were weighed and measured, and 11 were sacrificed for internal examination of gonadal state after parturition or the normal parturition period.

Fish were examined in the laboratory within 24 h of capture, to assess their physiological conditions and reproductive states. Comprehensive examination protocols included morphometrics (length, breadth, width), gravimetrics (total weight, visceral weight, gonad weight, liver weight) and meristics; external and internal examinations of organs for condition (pathologies, fat content, general appearance), diseases and parasites; subsampling of muscle, liver and gonads for proximate analyses, histology and fecundity; and age determination by the otolith break-and-burn method. Fecundity was gravimetrically estimated in triplicate after Gilson fluid fixation. For histology, ovaries were fixed in 10% buffered formaldehyde, dehydrated in ethanol, cleared in xylene and embedded in paraffin (Humason 1967). Testes were fixed in 2.5% glutaraldehyde, postfixed in 1% osmium tetroxide and embedded in epoxy resin (Spurr 1969). Tissues

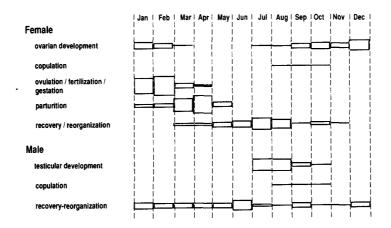


Fig. 2. Annual reproductive performance of male and female yellowtail rockfish from Cordell Bank, California.

were sectioned at  $6 \mu m$  and stained in hematoxylin and eosin.

Specimen-specific data were managed by using dBASE III +. Subsets were created for individual or group analyses depending on the subtask objectives. Statistical analyses included univariate descriptions, curve fitting, correlation and regression analyses, analysis of variance (ANOVA), analysis of covarience (ANACOV) and graphics, completed with the assistance of Number Cruncher Statistical System 5.01 for microcomputers.

## Results

## Reproductive performance

The annual sequence of reproductive performance in yellowtail rockfish from Cordell Bank (Fig. 2) followed general patterns described in other studies for many *Sebastes* spp. (DeLacy et al. 1964, Moser 1967, Ni & Templeman 1985, Wyllie Echeverria 1987). Both sexes shared common characteristics of gonadal development, namely a copulation period and a recovery-reorganization period. However, their seasonal patterns differed, and females underwent additional elaboration with the ovulation to parturition developmental sequence that is unique to *Sebastes*.

Ovarian development began just prior to the

copulation period and accelerated in September. From October through January, 75% of those females with progressively developing ovaries were observed. Most (89%) that had ovulated and were carrying developing embryos were collected in January and February, and parturition usually occurred in March and April (73%). The prolonged (9 months, March through November) recoveryreorganization period came next and was most obvious just prior to the onset of ovarian development. Male testicular development was rapid, occurring largely during July and August (67%), then declining rapidly with the ending of the copulation period in October. A varying portion of the population appeared in the recovery-reorganization state throughout the year.

#### Community-population performance

At Cordell Bank the fish community associated with yellowtail rockfish and available to hook and line consisted of 21 species, dominated numerically by yellowtail rockfish (41.5%) followed by *S. rosaceus* (13.9%), *S. paucispinis* (11.3%), *S. chlorostictus* (10.3%), *S. pinniger* (6.2%) and *Ophiodon elongatus* (4.7%). *Sebastes* spp. comprised 94.4% of the total catch. The mean number of species did not seasonally vary (Table 1), nor did the species composition. Catches also were not seasonally dif-

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	xj± SE
Sex ratio M:F	0.63	1.03	1.65	1.45	1.33	1.62	1.11	0.96	0.41	0.43	0.64	0.43	$0.97 \pm 0.47$
Yellowtail catch	175	117	206	108	41	145	136	98	49	99	82	162	118.2 ± 49.4
CPUE	3.19	2.53	3.44	1.63	1.68	3.78	2.80	3.54	1.83	2.31	2.09	2.02	$2.57 \pm 0.76$
No. of species	11	9	8	10	8	11	9	9	10	9	11	11	$9.7 \pm 1.2$

*Table 1.* Yellowtail rockfish sex ratio (males:females), total yellowtail catch, catch per unit effort (CPUE; No. of fish fisherman<sup>-1</sup>  $h^{-1}$ ) and number of total fish species collected on yellowtail rockfish cruises.

ferent; mean monthly catch per unit effort (CPUE) was 2.57. The yellowtail rockfish sex ratios changed throughout the year, despite an even (0.97) mean value for the year. The male to female ratio was approximately even in February and then again in July and August, the main copulation period. Females predominated in September – January and males in March – June.

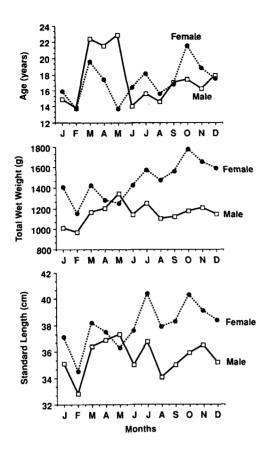
The male and female subadult yellowtail rockfish were similar in ages and size (Table 2), whereas adult females were heavier and longer than males despite identical mean ages of 17.2 years. The seasonal distribution of these parameters (Fig. 3) indicated that males were generally older than females during March – May and were younger in other months. Females on average were longer and heavier in all months except March, and their average size greatly increased after June while that of males slightly decreased. True sexual dimorphism was apparent (Fig. 4). Body depths at length were not significantly different (ANACOV,  $p \ge 0.05$ ) between males and females, but age-specific total wet weights and standard lengths diverged significantly (ANACOV,  $p \le 0.05$ ) in fish older than 8 years of age. Males also exhibited a narrower range of ages than did females (5–39 versus 4–45 years). All reproductive processes from ovulation and fertilization through parturition occurred from January through May (Fig. 2). The highest incidence of females with newly fertilized eggs and eyed embryos was found in January and February (Table 3), and spent fish were most frequent after February. It appeared that older fish spawned early in the season. Mean ages of females with either fertilized eggs, eyed embryos or newly spent ovaries were higher than those in succeeding months.

## Individual performance

Individual reproduction was best monitored in the laboratory. Maturation and spawning of experi-

Table 2. Means, standard deviation and range of ages (year; Rg), total wet weight (g) and standard length (cm) of subadult and adult male and female yellowtail rockfish.

Age			Total wet	weight		Standard length		
x	SD	Rg	x	SD	Rg	x	SD	Rg
7.2	2.0	5–11	710.1	212.1	425–1244	29.6	2.7	25.35
6.7	1.5	4-10	722.9	315.5	362–1879	28.7	3.1	23-36
17.2	7.1	6–39	1156.2	209.0	6691660	36.1	2.1	32-42
17.0	2.0	6 45	14/2 4	2011 0	500 <b>2</b> /02	20.0		29-49
	7.2 6.7	7.2 2.0   6.7 1.5   17.2 7.1	7.2 2.0 5-11   6.7 1.5 4-10   17.2 7.1 6-39	7.2 2.0 5-11 710.1   6.7 1.5 4-10 722.9   17.2 7.1 6-39 1156.2	7.2   2.0   5-11   710.1   212.1     6.7   1.5   4-10   722.9   315.5     17.2   7.1   6-39   1156.2   209.0	7.2   2.0   5-11   710.1   212.1   425-1244     6.7   1.5   4-10   722.9   315.5   362-1879     17.2   7.1   6-39   1156.2   209.0   669-1660	7.2   2.0   5-11   710.1   212.1   425-1244   29.6     6.7   1.5   4-10   722.9   315.5   362-1879   28.7     17.2   7.1   6-39   1156.2   209.0   669-1660   36.1	7.2   2.0   5-11   710.1   212.1   425-1244   29.6   2.7     6.7   1.5   4-10   722.9   315.5   362-1879   28.7   3.1     17.2   7.1   6-39   1156.2   209.0   669-1660   36.1   2.1



*Fig. 3.* Mean monthly age (years), total wet weight (g) and standard length (cm) of yellowtail rockfish from Cordell Bank, California.

mental fish held in the laboratory were similar to those in field-caught specimens. Seven of 22 laboratory fish with a mean age of 24 years completed maturation and released embryos. Fish that did not successfully spawn had a mean age of 9.5 years. Examination of these fish showed that they ceased ovarian development and resorbed their eggs. All seven females ceased feeding 3–5 days before parturition, and fish became reclusive and had high opercular ventilation rates. All releases occurred during the night. Examination of fish within 2–5 days after parturition showed that extrusion of embryos was nearly complete and that ovaries quickly began recovery and reorganization with the firming

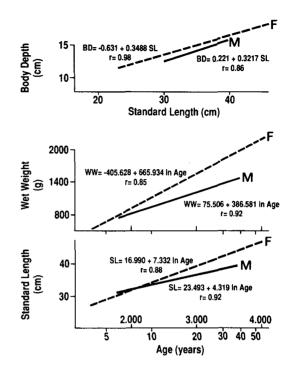


Fig. 4. Linear regression plots of standard length, wet weight by age and body depth by standard length of male (n = 97) and female (n = 340) yellowtail rockfish from Cordell Bank, California.

of tissues and reduction of the lumen and ovarian flaccidity.

Ages at maturity were estimated by contrasting individual subadults with undeveloped gonads with adults with gonads in late stages of development (Table 4). Males tended to be slightly, but not significantly (t-test,  $p \ge 0.05$ ), older than females. Adults that appeared mature by having gonads in advanced stages of maturation and adults that had fully developed ova, fertilized eggs or spent ovaries did not differ significantly in age (t-test,  $p \ge 0.05$ ), and they had broad age ranges (8–39 years for males; 6–45 years for females) and wide distributions (coefficients of variation, 36.2 - 39.8%).

By subtracting the minimum ages at maturity from the age frequencies of the males and females, we were able to plot the average distributions of reproductive lifespans within the male and female yellowtail rockfish stock (Fig. 5). Age distributions

Reproductive state	Month	N	% of total	Adult mean age (years)
Fertilized eggs	Jan	13	39	21.2
	Feb	17	52	15.8
	Mar	3	9	18.3
Eyed embryos	Jan	2	66	26.0
	Feb	1	33	9.0
Spent ovaries	Jan	3	4	28.0
	Feb	5	6	26.0
	Mar	25	32	20.7
	Apr	32	41	19.4
	May	10	13	15.7
	Jun	6	8	13.7

*Table 3.* Percent composition and adult mean ages, by month, of adult yellowtail rockfish with fertilized eggs, eyed embryos or spent ovaries.

and reproductive lifespans of males and females were polymodal. Potential reproductive lifespans were high, 31 years (range 8–39 years) for males and 39 years (range 6–45 years) for females. The mean reproductive lifespans were the same – 11 years (shaded area) for males (8–19 years) and females (6–17 years). Based on the age composition of the stock, 55% of the males and 59% of the females had reproductive lifespans of 0–11 years.

Whole body changes occurred with gonadal development, especially in females. Females increased in breadth and width as ovaries enlarged. Both sexes had seasonally enlarged urogenital papillae, males during the copulatory period and females during parturition.

#### Organ performance

The most easily quantifiable trait reflecting seasonal gonadal changes was the gonadosomatic index (GSI = gonad wet weight in grams (total body wet weight in grams)<sup>-1</sup>  $\times$  100). The low subadult GSI's and absolute gonad weights easily separated subadults from mature adults during the gonadal developmental period. Mean GSI value for adult males was 0.257 versus 0.098 for subadults; mean GSI value for adult females was 3.22 versus 0.486 for subadults. Seasonal GSI patterns for adults were distinctive (Fig. 6). Male GSI's remained low from January to June, were highest during testicular development and the copulation period and peaked in August. The GSI's of females were cyclic, but the increase in GSI's with gonadal development was more gradual, with a distinct peak in January and a graduated but rapid decline during early recovery.

Estimated fecundity by fish length, age or weight showed no significant difference among the 3 years (ANOVA,  $p \ge 0.01$ ; Fig. 7). The highest correlations were seen between fecundity and total body wet weight. A comparison of age-specific fecundity in pre-fertilized and fertilized fish indicated that there was no significant difference (ANOCOV,

Table 4. Age and standard length (SL) of male and female of yellowtail rockfish in all reproductive states, and comfirmed mature adults (those with fully mature or recently spent gonads). Rg = range.

	Male	Female				
	x	SD	Rg		SD	Rg
Subadults						
Age (years)	7.2	2.0	5-11	6.7	1.5	4-10
SL (cm)	29.6	2.7	25-35	28.7	3.1	23-36
All adults						
Age	17.2	7.1	6-39	17.2	7.2	6-45
SL	36.1	2.1	32-42	38.9	3.7	29-46
Confirmed adults						
Age	19.5	6.7	8-39	17.6	7.0	6-45
SL	36.6	2.7	32-42	37.6	3.7	29-46.0

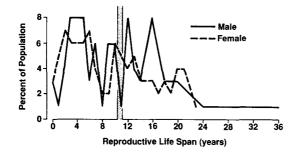


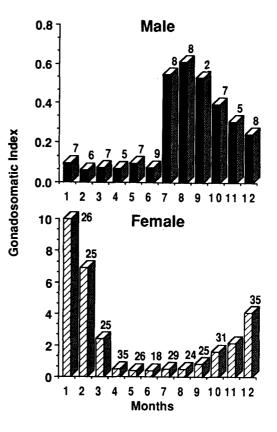
Fig. 5. Distribution, in percent of the population, of reproductive lifespans of male and female yellowtail rockfish from Cordell Bank, California. Shaded area represents mean reproductive lifespan for males and females.

 $p \ge 0.05$ ) between potential and real fecundity (Fig. 8).

Annual sequences of macroscopic gonadal changes were apparent. Most male subadult testes appeared small, translucent, elongated structures, triangular in cross section to threadlike. Colors ranged from translucent pink to yellowish white. With maturity, testes enlarged and became firm and triangular. The pink changed gradually to all white, the process beginning as a white line along the sperm duct. During the peak of the copulation period, testes contained free-flowing sperm. Associated with this ripened condition were large urinary bladders usually full of urine; the urogenital papillae were enlarged and distended. After the copulation period, testes gradually lost their white appearance, beginning at the periphery. Testes slowly became light brown to pink-gray and decreased in size.

Young, immature females had paired, translucent, ribbonlike ovaries ventral to the swim bladder. With the onset of maturity during the developmental period, ovaries enlarged and were circular. Ovaries changed from pale pink to yellowish orange as yolk accumulation progressed. No black pigmentation spots were visible. This process was reversed during the recovery-reorganization period.

Ovaries in mature females underwent notable seasonal changes. After the copulation period, ovaries began to enlarge and to change from a pale pink to yellow-orange. Ovaries gradually enlarged



*Fig. 6.* Mean monthly gonadosomatic index [gonad wet weight in grams (g) (total body wet weight (g))<sup>-1</sup> × 100] of male and female yellowtail rockfish from Cordell Bank, California.

to occupy over half the peritoneal cavity volume. As the time of ovulation approached, the large eggs could be easily teased from their clustered follicles. At ovulation and fertilization, eggs dramatically increased in clarity and became more yellowish blue. The thin ovarian walls encased ovaries turgid with free eggs. As gestation proceeded, the ovaries assumed a gray-green appearance largely due to the pigmentation of embryonic eyes.

After parturition, which probably occurred over a period of hours based on laboratory observations, the ovaries appeared as flaccid sacks with vacuous lumens. Residual embryos were occasionally visible in the lumen. Ovaries appeared dark red-brown at this stages. Recovery and reorganization occurred rapidly within a few days. Flac-

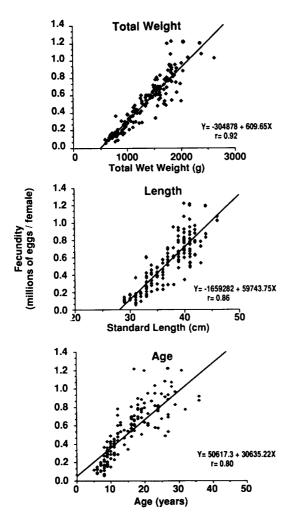


Fig. 7. Fecundity by total weight, standard length and age of yellowtail rockfish from Cordell Bank, California.

cidity decreased, lumens decreased, walls thickened, and colors changed to brown-pink. Often randomly placed, small, black spots were visible, especially along the ventral midline.

## Tissue performance

Histological examination confirmed that yellowtail rockfish were determinate spawners. At this level of organization, it was possible to closely monitor the annual reproductive cycle. This definitive examination served as a sensitive measure of the yellowtail rockfish's reproductive state.

Elongate testes had an unrestricted, tubulartype structure throughout (Grier 1981). Efferent seminiferous tubules branched off the central sperm ducts and became increasingly smaller towards the periphery. Intratubular spaces contained germinal epithelium composed of Sertoli cells and spermatogenic germ cells (cysts). Extratubular spaces were the site of Leydig cells, usually found in conjunction with capillaries, nerves, smooth muscle and fibroid cells, all in a connective tissue matrix, the stroma. Testes were bordered by squamous epithelium. Spermatogenesis occurred in cysts, progressing from the periphery to the sperm ducts. Early in testicular recrudescence, tubules contained cysts of primary and secondary spermatogonia, widely separated by Sertoli cells. Mitotic and meiotic divisions of secondary spermatogonia led to formation of spermatocytes, close apposition of cysts and crowding of tubules. As maturation proceeded, spermatogonia throughout the testes appeared tightly packed within the cysts. The developmental progression from spermatid to spermatozoan formation occurred within the cysts, which then burst and released spermatozoa into tubules. In these final stages, mature spermatozoa were found throughout collecting tubules and ducts. During the post-copulation period, gradual recovery and reorganization were observed wherein residual sperm and cytoplasm in the lumens, and the ducts were resorbed by Sertoli cells. Peripheral areas showed reformation of the cysts and the presence of primary and secondary spermatogonia. Immature testes also contained these initial spermatogonia. They differed from mature testes in that cysts were small along with tubular lumens, and they showed no evidence of residual spermatozoa.

Paired ovoid ovaries consisted of stroma and oogonial nests that underwent acinar development along margins of lamellar branches throughout the ovaries. The stroma-germ tissue complex was encased in a thin ovarian wall of squamous epithelium and smooth muscle that seasonally varied in thickness.

A seasonal developmental progression of follicle

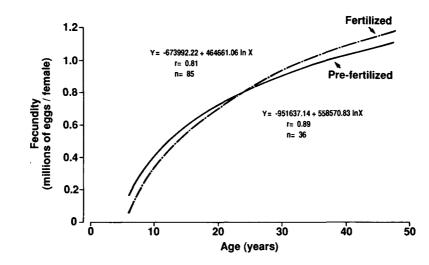


Fig. 8. Semilogarithmic plot of fecundities of yellowtail rockfish with pre-fertilized and fertilized eggs by age.

and oocyte growth was observed. Differentiation was accompanied by increased vascularization and movement of epithelial cells towards the surface of the oocytes. Small  $(5-25 \,\mu\text{m})$  nested oogonia with transparent cytoplasm, dark-stained nuclei and larger (20–100  $\mu$ m) early peri-nucleolus oocytes were found in ovarian tissues year-round. These were considered undeveloped or 'resting' stage oocytes (Bowers & Holliday 1961, Howell 1983). With the onset of recovery and reorganization, oocytes (ca. 50-140 µm diameter)-with numerous, randomly distributed, clear lipid vacuoles, increasingly large nuclei and peripherally arranged nucleoli-increased in frequency. By mid to late summer, cytoplasmic granulated yolk accumulated as oocytes enlarged (120–210  $\mu$ m). With increasing ovarian development, over half the interior of these oocytes became filled with large yolk globules, and lipid vacuoles coalesced and enlarged. In the final developmental stages, the large (600- $750 \,\mu\text{m}$ ) oocytes contained single, large lipid vacuoles and amoeboid nuclei. With ovulation, follicle components disintegrated while the capillary network was maintained and remained in close association with the egg. Embryos were observed as free from lamellae in the ovarian lumen. Spent ovaries quickly recovered and histologically displayed increased vascularization, with empty or collapsed

follicles in various resorptive stages. Occasional residual embryos and unfertilized oocytes were seen in various stages of degeneration. As ovaries reorganized, lamellar branches and associated stroma became compact and firm, and small nested oocytes as first described became most numerous. Ovaries of immature fish contained early developing oocytes, and there was no evidence of yolk accumulation nor recovering resorptive tissues.

## Discussion

The Cordell Bank yellowtail rockfish population's annual sex ratio reversal showed a pattern not previously observed in rockfishes. A coastwide study of yellowtail rockfish (Fraidenburg 1980) showed males dominated (56–74%) in each area with no latitudinal trend. This survey was conducted during mid to late summer, the transition period in our study when the sex ratio changed from male dominance to even ratios and then to predominantly females. Northwest Atlantic studies (Ni & Sanderman 1984, Ni & Templeman 1985) of three *Sebastes* species noted, as in our study, an overall even sex ratio for the year, but females were more abundant for all but 3 months (March, June and August). These species were behaviorally different in that the sexes were believed to segregate in different seasons. Yellowtail rockfish are believed to be nonmigratory and to remain close to areas that they colonize as juveniles (Carlson & Haight 1972, Calson 1986). Changes in sex ratios may have resulted from differences in feeding behavior or localized sex segregation. It is also possible that male aggression associated with territoriality, as noted by Shinomiya & Ezaki (1991), could account for more males being caught by hook and line.

The age and size composition of the Cordell Bank population appeared different from those of northern populations. This is important because the composition determines the reproductive capacity of the population. The coastwide rockfish survey of Fraidenburg (1980) showed a north to south cline of decreasing age and size. Since that study, a decade of monitoring of the commercial catches in Oregon and Washington has provided evidence of significant declines in mean ages and sizes (Tagart 1988). Preliminary results of our own field studies on Washington yellowtail rockfish support these findings (National Marine Fisheries Service, Tiburon Laboratory, unpublished data). Northern populations appeared younger overall but were larger than fish of similar ages from Cordell. For example, the mean age of females in northern populations was 12.1 years (versus 17.2 cm for Cordell Bank fish), and mean standard length was 46.6 cm (versus 38.9 cm).

A consistent trend among yellowtail rockfish populations was sexual dimorphism. Females were longer and heavier at age than males. Wyllie Echeverria (1986) provided details on this dimorphism in four *Sebastes* species, including yellowtail rockfish. As noted by Westrheim & Harling (1975), this dimorphism became apparent after fish reached 6–8 years of age (Fig. 4), the approximate ages that we found yellowtail rockfish to mature.

Sebastes usually have a protracted spawning season (Leaman 1988). The parturition period for Cordell Bank yellowtail rockfish occurred from January through May and peaked during March and April (Fig. 2). In the geographically larger study of Wyllie Echeverria (1987), yellowtail rockfish exhibited a similar seasonal pattern. One of our findings is relevant to management: the older fish spawned during the early part of the season. Restricted fishing seasons and selective exploitation in Washington fisheries could affect the reproductive potential of these populations.

Wyllie Echeverria (1987) estimated the ages and sizes at maturity for yellowtail rockfish (males; first = 4 years, 30 cm; 50% = 6 years, 35 cm; 100% = 11 years, 43 cm; females: first = 4 years, 27 cm; 50% = 7 years, 36 cm; 100% = 11 years,42 cm). Our research design did not allow such precision. Male and female yellowtail rockfish at Cordell Bank were older and larger at first maturity (males: first = 8 years, 32 cm; females: first = 6 years, 29 cm). Our smaller sample size and restricted sampling range could have biased our results. One problem that we are currently trying to resolve is whether the small, young females that appear to have maturing ovaries actually complete the process. Our laboratory observations of these fish and the occurrence of similarly developing fish in the field during the entire developmental period suggest that they remain functionally immature, as has been found in other Sebastes species (Westrheim 1958, Leaman 1988).

The duration of the reproductive lifespan is determined by the age at maturity and the life expectancy. Cordell Bank yellowtail rockfish had long potential reproductive lifespans of 31 and 39 years for males and females respectively. The maximum potential span for the species could be 52 years, given an age at maturity of 4 years (Wyllie Echeverria 1987) and a maximum age of 56 (Beamish 1979). Our study estimates over half of the population has real reproductive lifespans of 11 years for both sexes. This trait was largely due to the polymodal, wide-ranging age structure of the population. Fraidenburg's (1980) survey showed this to be a coastwide phenomenon. Long reproductive lifespans have been shown to be important for the persistence of populations in highly variable environments similar to those of the yellowtail rockfish habitats (Stearns 1977).

Fecundity is often used as an index of reproductive effort, and generally it is believed to increase with age (Williams 1966, Gadgil & Bossert 1970). Fecundity of yellowtail rockfish from Cordell Bank correlated well with age and size (Fig. 7). Earlier studies (Phillips 1964, Gunderson et al. 1980) of vellowtail rockfish have found considerably lower fecundity at age and size. These studies may possibly differ because Phillips (1964) presented estimates of fecundity at age based on low precision methods and Gunderson et al. (1980) examined adults over 43 cm using a volumetric subsampling method. Only 2% of our specimens were in that size range. Recent comparisons of methods for estimating fecundity have shown that gravimetric subsampling was more accurate than volumetric subsampling (Leaman 1988). Boehlert et al. (1983) observed decreased fecundity in Sebastes entomelas with the approach of parturition. Kusakari (1991) found declining fecundity during gestation in S. schlegeli. This suggests that fecundity estimates derived from ovaries in early stages of development do not accurately represent fertility. We found no evidence of this in our study (Fig. 8) although our ongoing histological studies are showing interannual variability in the occurrence of egg resorption. It is possible that our fecundity methodology is not sensitive enough to detect this phenomenon.

Our histological observations proved to be sensitive measures of the reproductive cycle. Structures and apparent functions were similar to those described in other Sebastes species (Moser 1967, Lisovenko 1978). They differed in that yellowtail rockfish showed a typical pattern of teleostean group synchronous ovarian development in contrast to the multiple-spawning pattern found in S. paucispinis. Histological changes in our yellowtail rockfish ovaries occurred throughout the year, similar to findings in S. alutus (Leaman 1988). These changes were easily observed in the cytoplasm, nucleus and follicle, indicating that there is no resting period between reproductive periods. Changes in the male spermatogenic sequence were less dramatic than in that for the females. Recruitment of a season's gametes from a pool of intratubular stem spermatogonia was rapid and of short duration. Wootton (1984) defined life history strategy as the overall pattern shown by an individual. Life history tactics then become the variations in the typical pattern that fish make in response to fluctuations in their environments. With the description and characterization we have provided on the Cordell Bank yellowtail rockfish, we now have the opportunity to expand our studies on spatial, temporal and populational scales to see how other populations have responded and adapted to different habitats. Through knowledge of life history performance, especially reproductive performance, it should be possible to determine the life history adaptive capacity of yellowtail rockfish as a species and to delimit the adaptive capacities of particular populations.

#### **References cited**

- Beamish, R.J. 1979. New information on the longevity of Pacific ocean perch (*Sebastes alutus*). J. Fish. Res. Board Can. 36: 1395–1400.
- Boehlert, G.W., W.H. Barss & P.B. Lamberson. 1983. Fecundity of the widow rockfish (*Sebastes entomelas*) off the coast of Oregon. U.S. Fish. Bull. 80: 881–884.
- Bowers, A.B. & F.G.T. Holliday. 1961. Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus* L.). Department of Agriculture and Fisheries Scotland, Marine Research 5: 1–16.
- Carlson, H.R. 1986. Restricted year-class structure and recruitment lag within a discrete school of yellowtail rockfish. Trans. Amer. Fish. Soc. 115: 490–492.
- Carlson, R.J. & R.E. Haight. 1972. Evidence for home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish Res. Board Can. 29: 1011–1014.
- DeLacy, A.C., C.R. Hitz & R.L. Dryfoos. 1964. Maturation, gestation, and birth of rockfish (*Sebastodes*) from Washington and adjacent waters. Washington Department of Fisheries, Research Paper 2: 51-67.
- Fraidenburg, M.E. 1980. Yellowtail rockfish, *Sebastes flavidus*, length and age composition off California, Oregon, and Washington in 1977. Mar. Fish. Rev. 42: 54–56.
- Gadgil, M. & W.H. Bossert. 1970. Life history consequences of natural selection. Amer. Nat. 102: 52-64.
- Grier, H.J. 1981. Cellular organization of the testis and spermatogenesis in fishes. Amer. Zool. 21: 345–357.
- Gunderson, D.R., P. Callahan & B. Goiney. 1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish Rev. 42: 74–79.
- Howell, W.H. 1983. Seasonal changes in the ovaries of adult yellowtail flounder, *Limanda ferrunginea*. U.S. Fish. Bull. 81: 341–355.
- Humason, G.H. 1967. Animal tissue techniques, 3rd. edition. W. H. Freeman, San Francisco. 641 pp.
- Kusakari, M. 1991. Mariculture of kurosoi, Sebastes schlegeli. Env. Biol. Fish. 30: 245–251.
- Leaman, B.M. 1988. Reproductive and population biology of

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Pacific ocean perch (Sebastes alutus (Gilbert)). Ph.D. Thesis, University of British Columbia, Vancouver. 200 pp.

- Lewontin, R.C. 1958. The adaptations of populations of varying environments. Cold Spring Harbor Symp. Quant. Biol. 22: 395-408.
- Lisovenko, L.A. 1978. Reproduction of rockfishes (family Scorpaenidae) off the Pacific coast of South America. J. Ichthyology 18: 262–268.
- Moser, H.G. 1967. Seasonal histological changes in the gonads of *Sebastes paucispinis* (Ayres), an ovoviviparous teleost (family Scorpaenidae). J. Morph. 123: 329–351.
- Ni, I-H. & E.J. Sandeman. 1984. Size at maturity for Northwest Atlantic redfishes (*Sebastes*). Can. J. Fish. Aquat. Sci. 41: 1753–1762.
- Ni, I-H. & W. Templeman. 1985. Reproductive cycles of redfishes (*Sebastes*) from southern Newfoundland waters. J. Northw. Atl. Fish. Sci. 6: 57–63.
- Phillips, J.B. 1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Cal. Dep. Fish and Game, Fish Bull. 126. 70 pp.
- Shinomiya, A. & O. Ezaki. 1991. Mating habits of the rockfish Sebastes inermis. Env. Biol. Fish. 30: 15-22.
- Spurr, A.R. 1969. A low viscosity epoxy resin embedding medium for electron microscopy. J. Ultra. Res. 26: 31–43.
- Stearns, S.C. 1977. The evolution of life history traits: a critique

of theory and a review of the data. Ann. Rev. Ecol. Syst. 8: 145–171.

- Tagart, J.V. 1988. Status of yellowtail rockfish stocks in the International North Pacific Fishery Commission Vancouver and Columbia areas. Wash. Dep. of Fisheries, Spec. Report. 114 pp.
- Westrheim, S.J. 1958. On the biology of Pacific ocean perch, Sebastes alutus (Gilbert). M.Sc. Thesis, University of Washington, Seattle. 106 pp.
- Westrheim, S.J. & W.R. Harling. 1975. Age-length relationships for 26 scorpaenids in the Northeast Pacific Ocean. Fish. Mar. Serv. Tech. Report 565. 12 pp.
- Williams, G.C. 1966. Adaptation and natural selection. Princeton University Press, Princeton. 307 pp.
- Wootton, R.J. 1984. Introduction: strategies and tactics in fish reproduction. pp. 1–12 *In*: G.W. Potts & R.J. Wootton (ed.) Fish Reproduction: Strategies and Tactics, Academic Press, London.
- Wyllie Echeverria, T. 1986. Sexual dimorphism in four species of rockfish genus *Sebastes* (Scorpaenidae). Env. Biol. Fish. 15: 181–190.
- Wyllie Echeverria, T. 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. U.S. Fish. Bull. 85: 229–250.