

**Abstract**—We summarize the life history characteristics of silvergray rockfish (*Sebastes brevispinis*) based on commercial fishery data and biological samples from British Columbia waters. Silvergray rockfish occupy bottom depths of 100–300 m near the edge of the continental shelf. Within that range, they appear to make a seasonal movement from 100–200 m in late summer to 180–280 m in late winter. Maximum observed age in the data set was 81 and 82 years for females and males, respectively. Maximum length and round weight was 73 cm and 5032 g for females and 70 cm and 3430 g for males. The peak period of mating lasted from December to February and parturition was concentrated from May to July. Both sexes are 50% mature by 9 or 10 years and 90% are mature by age 16 for females and age 13 years for males. Fecundity was estimated from one sample of 132 females and ranged from 181,000 to 1,917,000 oocytes and there was no evidence of batch spawning. Infection by the copepod parasite *Sarcotaces arcticus* appears to be associated with lower fecundity. Sexual maturation appears to precede recruitment to the trawl fishery; thus spawning stock biomass per recruit analysis (SSB/R) indicates that a  $F_{50\%}$  harvest target would correspond to an  $F$  of 0.072, 20% greater than  $M$  (0.06). Fishery samples may bias estimates of age at maturity but a published meta-data analysis, in conjunction with fecundity data, independently supports an early age of maturity in relation to recruitment. Although delayed recruitment to the fishery may provide more resilience to exploitation, managers may wish to forego maximizing economic yield from this species. Silvergray rockfish are a relatively minor but unavoidable part of the multiple species trawl catch. Incorrectly “testing” the resilience of one species may cause it to be the weakest member of the species complex.

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## Life history characteristics for silvergray rockfish (*Sebastes brevispinis*) in British Columbia waters and the implications for stock assessment and management

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Silvergray rockfish (*Sebastes brevispinis*) range from the Gulf of Alaska to central Baja California (Love et al., 2001) and are a minor part of the trawl and hook-and-line fisheries catch from northern Washington to the Gulf of Alaska (Alaska Fisheries Information Network,<sup>1</sup> Pacific Fisheries Information Network,<sup>2</sup> Pacific Biological Station<sup>3</sup>). Coastwide commercial landings averaged 2600 metric tons (t) from 1990 to 2000, and about two-thirds of these landings came from British Columbia (B.C.) waters, mostly from bottom trawling. Hook-and-line landings are the most common type in Alaskan waters (mostly from southeastern Alaska) and have averaged less than 20 t. Combined annual trawl landings from Washington and Oregon peaked at over 1000 t from 1977 to 1979, declined to an average of 210 t from 1990 to 1998, and since 1999 have further declined to negligible levels.

The B.C. bottom trawl fishery is currently managed through individual vessel quotas (IVQs) whereby a fixed proportion of the annual quota for each stock is allocated to each quota-holder. Because silvergray rockfish are currently assessed and managed as four separate stocks (Fig. 1: Pacific Marine Fisheries Commission areas 3CD, 5AB, 5CD, and 5E), a vessel may possess up to four area-specific quotas for silvergray rockfish. All bottom trawlers on the outer coastal waters of British Columbia are required to have an independent observer on the vessel. Once vessels have reached

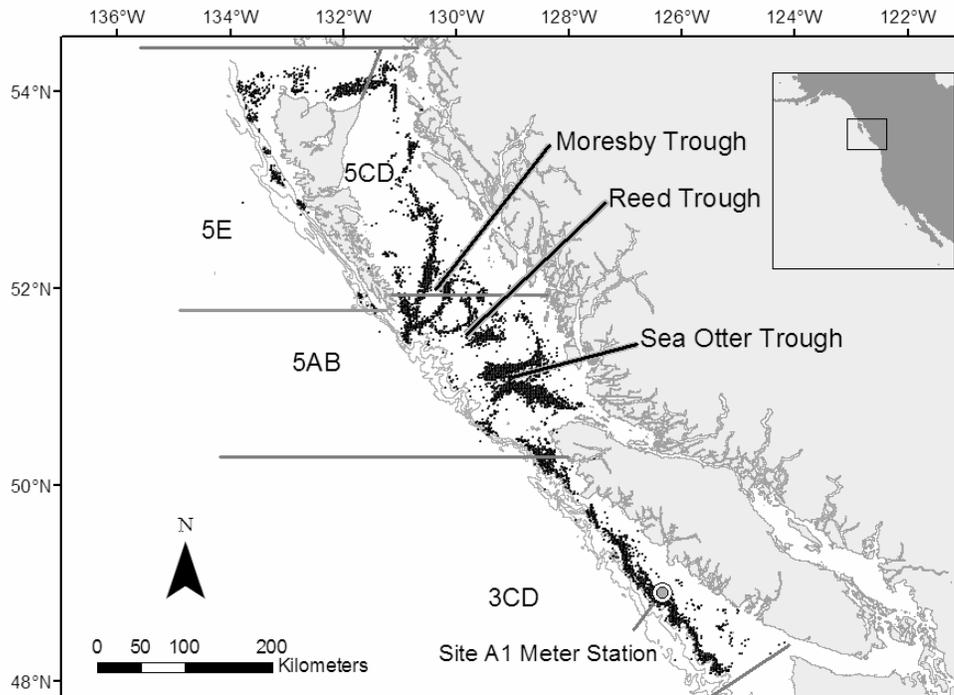
their IVQ for one area and species, and have exhausted their limited opportunity to temporarily lease quota from other lease-holders, they must cease all bottom trawling even though they may still have IVQ remaining for other species in that area.

The quotas for silvergray rockfish are relatively small compared with those for other species in the fishery; thus fishermen can fully fill their silvergray rockfish IVQs as they target other species. However, if silvergray rockfish become difficult to avoid through increased abundance or availability, or if the silvergray rockfish quota is reduced, even though catch rates remain constant, they become a nuisance in that fishermen cannot fulfill their IVQs for other species without exceeding their silvergray rockfish IVQ. Therefore, the quotas for minor species, such as silvergray rockfish, now assume more importance than would be gained from their landed value. Finally, the enactment of species-at-risk legislation in Canada has led to the requirement

<sup>1</sup> Alaska Fisheries Information Network. 2000. AKFIN Support Center, 612 W Willoughby Ave. Suite B. Juneau, Alaska 99801.

<sup>2</sup> Pacific Fisheries Information Network. 2000. Pacific States Marine Fisheries Commission, 205 SE Spokane Street, Suite 100, Portland, Oregon 97202.

<sup>3</sup> Pacific Biological Station. 2000. Unpubl. data. Fisheries and Oceans Canada. Nanaimo, British Columbia V9T 6N7, Canada.



**Figure 1**

Coastal waters of British Columbia showing boundaries of silvergray rockfish (*Sebastes brevispinis*) stocks, trawl capture locations of silvergray rockfish (black dots) for 1996–2000, mooring site for the oceanographic metering of temperature at-depth (A1 meter station), and 500-, 1000-, and 1500-m depth contours.

to assess and protect the status of any species affected by fishing, regardless of its commercial value.

Research on silvergray rockfish is an example of an area that has been neglected owing to the lack of economic importance of this species in the commercial fisheries. Even the data that are available have been collected incidentally during fishing operations targeting other species or during generic sampling programs. Nevertheless, we show in the present article that these data, in conjunction with detailed commercial catch and effort data, can be used to provide insight into the biology, assessment, and management of silvergray rockfish. This article summarizes this information and provides estimates of the various life history parameters needed for stock assessment. Some of the estimates represent updates from previous work, but we also for the first time present estimates of fecundity and maturity at age and size. Using these values, we also derive a target reference point.

## Materials and methods

### Data sources

Data for silvergray rockfish were collected from B.C. waters during port sampling, at-sea observer programs, and research cruises from 1977 through 2000. These

data reside at the Pacific Biological Station, Nanaimo, B.C., Fisheries and Oceans, Canada. As of June 2000, the database contains information on over 40,000 specimens. Of these specimens, we aged 13,671 representing most of the specimens from which we obtained otoliths, in addition to documenting length, sex, and maturity stage. We, also used catch observations from the commercial trawl observer program from 1996 through 2000.

### Habitat

Preferred depth distributions of silvergray rockfish were inferred from analyzing catch rates in the commercial data. We used all bottom tows that contained silvergray rockfish and included tow duration. Bottom depth of the tows was determined as the midpoint between beginning and end depth of the tows. We applied a nonparametric locally weighted regression smoothing function (LOESS) (Cleveland, 1979) to log-CPUE observations grouped by 20-m intervals.

Depth of peak catch rates by month were compared with temperature-at-depth estimates based on data collected from the site A1 meter station on the west coast of Vancouver Island (Fig. 1: 48°32'N by 126°12'W). These data, collected from 1986 to 2000 (excluding El Niño years), were taken from 35-, 100-, 175-, and 400-m depths. The temperatures at fixed depths were then

**Table 1**

Field classification of gonad maturity stages for silvergray rockfish (*Sebastes brevispinis*) used by the Groundfish Section, Pacific Region Science Branch, Fisheries and Oceans, Canada.

	Female ovaries	Male testes
1	Immature (translucent, small, color can be clear, amber, yellow, or pink)	Immature (translucent, string-like)
2	Developing (small, opaque or translucent, can be yellow, usually light pink)	Developing (swelling, brown-white)
3	Developed (eggs usually white or cream white, can be yellow or orange-yellow)	Not used
4	Fertilized (large, cream or orange-yellow eggs, translucent)	Developed (large, white, easily broken)
5	Embryos or larvae present (includes eyed eggs)	Ripe (running sperm)
6	Spent (flaccid, red, a few larvae may be present)	Spent (flaccid, creamy-brown, some milt present but not free-flowing)
7	Resting (moderate size, firm, red-grey, red-grey, pink, or purple to almost black)	Resting (ribbon-like, small brown)

converted through interpolation to provide depth at specific temperatures (Hourston<sup>4</sup>).

#### Aging and growth determinations

Ages were determined by using the otolith burnt-section technique (MacLellan, 1997) with a minor modification. A survey directed at studying juvenile rockfish in 1991 captured two 17-cm silvergray rockfish. An examination of these otoliths indicated that the previous application of the method had incorrectly assigned the first annulus to the age count in specimens. Therefore, some previously aged specimens were probably under-estimated by one year (MacLellan<sup>5</sup>). A faint first annulus is consistent with the late spring to mid-summer parturition of silvergray rockfish that appears to preclude significant summer growth in its first year. The method was modified in August of 1992, and we added one year to all previously aged specimens in the data set.

Most (85%) of the otoliths were aged by one reader. The remaining 15% were aged by two readers to monitor consistency. If there was a disagreement, the two readers agreed on a "resolved" age.

Age and length data were fitted to a generalized growth model (Schnute, 1981) (Appendix 1). Growth dimorphism was calculated as the ratio of the mid-points of fork length (maximum observed length minus minimum observed length) between males and females (Lenarz and Wylie Echeverria, 1991).

#### Reproductive maturity

Maturity stage was classified macroscopically in the field (Table 1). We examined the annual reproductive cycle

by tracking the proportions in each maturity stage by month. Lacking histological confirmation for characterizing maturity, we followed the suggestion of Wylie Echeverria (1987) and used only those specimens collected from the reproductive or gestation period of March to August. Within this subset, we grouped female stages 1 and 2 as immature, and stages 3–7 as mature. Because most mature females exhibited fertilized eggs by March, we assumed that females with small, nondeveloped ovaries in March through August would not complete parturition in the same calendar year.

We assumed that stage 1, during which testes are translucent and string-like, was the only male immature stage. Subsequent stages 2 and 4–7 were grouped as mature (stage 3 was not used in the field). The proportion of stage-2 males (in relation to males in other mature stages) decreased rapidly during the mating season (September–January) indicating that many of the specimens classified as stage 2 would become mature within the same calendar year. We emphasize, however, that without histological support for these classifications, the assumptions of maturity-at-age or maturity-at-length remain tentative.

The estimated proportions of maturity at age were computed by fitting a generalized additive model (GAM) to the binomial maturity classes (0=immature, 1=mature) (Hastie and Tibshirani, 1990). A logistic link with a binomial error structure was applied, as well as a second-degree nonparametric LOESS smoother.

#### Fecundity

Fecundity was estimated from a single sample ( $n=132$ ) of females captured by commercial bottom trawl in Sea Otter Trough in April 1989 (Fig. 1). The catch was stored in refrigerated seawater for four days prior to sampling. Sampling was stratified by length to obtain a range of ages, and from each fish we obtained measurements of fork length, gonad weight, and somatic weight. We also collected otoliths and counted the number of cysts con-

<sup>4</sup> Hourston, R. 2003. Personal commun. Institute of Ocean Sciences, Fisheries and Oceans Canada. 9860 West Saanich Road, P.O. Box 6000, Sidney, British Columbia. V8L 4B2, Canada.

<sup>5</sup> MacLellan S. 2000. Personal commun. Pacific Biological Station, Fisheries and Oceans Canada. Nanaimo, British Columbia. V9T 6N7, Canada.

taining the copepod parasite *Sarcotaces arcticus* in the coelomic cavity. All the oocytes of all the female gonads appeared to be in a prefertilized condition.

The ovaries that were used for fecundity estimation were fixed and stored in modified Gilson's solution (Leaman, 1988) and shaken weekly for one year. Fecundity estimates were derived gravimetrically (Leaman, 1988). Each ovary was drained and filtered through stacked sieves (100–750  $\mu\text{m}$ ); each clump was broken manually if possible. The ovarian membranes and connective tissue were teased away from eggs and discarded. The oocytes were transferred to millipore filters, vacuum-dried for 15 minutes, and the oocytes and filter were weighed to 0.01 g. Four subsamples of approximately 0.1 g and 1000 oocytes were weighed to 0.0001 g. Total fecundity was estimated for each fish by multiplying total vacuum-dried ovary weight by the mean density of the four samples. Fecundity relationships against age, weight, and length were examined with a generalized additive model (GAM) (Hastie and Tibshirani, 1990). An identity link with a Gaussian error structure was used in each case. Ovaries to be used for histological examination were fixed in Smith's formal dichromate solution and then stored in 3% formaldehyde. Histology samples were imbedded, sectioned, mounted, stained with Harris' haematoxylin, and counterstained with alcoholic eosin (Gray, 1954).

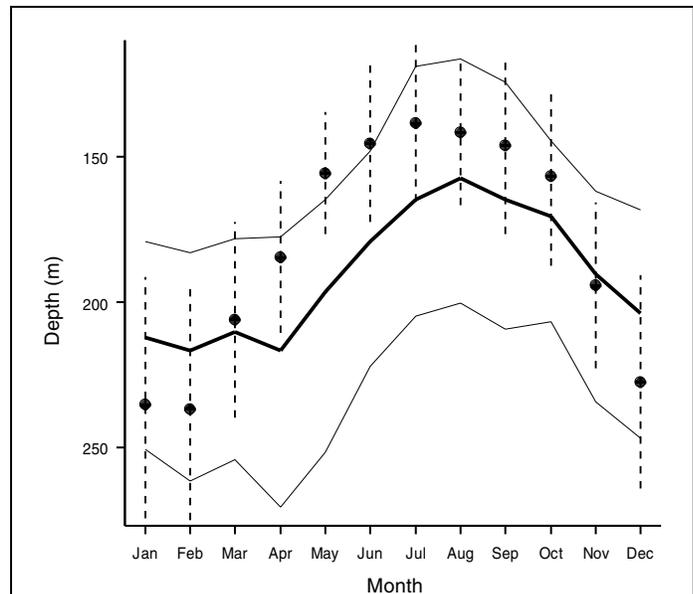
### Spawning stock biomass per recruit (SSB/R)

We combined estimates of instantaneous natural mortality rate ( $M$ ) of 0.06 and partial recruitment from Stanley and Kronlund (2000) with our estimates of the proportion mature at age and predicted fecundity at age in order to derive estimates of the expected population fecundity of unfished populations (Appendix 2). The impact of fishing on spawning stock biomass per recruit (SSB/R) can then be explored by comparing the ratio of predicted cumulative fecundity of a cohort under exploitation to predicted cumulative fecundity under no fishing pressure (Gabriel et al., 1989; Clark, 1991).

## Results

### Habitat

The commercial data indicated that the highest catch rates and most of the landings of silvergray rockfish come from the edge of the continental shelf or along the edges of deep troughs (Fig. 1). These tows were typically conducted in bottom depths of 100 to 300 m, although silvergray rockfish have been reported from tows with mid-point bottom depths greater than 580 m. Monthly catch rates by depth indicate a seasonal trend wherein peak catch rates are highest in depths of 180–280 m in March and April, but highest in depths of 100–200 m in September and October (Fig. 2).



**Figure 2**

Silvergray rockfish (*Sebastes brevispinis*) seasonal depth distribution. The solid lines show the median (heavy line) and 25th and 75th percentiles (thin lines) for the number of silvergray rockfish catch observations (observed commercial trawl sets) at depth, between 1996 and 2003. The dots indicate the estimated depth at  $7.2^{\circ}\text{C} \pm 1$  standard deviation (dotted line).

If the shift in catch rates correctly indicates seasonal movement, and the interpolated temperatures at site A1 characterize bottom temperatures on the coast, together they indicate that silvergray rockfish tend to maintain peak densities at bottom water temperatures centered around  $7.2^{\circ}\text{C}$  (Fig. 2). The move to shallower water in the late spring, however, seems to lag behind the cooling of shallower water that results from summer upwelling (Thomson<sup>6</sup>). The return to deeper water in the fall is coincident with the warming of water at greater depths.

The cohabitants of silvergray rockfish were also inferred from commercial trawl observations. For these data, we selected tows with at least 50 kg of silvergray rockfish. Silvergray rockfish represented 12.8% of the total catch of over 36,000 t (Table 2). The dominant species by weight in these tows were Pacific ocean perch (*Sebastes alutus*), arrowtooth flounder (*Atheresthes stomias*), yellowmouth rockfish (*S. reedi*), yellowtail rockfish (*S. flavidus*), redstripe rockfish (*S. proriger*), and canary rockfish (*S. pinniger*). The species most frequently co-occurring in the tows were arrowtooth flounder, lingcod (*Ophiodon elongatus*), spiny dogfish

<sup>6</sup> Thomson, R. 2003. Personal commun. Institute of Oceans Sciences, Fisheries and Oceans Canada. 9860 West Saanich Road, P.O. Box 6000. Sidney, British Columbia V8L 4B2, Canada.

**Table 2**  
Fish species captured in 1996–99 B.C. bottom trawl tows that contained silvergray rockfish (*Sebastes brevispinis*).

Common name	Species	% of total catch (36,489,773 kg)	% frequency (10,820 tows)
Silvergray rockfish	<i>Sebastes brevispinis</i>	12.8	100.0
Arrowtooth flounder	<i>Atheresthes stomias</i>	13.0	77.2
Lingcod	<i>Ophiodon elongatus</i>	2.8	65.1
Spiny dogfish	<i>Squalus acanthias</i>	2.5	58.4
Yellowtail rockfish	<i>Sebastes flavidus</i>	11.3	57.4
Canary rockfish	<i>Sebastes pinniger</i>	5.4	55.2
Redstripe rockfish	<i>Sebastes paucispinis</i>	1.3	54.0
Pacific cod	<i>Gadus macrocephalus</i>	1.1	53.7
Pacific halibut	<i>Hippoglossus stenolepis</i>	0.6	48.2
Redstripe rockfish	<i>Sebastes proriger</i>	7.2	47.3
Rex sole	<i>Errex zachirus</i>	0.8	46.6
Sablefish	<i>Anoplopoma fimbria</i>	0.6	46.2
Spotted ratfish	<i>Hydrolagus colliei</i>	0.6	43.7
Pacific ocean perch	<i>Sebastes alutus</i>	13.9	40.4
Yellowmouth rockfish	<i>Sebastes reedi</i>	12.7	39.2
Dover sole	<i>Microstomus pacificus</i>	1.1	36.0
Petrале sole	<i>Eopsetta jordani</i>	0.4	34.5
Redbanded rockfish	<i>Sebastes babcocki</i>	0.9	33.7
English sole	<i>Pleuronectes vetulus</i>	0.5	28.3
Widow rockfish	<i>Sebastes entomelas</i>	3.9	27.1
Greenstriped rockfish	<i>Sebastes elongatus</i>	0.3	27.0
Longnose skate	<i>Raja rhina</i>	0.3	26.0
Others		6.2	—

(*Squalus acanthias*), yellowtail rockfish, canary rockfish, redstripe rockfish, and Pacific cod (*Gadus macrocephalus*). All of these species were observed in more than 50% of the selected tows.

The cohabitants varied with depth. Tows conducted in depths less than 200 m tended to include lingcod, dogfish, canary rockfish, and yellowtail rockfish, whereas catches from greater than 200 m were dominated by arrowtooth flounder, Pacific ocean perch, redstripe rockfish, and yellowmouth rockfish. Fishermen report that silvergray rockfish are typically found over relatively "hard" bottom, often in proximity to bottom that was not trawlable because it was too rough. They are rarely caught in midwater trawls.

#### Aging and growth estimates

The maximum ages observed in Canadian samples were 81 and 82 years for females and males, respectively. The corresponding ages at the 99.9% percentiles were 76 and 77 years.

Although we assumed that our aging methods for silvergray rockfish provided unbiased estimates of age, agreement between readers was poor. Agreement to  $\pm 1$

year was 60–80% for ages less than 20 years and then declined with age.

The standard errors of the growth parameter estimates show that there is a significant, albeit modest, difference in growth rates; females grow faster and to a larger size (Table 3, Fig. 3). Maximum observed length was 73 and 70 cm for females and males, respectively. We estimated the length-weight relationship for females and males separately and combined from 476 total specimens (Table 3, Fig. 3). The ratio of the mid-point lengths for males and females was 97.2 (Table 4), indicating little sexual dimorphism.

#### Maturation cycle

The field maturity observations were congruent for females and males (Fig. 4). Testes began developing (stage 2) in September and October and were large and swollen by November and December (stage 4) (Fig. 4). January and March testes were in the late stages of mating (stage 6), whereas from April through August testes appeared to be in a resting phase for males (stage 7). The few observations of large swollen testes with running sperm (stage 5) occurred from October through February. The

**Table 3**

Growth and fecundity parameter estimates and standard errors for silvergray rockfish (*Sebastes brevispinis*) (see Appendix 1 for parameter definitions).

Equation	Parameter	Females		Males		Combined	
		Estimate	SE	Estimate	SE	Estimate	SE
Length-at-age	$y_1$	48.985	0.048	47.887	0.041	48.468	0.034
	$y_2$	60.628	0.015	56.108	0.091	57.719	0.083
	$a$	0.0581	0.002	0.0708	0.002	0.0709	0.002
	$b$	1.0000		1.000		1.000	
	$\tau_1$	15.000		15.000		15.000	
	$\tau_2$	60.000		60.000		60.000	
Length/Weight (ln scale)	$\alpha$	-4.000	0.137	-2.506	0.411	-3.634	0.157
	$\beta$	2.924	0.034	2.547	0.105	2.833	0.040
Fecundity/Somatic weight (ln scale)	$\alpha$	3.014	0.572				
	$\beta$	1.367	0.073				
Fecundity/Length	$\alpha$	-3.454	1.007				
	$\beta$	4.2833	0.251				

**Table 4**

Comparison of silvergray rockfish (*Sebastes brevispinis*) fork length ratio (group 1) with results from Lenarz and Echevarria (1991) (groups 2–4).

Species group		Deep (>125m)	Shallow ( $\leq$ 125 m)	All rockfish species combined
1	Silvergray rockfish (present study)	Fork length ratio	0.97	
2	Water-column species	Number of species	12	5
		Standard length ratio	0.88	0.91
3	Demersal species	Number of species	5	12
		Standard length ratio	0.95	0.98
4	All rockfish species combined	Number of species	17	17
		Standard length ratio	0.90	0.96

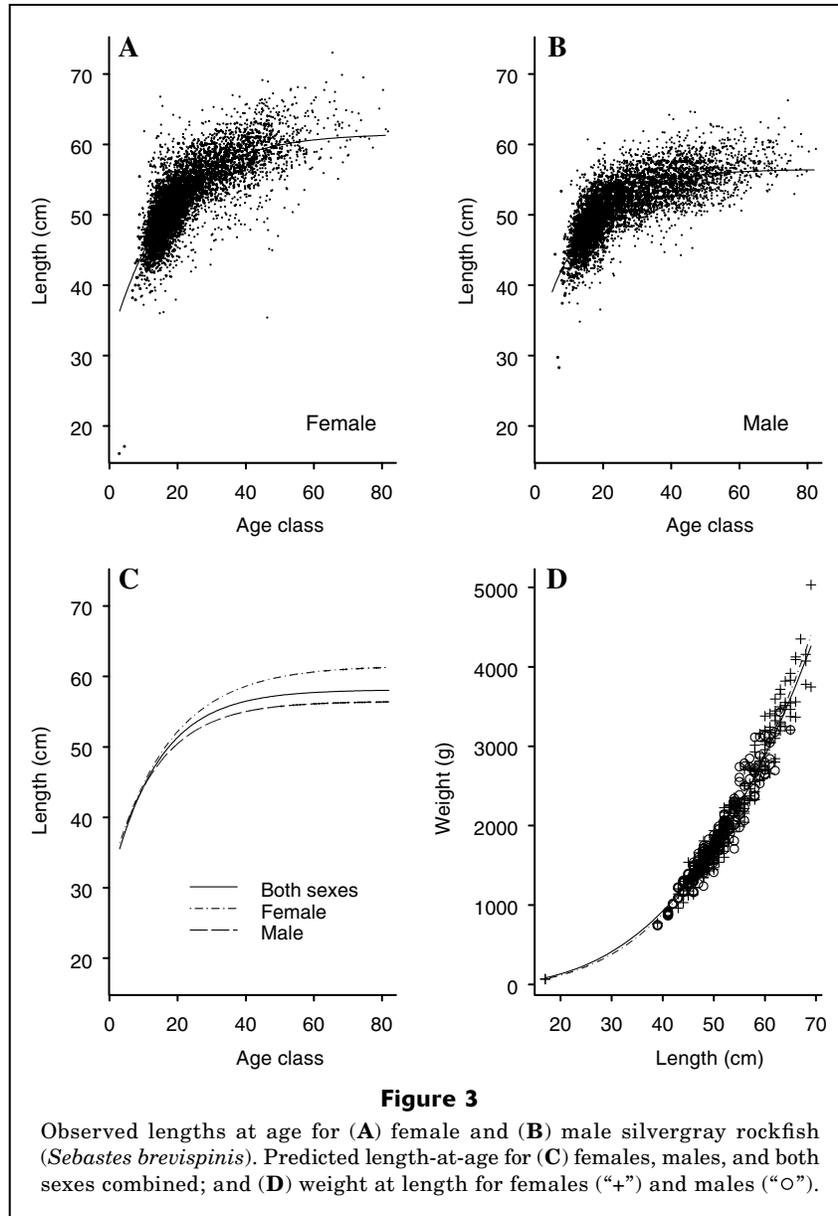
peak period of mating is presumably December to February. One sample of 109 males, collected in March 1988, was recorded entirely as maturing. This one sample accounted for all but two records of stage-4 males collected in March and, therefore, contradicted the results of 20 other March samples, totalling 364 specimens. Although we found no evidence of a recording error, we suggest that these specimens were misclassified and were probably recovering instead of developing males.

The developing ovaries (stages 2 and 3), observed from January to April, shifted to fertilized through to resting stages (stages 3–7) in April to June. Eyed larvae were commonly observed from May to July although a few individuals with eyed larvae were observed in February, August, and October.

We examined whether there was a relationship between the size of the female and the timing of parturition by categorizing July observations as either

“parturition not completed” (stages 3–5) or “parturition completed” (stages 6–7) (Fig. 5). The results indicated a dome-shaped relationship with length wherein it appears that a higher proportion of the smaller and larger females had not completed parturition. There were too few observations from June to examine the transition in more detail or to examine whether timing varied with latitude within B.C. waters.

Age observations from the commercial fishery indicate that both sexes are 50% mature at about 10 years of age and over 90% are mature at age 16 for females, and age 13 for males (Table 5, Fig. 6). However, the analysis was limited by the lack of young fish in the samples. For example, there were only five 8-year old and thirteen 9-year old females in the data set. Comparison of the age at maturity and partial recruitment at age indicates that silvergray rockfish mature prior to recruitment (Table 5, Fig. 7).



### Fecundity and stock-assessment-parameter estimates

The total number of large oocytes ranged from 181,000 to 1,917,000 (Fig. 8). A general linear model (GLM) treatment of log fecundity against log somatic weight and age indicated that age was not a significant variable after accounting for somatic weight. Although size is a better predictor of fecundity than age, we also provide the predicted fecundity with age (Table 5) for subsequent calculation of SSB/R.

We examined histological cross-sections from 11 mature specimens in the sample. All appeared to be late in the process of vitellogenesis, the late stage 3 of Wylie Echeverria (1987) or stage V of Bowers (1992). The oocytes in each ovary were either large, with diameters ranging from 300 to 600  $\mu\text{m}$  or smaller than 150  $\mu\text{m}$ .

There was little variation within ovaries in the diameter of the larger eggs ( $\pm 50 \mu\text{m}$ ) and thus no evidence of additional maturing batches.

The SSB/R analysis indicated that an instantaneous fishing mortality ( $F$ ) that reduces the SSB/R to 50% of what could be expected with no fishing, ( $F_{50\%}$ ) equates to an  $F$  of 0.072 (Fig. 9).

### Discussion

#### Data sources

The opportunistic assemblage of samples collected from the commercial fishery and research cruises has two implications if one attempts to draw inference from these

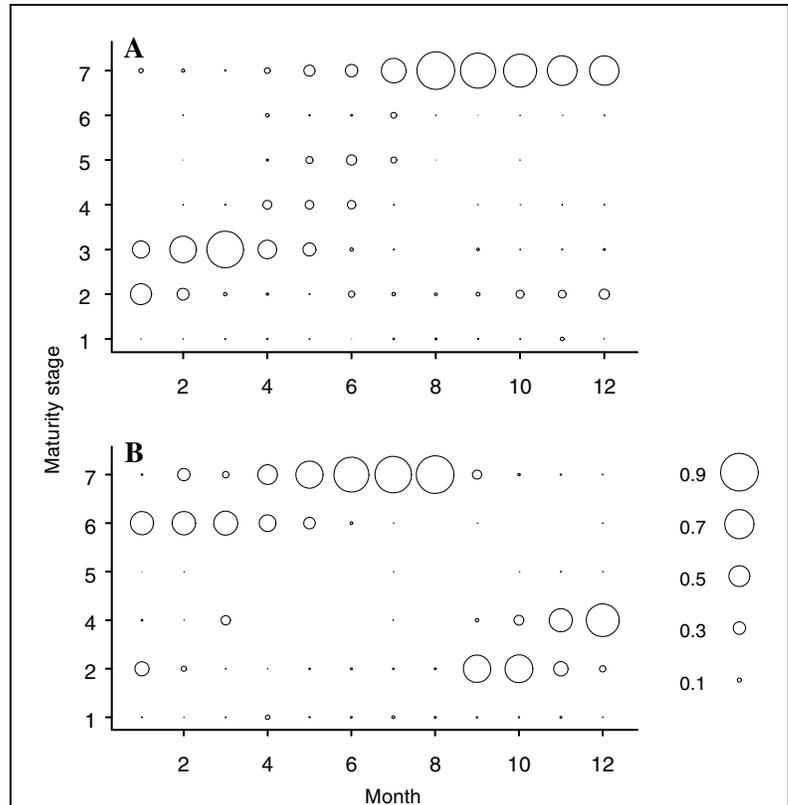
data. The first is that while the overall number of samples and specimens is large, they are not equally distributed over time and space. Thus, for example, we cannot examine whether larger or older males complete the mating earlier in the season because of the lack of winter samples. The second implication is that the results are influenced by the fishing practices. This is particularly the case for inferring depth distribution from trawl catches.

**Habitat**

Silvergray rockfish appeared to be concentrated in the 100–300 m depth interval. Their distribution tended to overlap the distribution of “slope” and “shelf” assemblages of Weinberg (1994) that were based on survey results from northern California to southern British Columbia. The distribution also agrees with observations from research surveys in B.C. waters (Nagtegaal, 1983). Peak catch rate at depth indicates an annual depth migration, noted by fishermen, of about 80 m. The timing and range of this movement is considered by fishermen to be typical for rockfish (Dickens<sup>7</sup>).

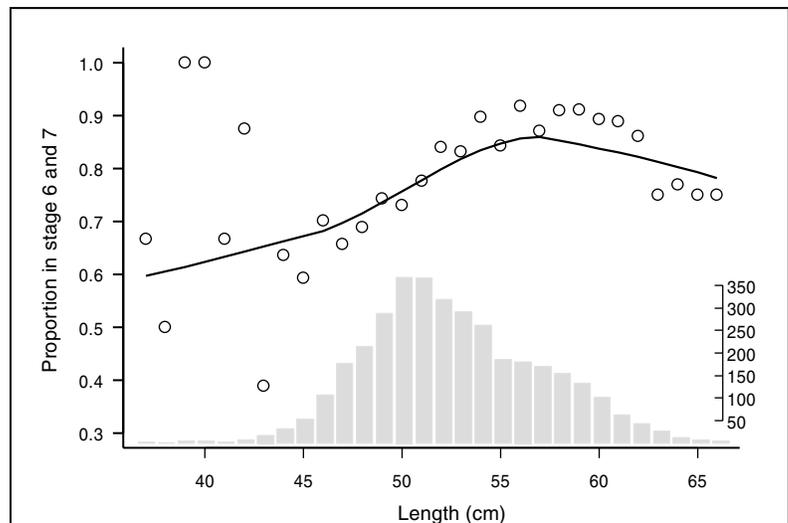
The movement appears correlated with temperature. Bottom temperature increases in winter owing to downwelling (Fig. 2) (Thomson<sup>6</sup>). Thus, the shift to shallower water in the summer means that peak catch rates throughout the year are found in waters centered at just over 7°C. The apparent seasonal movement has obvious implications for stock assessments. Surveys designed to track abundance among years need to be consistent with respect to their timing and depth. More importantly, those who attempt to use CPUE to monitor abundance must consider changes in the distribution of fishing effort by season among years.

There has been no research on the larger scale movements of silvergray rockfish. Barotrauma induced during traditional trawl or hook-and line-fishing precludes tag-recapture studies, although recent work on other rockfish indicates there is potential for tagging *in situ* (Schrope, 2000; Starr et al., 2001). Nor do we know of any genetic studies on silvergray rockfish to determine stock structure, although the



**Figure 4**

The proportion of each maturity stage within each month for (A) female and (B) male silvergray rockfish (*Sebastes brevispinis*) (see Table 1 for definition of stages represented by the numbers on the y axis).



**Figure 5**

The proportion of all mature (stages 3–7, see Table 1) female silvergray rockfish (*Sebastes brevispinis*) in July samples that were classified as spent or resting (stages 6–7) against length. The number of observations is shown in the histogram.

<sup>7</sup> Dickens, B. 2000. Personal commun. 1678 Admiral Tryon Boulevard, Qualicum Beach, British Columbia V0R 2T0, Canada.

**Table 5**

Summary of the predicted values of life history parameters at age for silvergray rockfish (NA: not applicable), partial recruitment values from Stanley and Kronlund (2000).

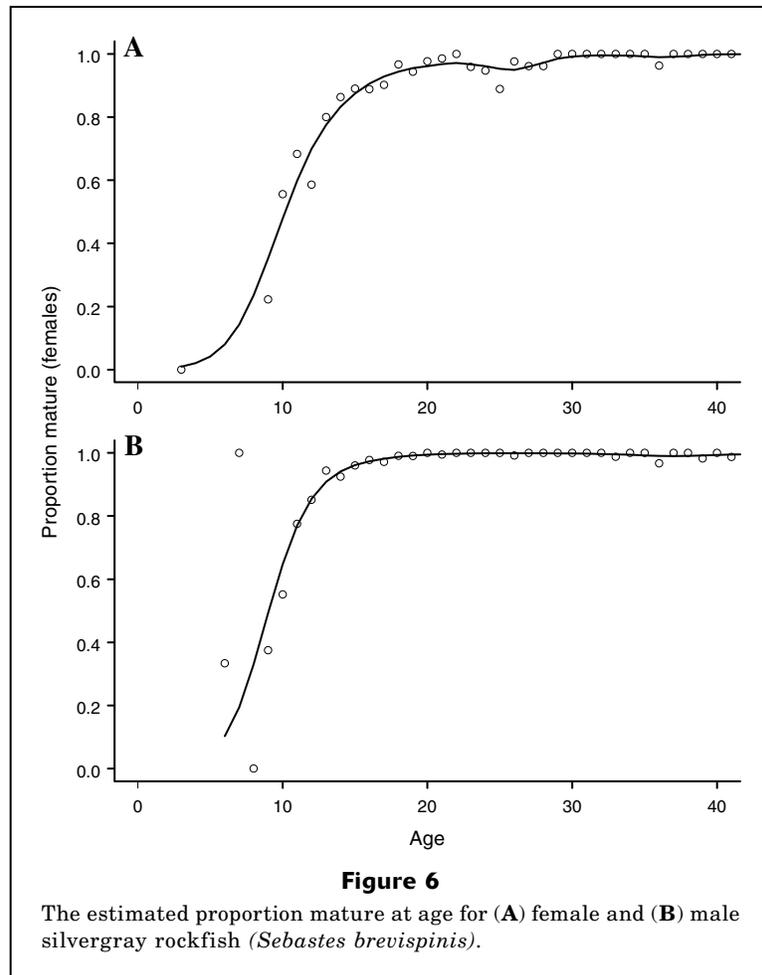
Age (years)	Both sexes		Females			Males		
	Partial recruitment	Length (cm)	Weight (g)	% mature	Fecundity (10 <sup>6</sup> )	Length (cm)	Weight (g)	% mature
1	0.000	NA	NA	0.000	NA	NA	NA	0.000
2	0.000	NA	NA	0.000	NA	NA	NA	0.000
3	0.000	NA	NA	0.010	NA	NA	NA	0.000
4	0.000	NA	NA	0.020	NA	NA	NA	0.000
5	0.000	NA	NA	0.041	NA	NA	NA	0.000
6	0.000	NA	NA	0.080	NA	NA	NA	0.103
7	0.000	NA	NA	0.143	NA	NA	NA	0.195
8	0.000	42.680	1158	0.235	NA	42.386	1138	0.330
9	0.000	44.750	1233	0.352	NA	43.348	1205	0.492
10	0.002	45.698	1307	0.479	NA	44.245	1270	0.647
11	0.151	46.593	1379	0.599	NA	45.080	1332	0.770
12	0.283	47.437	1448	0.700	0.496	45.858	1391	0.855
13	0.401	48.233	1516	0.776	0.536	46.583	1448	0.909
14	0.505	48.985	1582	0.833	0.576	47.258	1502	0.942
15	0.596	49.694	1645	0.875	0.616	47.887	1553	0.961
16	0.674	50.363	1707	0.906	0.656	48.473	1602	0.974
17	0.742	50.994	1766	0.928	0.696	49.019	1648	0.982
18	0.799	51.590	1823	0.944	0.736	49.528	1692	0.988
19	0.847	52.152	1877	0.955	0.776	50.002	1734	0.992
20	0.887	52.682	1930	0.962	0.817	50.444	1773	0.995
21	0.919	53.183	1980	0.968	0.857	50.855	1810	1.000
22	0.944	53.655	2029	0.971	0.898	51.238	1845	1.000
23	0.963	54.101	2075	0.967	0.939	51.595	1878	1.000
24	0.977	54.521	2119	0.962	0.981	51.928	1909	1.000
25	0.987	54.917	2161	0.953	1.022	52.238	1938	1.000
26	0.994	55.292	2201	0.949	1.057	52.527	1965	1.000
27	0.999	55.645	2240	0.960	1.087	52.796	1991	1.000
28	0.999	55.978	2276	0.972	1.117	53.046	2015	1.000
29	1.000	56.292	2311	0.985	1.145	53.280	2038	1.000
30	1.000	56.589	2345	0.992	1.166	53.497	2059	1.000
40	1.000	58.774	2598	1.000	1.252	55.002	2210	1.000
50	1.000	59.996	2747	1.000	1.228	55.743	2287	1.000
60	1.000	60.680	2832	1.000	1.069	56.108	2325	1.000
70	1.000	61.030	2881	1.000	NA	56.288	2344	1.000

relationship of silvergray rockfish to other rockfish species was examined by Gharrett et al. (2001).

### Growth

Silvergray rockfish age estimates have not been validated as they have been for other rockfish (Bennett et al., 1982; Culver, 1987; Leaman and Nagtegaal, 1987; Andrews et al. 2002; Kerr et al. 2004); however, there is evidence of a modal progression in the year classes (Stanley and Kronlund, 2000).

Our estimated growth rates were similar to those reported by Archibald et al. (1981), who used a small subset of the current data. The maximum recorded size of 73 cm for silvergray rockfish is larger than that for most rockfish but smaller than that reported for the largest rockfishes, such as yelloweye rockfish (*S. ruberrimus*), cowcod (*S. levis*), shortraker (*S. borealis*), and bocaccio (*S. paucispinis*), all of which can exceed 91 cm (Haldorson and Love, 1991). The growth rate of silvergray rockfish is similar to that of other rockfishes (Haldorson and Love, 1991), and weight at length was



similar between sexes as is common for most rockfishes (Love et al., 1990).

Lenarz and Wylie Echeverria's (1991) examination of growth dimorphism led them to categorize rockfish as demersal versus water column, and shallow ( $\leq 125$  m) versus deepwater species ( $>125$  m). Table 4 shows that silvergray rockfish are consistent with other demersal rockfish in that they show relatively little sexual dimorphism in growth. Lenarz and Wylie Echeverria (1991) suggested that the size dimorphism may result from trade-offs between fecundity and size; they suggest that among water-column species, males may optimize size solely for survival, whereas added size for a female may confer advantages in egg production.

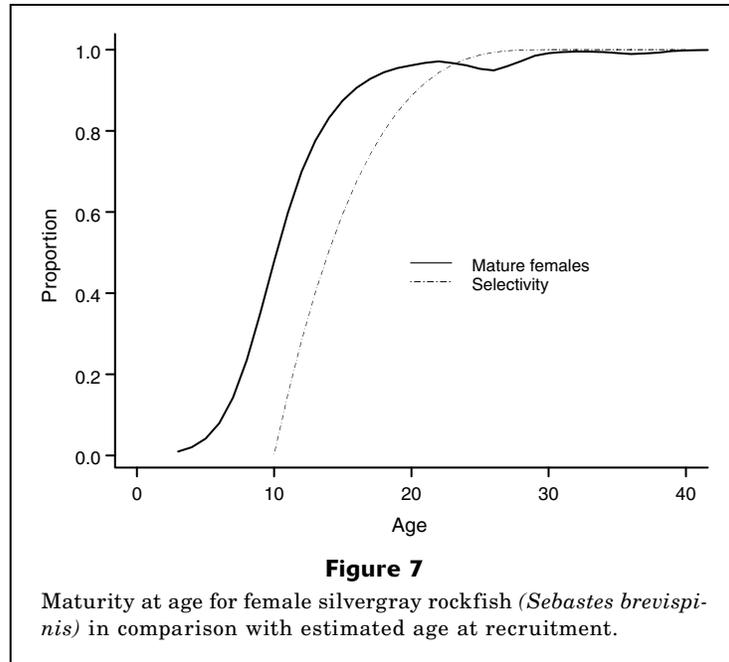
#### Seasonal maturation and age at maturity

The difficulties in the macroscopic staging of rockfish maturity have been widely discussed (Gunderson et al., 1980; Love and Westphal, 1981; Wylie Echeverria, 1987; Love et al., 1990; Nichol and Pickett, 1994). These authors are consistent in suggesting that maturity stages should be verified by histological examination of samples collected through all seasons.

More problematic than the staging is the possibility that commercial fishery samples may not be representative of the overall population. If only the mature fraction of an age class recruits to the fishery, then age at maturity derived from commercial samples will underestimate actual age at maturity. For the trawl nets used in the rockfish fishery in British Columbia, size at 100% retention for rockfish is about 30 cm. Silvergray rockfish do not begin to recruit to the fishery until about 35 cm; thus age or size at recruitment is conditioned by behavior of the silvergray rockfish and not by mesh size.

Given the discussion above, our conclusions on age and length at maturity should be viewed as tentative. Nevertheless, the available observations indicate that most females are mature by age nine and most males by age nine or ten. Lenarz and Wylie Echeverria (1991) noted that in 21 of 31 rockfish species, females and males matured at similar ages.

Mating appears to take place from September through January and peaks from December through January. This time range differs from the range derived from observations for southeastern Alaska where ripe male silvergray rockfish were observed from January to March



(O'Connell<sup>8</sup>). Significant proportions of females with fertilized eggs began to appear 2–3 months later in March and peaked from April to May. This lag time does not differ noticeably from that for other rockfish. Wyllie Echeverria (1987) reported that fertilized eggs are usually found 1–3 months after mating. A few specimens with eyed larvae have been observed in February and March but significant proportions are not observed until April. Parturition lasts through July and peaks in June. Westrheim (1975) suggested that the principal month of parturition was later than June for Oregon–B.C. waters, and later than May for the Gulf of Alaska. Phillips (1964) suggested that the timing of rockfish reproduction could be classified into two broad seasons: early (winter) or late (spring–summer). Silvergray rockfish clearly fall within the latter category.

A mating period from December to January and parturition in June implies a 5–6 month process. This is longer than the average period reported for rockfish by Wyllie Echeverria (1987) but similar to those reported for greenstripe rockfish (*S. elongatus*) (Dec–Feb to June), redstripe rockfish (Nov–Jan to June) and sharpchin rockfish (*S. zacentrus*) (Oct–Jan to Apr–May) (Shaw, 1999). The longer periods may reflect that these species and samples were from higher latitudes than the California observations prevalent in Wyllie Echeverria's work. However, Shaw (1999) pointed out that

rosethorn rockfish (*S. helvomaculatus*) samples from the same latitudes indicated a maturation process of 1–2 months. Batch spawning has been reported by Moser (1967a, 1967b) for some rockfish species but our histological examination of 11 specimens taken from the April sample provided no indication of this in silvergray rockfish. Samples taken closer to parturition would be more conclusive.

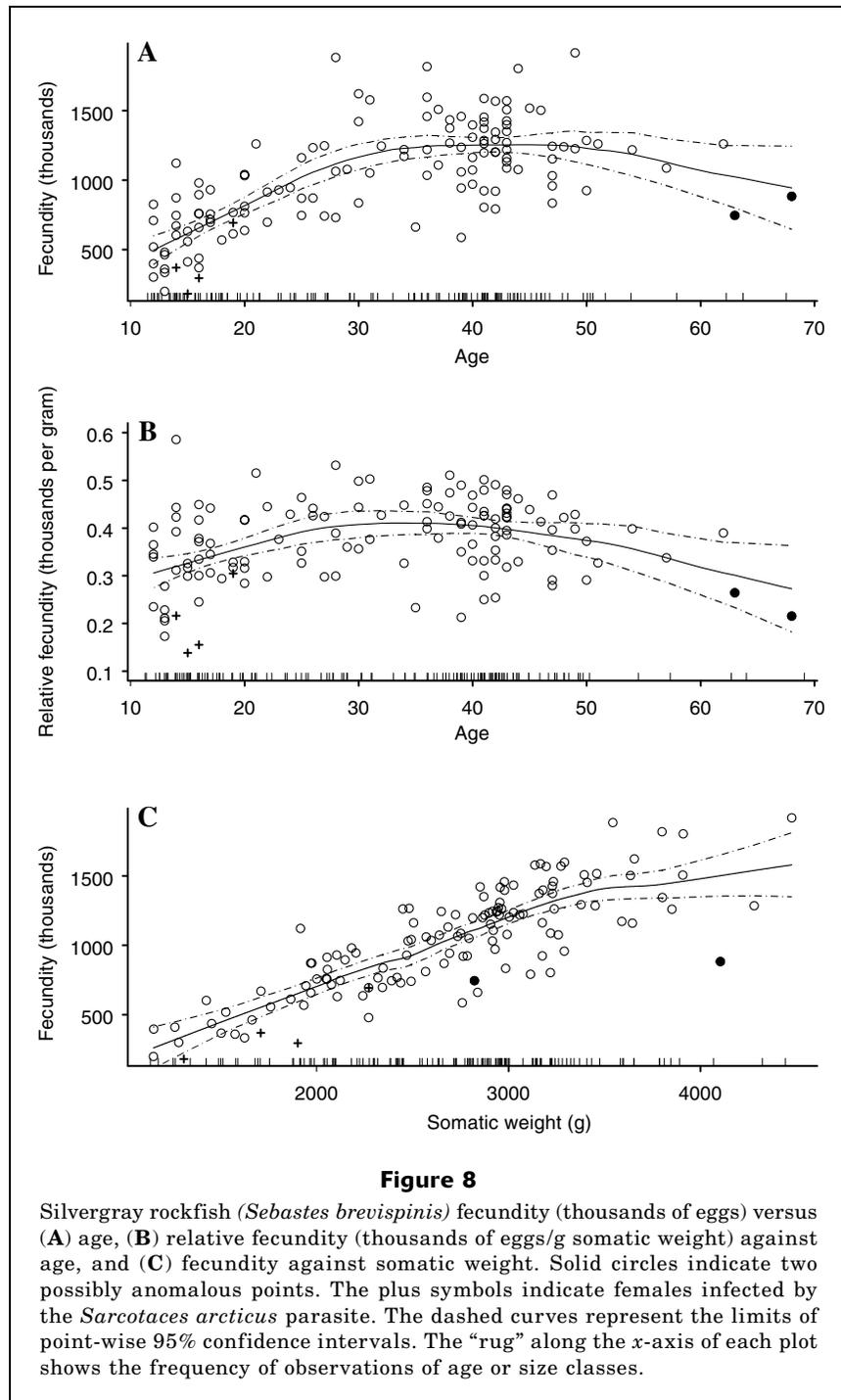
The July samples indicated a dome-shaped relationship in the timing of parturition. As reported for dark-blotched rockfish (Nichol and Pikitch, 1994) and yellowtail rockfish (Eldridge et al., 1991), we observed that the smaller females tended to complete parturition later. However, unlike the results from previous studies, our results indicates that the largest females also tended to complete parturition later.

### Fecundity

Different authors have emphasized that actual fecundity at parturition may be lower than estimates derived prior to fertilization (MacGregor, 1970; Boehlert et al., 1982; Haldorson and Love, 1991; Gunderson, 1997), although this was not observed in yellowtail rockfish (Eldridge et al. 1991). Future studies could examine fecundity closer to parturition; however, it is difficult to capture specimens on the verge of parturition without inducing extrusion (Boehlert et al., 1982). We also caution that our estimates are from one sample and Guillemot et al. (1985) reported significant interannual variation in gonadal development among five species of northern California rockfish.

The presence of the *Sarcotaces arcticus* parasite, previously reported for silvergray rockfish (Sekerak, 1975),

<sup>8</sup> O'Connell, V. 1986. Spawning seasons for some *Sebastes* species landed in the Southeast Alaska longline fishery for nearshore rockfishes (1982–1985). Unpublished report, 21 p. Alaska Department of Fish and Game, Division of Commercial Fisheries, 304 Lake St., No. 103, Sitka, AK 99835-7563.

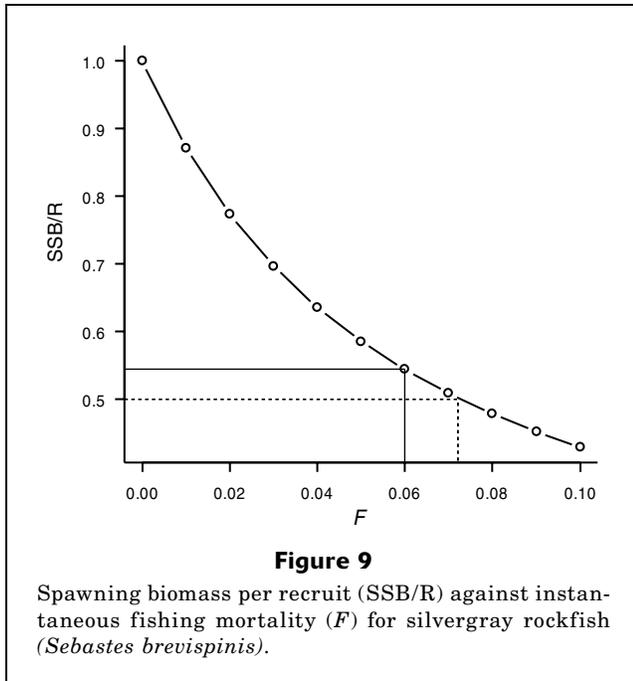


appears to be associated with reduced fecundity, albeit this conclusion is based on three observations. This conclusion is consistent with qualitative observations by the senior author that the gonads of infected silvergray rockfish tend to be smaller.

Silvergray rockfish fecundity appears typical of the genus as summarized in the meta-data treatment by Haldorson and Love (1991). Predicted fecundity for a

40-year old female exceeds 1,250,000 oocytes, although the maximum observed fecundity in a small sample was almost 2,000,000. The slope of the relationship of log fecundity to log length from our study was 4.283, close to the mean of 4.10 reported for other rockfish (Haldorson and Love, 1991).

Haldorson and Love (1991) noted that the ratio of fecundity at the age of 50% maturity versus fecundity



at the age of maximum fecundity ranged from 0.01 to 0.25 for rockfish. Fecundity at 50% maturity could not be determined because we had no observations for females less than 12 years of age. However, if we use fecundity at age 12 (the youngest fish in our sample) and fecundity at age 40 (the predicted age of maximum fecundity), the ratio exceeds 0.40. This finding supports the contention that age at 50% maturity for silvergray rockfish is less than 12 years and adds credibility to the observation that the age of 50% maturity is lower than the age at 50% selectivity.

Estimates of specific fecundity (fecundity/somatic weight) were 356 and 482 ova/g for the 12-year-old and 40-year-old females, respectively. Given that the age at 50% maturity is probably less than 12 years; this range in “relative investment” in reproduction appears average for rockfish (Haldorson and Love, 1991). As with other rockfish, specific fecundity increases with size, although it appears to reach an asymptote at age 40 for silvergray rockfish.

#### Age at maturity and SSB/R

An  $M$  of 0.06 places silvergray rockfish in the middle to lower end of the mortality range for rockfishes. It is higher than the estimates of 0.02–0.04 reported for yelloweye rockfish (O’Connell and Fujioka<sup>9</sup>; O’Connell et

al.<sup>10</sup>; Yamanaka and Lacko, 2001) but much less than 0.14 that has been used for yellowtail rockfish, or 0.28 used for black rockfish (*S. melanops*) (Dorn, 2002).

The analysis of SSB/R indicates that an  $F_{50\%}$  corresponds to  $F=0.072$  or  $F=1.2M$ . This  $F$  to  $M$  ratio represents a more aggressive harvest strategy than the range of 0.5–1.0 currently supported in the literature (Patterson, 1992; Walters, 1998). This result is caused by the special case of silvergray rockfish, anticipated by Clark (1991), wherein recruitment at age is delayed in comparison to maturity at age. If most females actually mature by age 11 or 12 years, but are still not 50% vulnerable at age 14 (Fig. 9), then even at a relatively high fishing mortality, most females can reproduce a few times prior to capture.

As stated above, recruitment to the fishery may be driven more by the stage of maturation than by size or age. Movement to areas and depths that are the source for most fishery samples may be governed by behavioral issues associated with maturation. If fish tend to recruit as they become mature, somewhat independent of size or age, then we may underestimate the age of 50% maturity. In this respect, it is interesting that the fecundity data, compared to other rockfish data, also indicate that the age of 50% maturity may be much less than 12 years.

Our suggestion to managers is that unless the non-recruited population can be sampled to verify maturity-at-age assumptions, then a more precautionary approach is warranted than is implied by an  $F=1.2M$  logic for harvest strategy. This silvergray rockfish example emphasizes the sensitivity of an SSB/R harvest logic to estimating age at maturity, which in turns emphasizes the often neglected issues of field classification of maturity and the representativeness of samples. The task of estimating age at maturity is perhaps too often ignored at the expense of estimating other life history parameters.

#### Conclusion

Owing to the small role that silvergray rockfish has played in groundfish fisheries of the eastern North Pacific Ocean, this species has received little research attention. However, these less valuable stocks are beginning to attract more attention owing to their potential to disrupt precautionary management objectives within the context of a multispecies fishery. With the shift to a more precautionary paradigm, a lack of stock knowledge about the status of any of the incidental species, such as silvergray rockfish, can be a basis for restricting the overall fishery. Strategic allocation of resources by species or stock can no longer be predicated on landed value.

<sup>9</sup> O’Connell, V., C. Brylinsky, and D. Carlile. 1991. Demersal shelf rockfish stock assessment and fishery evaluation report for 2004. Alaska Dep. Fish and Game Regional Information Report J03-39, 44 p. 304 Lake St. #103, Sitka, AK 99835-7563.

<sup>10</sup> O’Connell, V., and J. Fujioka. 1991. Demersal shelf rockfish. In Status of living resources off Alaska as assessed in 1991, p. 46–47. NOAA Tech. Memo. NOAA-TM-NMFS-F/NWC-211. 304 Lake St. #103, Sitka, AK 99835-7563.

Finally, we note how a meta-data analysis such as that provided by Haldorson and Love (1991) can provide values for stock assessment parameters in the absence of direct estimation. By summarizing the basic life history characteristics for silvergray rockfish in B.C. waters, we add to the research on rockfish and improve the basis for effective management of at least one more minor, but potentially fishery-limiting, species in the eastern Pacific groundfish complex.

## Acknowledgments

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## Literature cited

- Andrews, A. H., G. M. Cailliet, K. H. Coale, K. M. Munk, M. M. Mahoney, and V. M. O'Connell.  
2002. Radiometric age validation for the yelloweye rockfish (*Sebastes ruberrimus*) from southeastern Alaska. *Mar. Freshw. Res.* 53:139–146.
- Archibald, C. P., W. Shaw, and B. M. Leaman.  
1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters, 1977–1979. *Can. Tech. Rep. Fish. Aquat. Sci.* 1048, 57 p.
- Bennett, J. T., G. W. Boehlert, and K. K. Turekian.  
1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from 210 Pb/226 Ra measurements on otoliths. *Mar. Biol.* 71:209–215.
- Boehlert, G. W., W. H. Barss, and P. B. Lamberson.  
1982. Fecundity of the widow rockfish, *Sebastes entomelas*, off the coast of Oregon. *Fish. Bull.* 80:881–884.
- Bowers, M. J.  
1992. Annual reproductive cycle of oocytes and embryos of yellowtail rockfish *Sebastes flavidus* (Family Scorpaenidae). *Fish. Bull.* 9:231–242.
- Clark, W. G.  
1991. Groundfish exploitation rates based on life history parameters. *Can. J. Fish. Aquat. Sci.* 48:734–750.
- Cleveland, W. S.  
1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* 38:261–269.
- Culver, B.  
1987. Results from tagging black rockfish (*Sebastes melanops*) off the Washington and northern Oregon coast. In *Proceedings of the international rockfish symposium*; Anchorage, Alaska, October 20–22, 1986, p. 155–170. Univ. Alaska, Alaska Sea Grant Report 87-2, Anchorage, Alaska.
- Dorn, M. W.  
2002. Advice on west coast rockfish harvest rates from bayesian meta-analysis of stock-recruit relationships. *N. Am. J. Fish. Manag.* 22:280–300.
- Eldridge, M., J. A. Whipple, M. J. Bowers, B. Jarvis, and J. Gold.  
1991. Reproductive performance of yellowtail rockfish, *Sebastes flavidus*. *Environ. Biol. Fishes* 30:91–102.
- Gabriel, W. L., M. P. Sissenwine, and W. J. Overholz.  
1989. An analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. *N. Am. J. Fish. Manag.* 9:383–391.
- Gharrett, A. J., A. K. Gray, and J. Heifetz.  
2001. Identification of rockfish (*Sebastes* spp.) by restriction site analysis of the mitochondrial ND-3/ND-4 and 12S/16S rRNA gene regions. *Fish. Bull.* 99:49–62.
- Gray, P.  
1954. *The microtometist's formulary and guide*, 794 p. Blakiston, New York, NY.
- Guillemot, P. J., R. J. Larson, and W. H. Lenarz.  
1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae: *Sebastes*). *Fish. Bull.* 83:299–311.
- Gunderson, D. R.  
1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Can. J. Fish. Aquat. Sci.* 54:990–998.
- Gunderson, D. R., P. Callahan, and B. Goiney.  
1980. Maturation and fecundity of four species of *Sebastes*. *Mar. Fish. Rev.* 42:74–79.
- Haldorson, L., and M. Love.  
1991. Maturity and fecundity in the rockfishes, *Sebastes* spp., a review. *Mar. Fish. Rev.* 53:25–31.
- Hastie, T. J., and R. J. Tibshirani.  
1990. *Generalized additive models*, xv+335 p. Chapman and Hall, New York, NY.
- Kerr, L. A., A. H. Andrews, B. R. Frantz, K. H. Coale, T. A. Brown, and G. M. Cailliet.  
2004. Radiocarbon in otoliths of yelloweye rockfish (*Sebastes ruberrimus*): a reference time series for the coastal waters of southeast Alaska. *Can. J. Fish. Aquat. Sci.* 61:443–451.
- Leaman, B. M.  
1988. Reproductive and population biology of Pacific ocean perch (*Sebastes alutus* (Gilbert)). Ph.D. diss, 199 p. Univ. British Columbia, British Columbia, Canada.
- Leaman, B. M., and D. A. Nagtegaal.  
1987. Age validation and revised natural mortality rate for yellowtail rockfish. *Trans. Am. Fish. Soc.* 116:171–175.
- Lenarz, W. H., and T. Wylie Echeverria.  
1991. Sexual dimorphism in *Sebastes*. *Environ. Biol. Fishes* 30:71–80.
- Love, M. S., P. Morris, M. McCrae, and R. Collins.  
1990. Life history aspects of 19 rockfish species (Scorpaenidae: *Sebastes*) from the Southern California Bight. *NOAA Tech. Rep. NMFS* 87, 38 p.
- Love, M. S., and W. V. Westphal.  
1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off Central California. *Fish. Bull.* 79:533–545.
- Love, M. S., M. Yoklavich, and L. Thorsteinson.  
2001. *Rockfishes of the northeast Pacific*, 406 p. Univ. Cal. Press, London.
- MacGregor, J. S.  
1970. Fecundity, multiple spawning, and description of the gonads in *Sebastes*. *Mar. Fish. Rev.* 42:74–79.
- MacLellan, S. E.  
1997. How to age rockfish (*Sebastes*) using *S. alutus* as

- an example—the otolith burnt section technique. Can. Tech. Rep. Aquat. Sci. 2146, 39 p.
- Moser, H. G.  
1967a. Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773–797.  
1967b. Seasonal histological changes in the gonads of *Sebastes paucispinis* Ayres, an ovoviviparous teleost (Family Scorpaenidae). J. Morph. 123:329–354.
- Nagtegaal, D. A.  
1983. Identification and description of assemblages of some commercially important rockfishes (*Sebastes* spp.) off British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. no. 1183, 88 p.
- Nichol, D. G., and E. K. Pikitch.  
1994. Reproduction of darkblotched rockfish off the Oregon coast. Trans. Am. Fish. Soc. 123:469–481.
- Patterson, K.  
1992. Fisheries for small pelagic species: an empirical approach to management targets. Rev. Fish. Biol. Fisheries 2:321–338.
- Phillips, J. B.  
1964. Life history studies on ten species of rockfish (genus *Sebastes*). Calif. Dep. Fish Game, Fish. Bull. 126, 70 p.
- Schnute, J.  
1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38:1128–1140.
- Schrope, M.  
2000. Deep background. New Scientist 165:12.
- Sekerak, A. D.  
1975. Parasites as indicators of populations and species of rockfishes (*Sebastes*: Scorpaenidae) of the Northeastern Pacific Ocean. Ph.D. diss, 251 p. Univ. Calgary, Alberta, Canada.
- Shaw, F. R.  
1999. Life history traits of four species of rockfish (Genus *Sebastes*). M.Sc. thesis, 178 p. Univ. Washington, Seattle, WA.
- Stanley, R. D., and A. R. Kronlund.  
2000. Silvergray rockfish (*Sebastes brevispinis*) assessment for 2000 and recommended yield options for 2001/2002. Can. Stock Assess. Sec. Res. Doc. 2000/173, 116 p.
- Starr, R. M., J. N. Heine, J. M. Felton, and G. M. Cailliet.  
2001. Movements of bocaccio (*Sebastes paucispinis*) and greenspotted rockfishes (*Sebastes chloristicus*) in a Monterey submarine canyon: implications for the design of marine reserves. Fish. Bull. 100:324–337.
- Walters, C.  
1998. Evaluation of quota management policies for developing fisheries. Can. J. Fish. Aquat. Sci. 55:2691–2705.
- Weinberg, K. L.  
1994. Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington. Fish. Bull. 92:620–632.
- Westrheim, S. J.  
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399–2411.
- Wyllie Echeverria, T.  
1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. Fish. Bull. 85:229–250.
- Yamanaka, K. L., and L. C. Lacko.  
2001. Inshore rockfish (*Sebastes ruberrimus*, *S. maliger*, *S. caurinus*, *S. melanops*, *S. nigrocinctus*, and *S. nebulosus*) stock assessment for the west coast of Canada and recommendations for management. Can. Stock Assess. Sec. Res. Doc. 2002/139, 102 p.

## Appendix 1—Growth formula from Schnute (1981)

$$Y(t) = \left[ y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{1/b}$$

The model involves six parameters,  $\Theta = (\tau_1, \tau_2, y_1, y_2, a, b)$ , where  $\tau_1$  and  $\tau_2$  are two arbitrary ages in the life of a fish, such that  $\tau_2 > \tau_1$ . The parameter  $y_1$  is the size of a fish at time  $\tau_1$ , and  $y_2$  is the size of a fish at time  $\tau_2$  with  $y_2 > y_1 > 0$ . Parameters  $a$  and  $b$  determine the shape of the growth curve by controlling the acceleration (deceleration) in growth from times  $\tau_1$  to  $\tau_2$ . The parameter  $a$  has units (in time), and  $b$  is dimensionless. Although the mathematical expression of the model has four cases, these four cases actually represent the limiting forms of a single equation as  $a$  or  $b$  (or both) approach 0.

## Appendix 2—Spawning stock biomass per recruit

If  $N_a$  is a vector of the numbers of females at each age under constant conditions, such that

$$N_{a+1} = N_a e^{-(FS_a + M)},$$

where  $F$  = the instantaneous fishing mortality rate;  
 $S_a$  = the partial recruitment at age  $a$ ; and  
 $M$  = the instantaneous natural mortality rate;

then the cumulative spawning potential of a cohort of females over the lifetime of the cohort (under constant  $F$  and  $M$  and  $S_a$ ) is

$$SSB/R = \sum_1^a N_a Fec_a Mat_a,$$

where  $Fec_a$  = fecundity at age  $a$ , and  
 $Mat_a$  = proportion mature at age  $a$ .

The spawning potential per recruit (SSB/R) can then be calculated under various estimates of  $F$  and compared with the unfished SSB/R ( $F=0$ ) as shown in Figure 9.