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SEASONAL CYCLES OF FAT AND GONAD VOLUME IN FIVE SPECIES OF NORTHERN CALIFORNIA ROCKFISH (SCORPAENIDAE: *SEBASTES*)

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ABSTRACT

Seasonal changes in visceral fat volume and gonad volume are compared in five species of rockfish from northern and central California: *Sebastes entomelas*, *S. paucispinis*, *S. goodei*, *S. pinniger*, and *S. flavidus*. In these species, visceral fat was deposited between spring and fall, at the same time as gametogenesis. Visceral fat declined in volume between fall and spring, coinciding with the decline in volume of testes and preceding the release of embryos in females. We suggest that increased feeding during the summer upwelling season provides the energy for simultaneous fat accumulation, gametogenesis, and perhaps somatic growth. During subsequent seasons of presumed food storage, these rockfishes may utilize visceral fat reserves for maintenance. This pattern of fat deposition and utilization may contribute to the long life and repeated reproduction of rockfishes, at the expense of current fecundity and growth.

Our data also suggest that rockfishes which spawn only once during the reproductive season have fat cycles of greater magnitude than those spawning more than once a year. Of the species that we studied, the apparent single spawners *S. entomelas* and *S. flavidus* have more northerly geographic distributions and larger fat cycles than the multiple spawners *S. goodei* and *S. paucispinis*. It is possible that the shorter and more pronounced productive season in the north leads to a greater need for fat reserves during winter and makes the wintertime production of additional batches of eggs energetically difficult.

The seasonal storage and utilization of lipid (and nonlipid) reserves are important in the metabolic activities and overall life histories of many animals (Love 1970; Shul'man 1974; Derickson 1976a and associated papers). While cycles of lipid storage and utilization are generally associated with seasonal changes in food availability (Derickson 1976b) or metabolic demands (Lawrence 1976), the functions of lipid storage are varied.

In many fishes, reserves are used primarily in reproduction, as indicated by complementary cycles of lipid content and reproductive activity (Lasker 1970; Shchepkin 1971a, b; Schevchenko 1972; Shul'man 1974; Tyler and Dunn 1976; Wootton and Evans 1976; Lasker and Smith 1977; Diana and MacKay 1979; Delahunty and de Vlaming 1980; Patzner 1980; Hunter and Leong 1981). The seasonal accumulation of sufficient reserves may be a prerequisite for sexual maturity in some fishes (Iles 1974), and the amount of material stored may influence fecundity (Tyler and Dunn 1976). Reserves may also be used in migration (Robertson and Wexler 1960; Dotson 1978; Glebe and Leggett 1981 a, b), and, when used in spawning migrations, may contribute indirectly to reproduction.

Slobodkin (1962) and Calow (1977), however, noted that fat deposition may actually detract from reproduction, particularly when fat deposition and reproduction are concurrent. In such cases, reserves are often used instead for maintenance during periods of food scarcity (Calow and Jennings 1977), enhancing the opportunity to reproduce in the future. Some fishes seem to use reserves both for reproduction and maintenance, when spawning occurs during periods of food scarcity or fasting (Wilkins 1967; MacKinnon 1972; Iles 1974; Newsome and Leduc 1975; Foltz and Norden 1977; Dawson and Grimm 1980; Pierce et al. 1980; Glebe and Leggett 1981 a, b). The interpretation of such cases is complex, since reproduction and maintenance may be competing concurrently for reserves.

Roberts (1979) noted that fat was deposited seasonally around the viscera of two species of shallow-water rockfish, *Sebastes mystinus* and *S. melanops*. He suggested that the cycle of fat deposition and utilization was related to seasonal changes in the abundance of food and to reproduction.

In this paper we examine the seasonal relationship

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between visceral fat volume and gonad volume in five offshore species of rockfish: *Sebastes entomelas*, *S. paucispinis*, *S. goodei*, *S. pinniger*, and *S. flavidus*. Based on Roberts' suggestion and the general literature on fat cycles in fishes, we expected to find complementary cycles of fat and gonad volume, indicating that reserves are used in reproduction. We used visceral fat volume as a convenient index of the timing and magnitude of seasonal changes in reserves, explicitly assuming that reserves stored elsewhere would change coincidentally (Delahunty and de Vlaming 1980). Since we did not measure total reserves, our data on visceral fat volume cannot be applied to quantitative studies of energy budgets, but are most useful for examining seasonal changes and making comparisons within a group of closely related species.

The use of gonadal volume as an index of reproductive activity requires some explanation. In males, gonadal volume is a good index of the timing of gametogenesis. In females of this live-bearing genus, however, gametogenesis is often reflected only in the initial increase of gonadal volume. Following fertilization (which may occur some time after copulation, due to sperm storage [Sorokin 1961; Echeverria 1981[4]; Boehlert and Yoklavich 1984]), ovarian volume continues to increase during a gestation period that lasts a month or so (Moser 1967). There may be some postzygotic nutrition of embryos during this time (Boehlert and Yoklavich 1984), but much of the increase in volume is due to the accumulation of water (Moser 1967). In some species of *Sebastes* that spawn more than once a year, gametogenesis takes place again late in the reproductive season of females. Among the species considered here, *S. paucispinis* and *S. goodei* are clearly multiple spawners (Moser 1967; MacGregor 1970), and Echeverria[5] has presented some evidence for multiple spawning in *S. pinniger*.

MATERIALS AND METHODS

Party boat and commercial rockfish catches were sampled weekly, as a part of a large-scale study, by personnel from the National Marine Fisheries Service (Tiburon Laboratory) and the California Department of Fish and Game, at northern California fishing ports between Crescent City (lat. 41°N) and Morro Bay (35°N). The species sampled depended on the day's catch. Samplers measured the total length of each specimen to the nearest millimeter and removed the viscera and gonads for preservation in 10% Formalin[6] in seawater.

In the laboratory, fat tissue was dissected from the viscera and its volume estimated by water displacement in graduated cylinders. In some samples, a small amount of fat had liquified. The volume of this liquid was estimated and added to total fat volume. Gonads were also removed and their volume measured as above. The state of development of ovaries and testes was scored according to indices based mainly on gonad morphology and coloration (Moser 1967; Gunderson et al. 1980). Histological preparations of small gonads were used to confirm sex and state of maturity. Data for species, sex, total length, stage of maturity, and fat and gonad volume were stored using a computer.

Data on visceral fat volume were analyzed for collections made between March 1980 and February 1981, inclusive. Measurements of gonad volume were begun in June 1980 and continued until May 1981 to obtain a full year of data. For each species, data were pooled over all ports of collection and divided quarterly, as follows: spring (March-May), summer (June-August), fall (September-November), and winter (December-February). Quarterly division of data gave good sample sizes for most seasons, yet still allowed seasonal separation. Primary production is relatively low off California during fall and winter, but is greater during most of spring and summer, when coastal upwelling occurs (Bolin and Abbott 1963).

To facilitate comparisons, visceral fat volume and gonad volume were expressed as log-transformed power-function regressions of volume on fish length. The power equation is:

$$V = aL^b,$$

where V is volume, L is total length, and a and b are estimated parameters. This equation is often used to express the relationship between volumetric measures, such as fecundity, and linear measures, such as length (Bagenal 1978; Glebe and Leggett 1981a; de Vlaming et al. 1982). Logarithmic transformation to

$$\ln V = \ln a + b \ln L$$

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[4] Echeverria, T. 1981. Maturity in six species of rockfish (Pisces, Scorpaenidae, *Sebastes*). [Abstr.] Proceedings of the 1981 Western Groundfish Conference.

[5] Echeverria, T. 1983. Maturity and seasonality of the rockfishes (Scorpaenidae: *Sebastes*) of central California. Unpubl. manuscr., 60 p. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

allows the use of standard least-squares regression techniques, and stabilizes variances (Bagenal 1978). Thus, rather than using ratios of fat or gonad volume to fish weight or length, which can be biased by allometric relationships between the measurements (Bagenal 1978; de Vlaming et al. 1982), we employed empirically derived regression lines. The use of power equations also allowed us to test hypotheses with standard statistical procedures. Regressions were calculated for each sex during each season. Although most of the analyses were for adults, seasonal regressions of visceral fat volume were also computed for juveniles when samples were large.

Differences between regressions of fat or gonad volume were tested by analysis of covariance, using the ratio:

$$F = \frac{(N - 4)(SS_{com.} - SS_1 - SS_2)}{2(SS_1 + SS_2)}$$

where SS_1 and SS_2 are the residual sums of squares about the separate regressions, $SS_{com.}$ is the residual sum of squares for a common regression, and N is the number of specimens (Kleinbaum and Kupper 1978). When regressions differed significantly, the direction of differences was assessed by examining the positions of the regression lines and of calculated volumes at mean fish length. We chose to display only the calculated volumes at mean length, to simplify the presentation of data. The mean of ln (total length) was determined for all specimens of a sex and species included in the annual analysis. For each season and sex, the estimated value of ln (volume) at the mean of ln (length) (designated $\hat{Y}$) was calculated from the appropriate regression. We intend these point values to be used only for making comparisons within our data. The regression lines themselves best represent fat or gonad volume, and we present the parameters for these regressions. See Guillemot (1982) for scatter diagrams of raw data and regression plots.

The estimated values of fat volume at mean length were also used in an index of the relative amplitude of fat cycles. This index was the antilog of the difference between estimated ln (fat volume) in peak and low seasons, and is equivalent to the ratio of peak season:low season fat volume.

We compared fat cycles of males and females within a species by qualitatively noting differences in the timing and amplitude of fat cycles, and by statistically comparing fat regressions during peak and low seasons of fat volume. The latter comparisons were carried out by analysis of covariance, as above.

In comparing fat cycles among species, we noted differences in the timing of fat cycles and differences in the amplitude of cycles. We also assessed differences in the absolute volume of fat stored by applying analyses of covariance to the peak-season fat regressions of the different species.

RESULTS

Seasonal Cycles of Fat and Gonad Volume in Adults

In most seasons, moderate to low correlations (0.5 and below) existed between ln (visceral fat volume) and ln (total length), indicating a fair amount of scatter about the regressions (Table 1). Lower correlations occurred mainly in seasons of low fat volume (cf. Fig. 1). The slopes of most regressions were not significantly different from 3.0 (Table 1), indicating a proportionate relationship between fat volume and fish length. Slopes significantly smaller than 3 occurred in seasons of low fat volume (winter and spring), and in general slopes from seasons of low fat volume were smaller than those from seasons of higher fat volume. During seasons of low fat volume, fish of all sizes tended to have little fat, accounting in part for some of the lower correlations. Some slopes were significantly greater than 3 during seasons of high fat content (*S. entomelas* females, *S. paucispinis* males, *S. pinniger* females, and *S. flavidus* females), indicating disproportionately greater fat content in larger fish. Correlations between ln (gonad volume) and ln (total length) were generally high (Table 2), and showed no marked relation with season (Fig. 2). Below, we first examine the fat and gonad cycles for adults of each species separately, and then briefly compare the cycles of different species.

Sebastes entomelas

Visceral fat content changed significantly during the year in both male and female *S. entomelas* (Fig. 1). In females, where all seasonal regressions of ln (visceral fat volume) on ln (total length) differed significantly from each other, fat content increased from a low in spring to a peak in fall, and then declined in winter (Fig. 1). In males, neither the spring and winter nor the summer and fall fat regressions differed significantly (Fig. 1). Visceral fat volume in males increased after spring to a peak spread through summer and fall, and then declined in winter (Fig. 1). During the fall, when both sexes had large volumes of visceral fat, fat content of males barely

TABLE 1.—Seasonal regressions of ln (visceral fat volume, ml) on ln (total length, mm) in adults of five species of *Sebastes* from northern and central California. Slopes significantly different from 3 are indicated (? = $P < 0.1$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Species and season	Females				Males			
	Sample size	Intercept	Slope	*r*	Sample size	Intercept	Slope	*r*
S. entomelas								
Spring	118	^{1}21.752	3.845	0.240	88	−12.267	2.341	0.138
Summer	102	−23.875	4.335*	0.578	58	−32.427	5.795?	0.456
Fall	81	−28.715	5.184**	0.581	57	−20.654	3.908	0.459
Winter	163	−18.442	3.400	0.428	84	−19.524	3.538	0.251
S. paucispinis								
Spring	117	−10.334	1.988?	0.314	115	−17.544	3.150	0.443
Summer	116	−16.415	2.982	0.576	127	−16.120	2.978	0.553
Fall	75	−12.957	2.500	0.462	101	−24.053	4.259**	0.693
Winter	82	−1.269	0.633***	0.165	83	−9.847	1.942*	0.389
S. goodei								
Spring	193	−12.741	2.220	0.272	51	−14.555	2.671	0.281
Summer	219	−10.780	2.027	0.221	80	−11.827	2.299	0.403
Fall	140	−14.895	2.763	0.499	68	−17.686	3.228	0.334
Winter	183	0.253	0.155***	0.020	55	0.783	−0.026?	−0.002
S. pinniger								
Spring	23	−16.134	2.980	0.400	38	−16.581	3.006	0.445
Summer	61	−28.391	4.957***	0.786	103	−17.213	3.152	0.455
Fall	32	−24.771	4.453	0.579	37	−14.859	2.825	0.593
Winter	18	−24.371	4.289	0.529	14	−28.849	5.063	0.538
S. flavidus								
Spring	73	8.221	−1.038**	−0.099	71	−18.255	3.298	0.259
Summer	143	−24.044	4.323**	0.605	88	−10.960	2.152	0.240
Fall	147	−14.050	2.771	0.468	112	−8.652	1.777	0.212
Winter	69	−2.946	0.743*	0.092	72	−14.442	2.575	0.227

exceeded that of females. Fat regressions at the low point in spring did not differ significantly (Table 3).

As expected, gonad volume changed significantly during the year in both sexes of *S. entomelas* (Fig. 2). In males, the volume of testes increased dramatically from a low in spring to a peak in summer, and then declined through fall and winter (Fig. 2). In females, the volume of ovaries increased very slightly between spring and summer, and then increased greatly in fall and winter (Fig. 2).

Sebastes paucispinis

Visceral fat volume changed significantly during the year in males and females of *S. paucispinis* (Fig. 1). In females, fat content did not change significantly between spring and summer, but increased from summer to a peak in fall, to decline slightly in winter (Fig. 1). In males, visceral fat accumulated between spring and summer, remained about constant from summer to fall, and declined in winter (Fig. 1). During the nominal peak season in fall, fat content of females was significantly greater than that of males, while the regressions for fat content during the nominal low points in spring did not differ significantly (Table 3).

Ovarian volume in *S. paucispinis* reached its low point during summer, increased with vitellogenesis in fall, increased again with embryogenesis and/or further vitellogenesis in winter, and then declined in spring (Fig. 2). The volume of testes increased from spring into summer, continued to increase slightly in fall, and declined in winter (Fig. 2).

Sebastes goodei

Visceral fat volume in female *S. goodei* increased from spring through summer to a peak in fall, and declined in winter (Fig. 1). In male *S. goodei*, visceral fat volume increased from low levels in spring to a peak in summer, declined slightly in fall, and decreased again in winter (Fig. 1). The fat content of females during their fall peak exceeded that of males during their summer peak, while there was no significant difference in fat content during the low seasons of spring for females and winter for males (Table 3).

Ovarian volume increased slightly between spring and summer in females of *S. goodei*, and then grew more rapidly through fall and winter (Fig. 2). The volume of testes increased greatly between spring and summer in males of *S. goodei*, and then declined through fall and winter (Fig. 2).

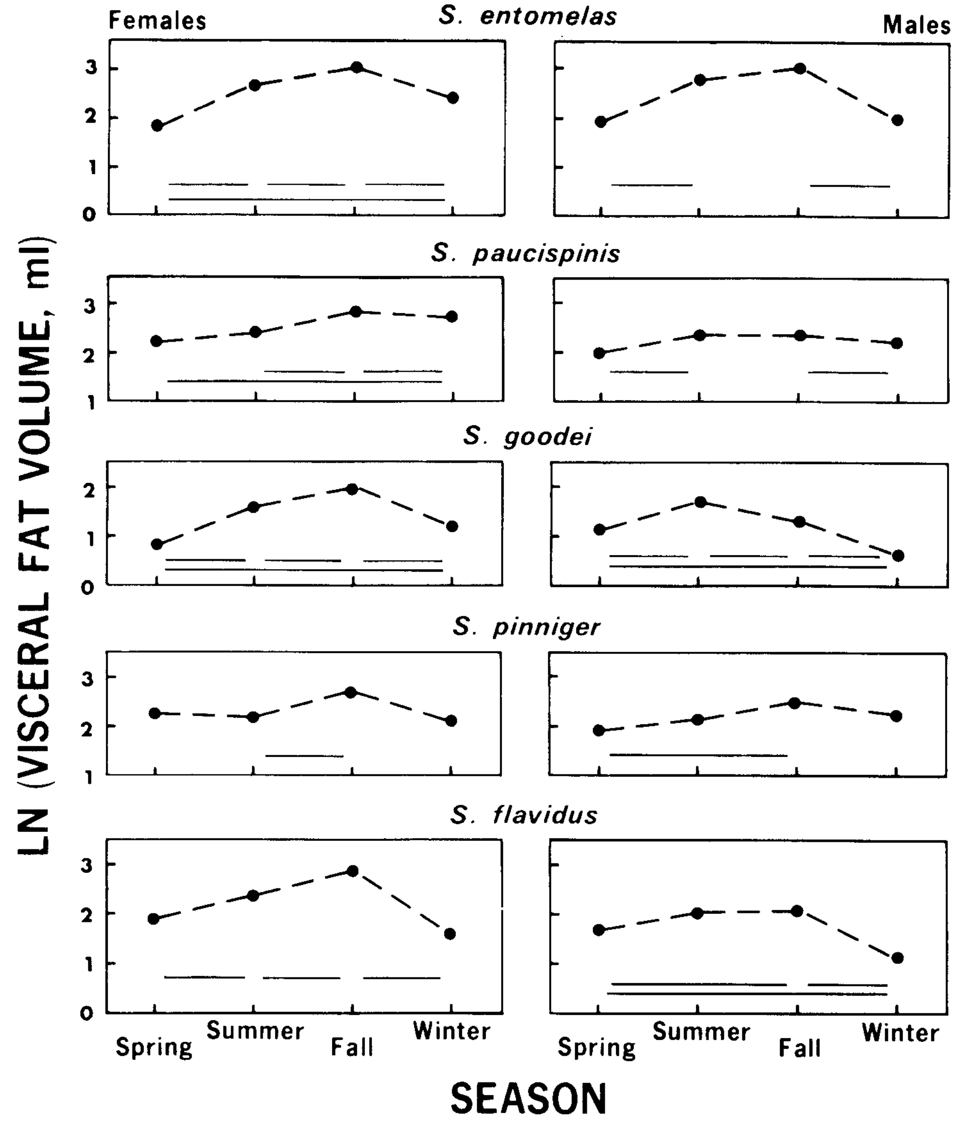

FIGURE 1. – Seasonal variation of visceral fat volume in adults of five species of *Sebastes* from northern and central California. For each species and sex, points are estimates of ln (fat volume) at the overall average of ln (total length) for specimens of that species and sex examined during the year. Estimates were derived from the seasonal regressions of ln (visceral fat volume) on ln (total length) (Table 1). A horizontal line between two seasons means that the fat regressions for those two seasons differed significantly ($P \leq 0.05$) by analysis of covariance. The upper of the two rows of horizontal lines are for adjacent seasons in the graph. The lower horizontal line is for winter and spring. The absence of a horizontal line means that the regressions did not differ significantly. Annual averages of ln (total length, mm) are *S. entomelas* females, 6.13, and males, 6.08; *S. paucispinis* females, 6.31, and males, 6.20; *S. goodei* females, 6.11, and males, 5.88; *S. pinniger* females, 6.11, and males, 6.14; and *S. flavidus* females, 6.11, and males, 6.04. Seasons: spring (March-May 1980), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

TABLE 2.—Seasonal regressions of ln (gonad volume, mL) on ln (total length, mm) in adults of five species of *Sebastes* from northern and central California.

Species and season	Females				Males			
	Sample size	Intercept	Slope	*r*	Sample size	Intercept	Slope	*r*
S. entomelas								
Spring	217	−36.259	6.226	0.787	93	−40.725	6.738	0.709
Summer	17	−50.148	8.148	0.908	18	−42.341	7.386	0.644
Fall	65	−58.734	10.187	0.781	33	−10.442	1.930	0.191
Winter	177	−40.049	7.249	0.532	115	−18.856	3.207	0.403
S. paucispinis								
Spring	113	−26.341	4.541	0.640	163	−36.055	5.933	0.855
Summer	78	−34.265	5.767	0.919	105	−36.360	6.130	0.807
Fall	78	−37.533	6.386	0.833	118	−28.802	4.935	0.845
Winter	118	−34.058	5.946	0.647	127	−17.757	3.014	0.508
S. goodei								
Spring	146	−34.372	5.961	0.785	60	−20.612	3.552	0.332
Summer	166	−32.127	5.617	0.798	63	−12.733	2.386	0.283
Fall	176	−17.064	3.293	0.460	93	−29.433	5.095	0.772
Winter	184	−27.812	5.151	0.495	71	−17.172	2.886	0.214
S. pinniger								
Spring	21	−23.843	4.181	0.694	35	−49.963	8.230	0.799
Summer	22	−51.129	8.611	0.902	43	−60.352	10.175	0.939
Fall	31	−50.164	8.448	0.889	40	−45.336	7.564	0.845
Winter	21	−34.798	6.022	0.538	14	−65.227	10.657	0.904
S. flavidus								
Spring	100	−29.422	5.083	0.707	138	−31.837	5.228	0.499
Summer	83	−33.961	5.892	0.852	50	−54.152	9.204	0.759
Fall	162	−47.425	8.155	0.822	134	−38.906	6.649	0.690
Winter	53	−30.680	5.592	0.575	80	−23.743	3.927	0.555

TABLE 3.—Comparisons of fat volume between males and females during peak and low fat seasons in five species of *Sebastes*. If not defined statistically, peak and low seasons were selected on the basis of regression positions. $\hat{Y}$, the estimated ln (fat volume) at the overall average of ln (total length), is presented as an indication of regression position (Fig. 1). If male and female fat regressions differed significantly ($P \leq 0.05$) by analysis of covariance, their relative fat volumes are indicated. NS denotes regressions that did not differ significantly.

Species	Females		Males		Comparison
	Season	$\hat{Y}$	Season	$\hat{Y}$	
S. entomelas					
Peak	Fall	3.07	Fall	3.09	♂ > ♀
Low	Spring	1.82	Spring	1.96	NS
S. paucispinis					
Peak	Fall	2.81	Fall	2.35	♀ > ♂
Low	Spring	2.20	Spring	1.99	NS
S. goodei					
Peak	Fall	1.98	Summer	1.70	♀ > ♂
Low	Spring	0.82	Winter	0.63	NS
S. pinniger					
Peak	Fall	2.69	Fall	2.49	NS
S. flavidus					
Peak	Fall	2.87	Fall	2.08	♀ > ♂
Low	Winter	1.59	Winter	1.12	NS

Sebastes pinniger

Cycles of visceral fat volume were poorly defined in *S. pinniger*. In females, only the summer and fall fat regressions differed significantly, suggesting a peak in fat content during the fall (Fig. 1). In males, no two consecutive seasons differed significantly in fat content, and the only two seasons that differed significantly at all were spring and fall (Fig. 1). Thus, males may also have had peak fat content during fall, but their fat cycle was not pronounced. The visceral fat content of males and females did not differ significantly during their apparent fall peaks (Table 3).

The ovarian cycle of *S. pinniger* was also poorly defined in our data. Ovaries increased significantly in volume between spring and summer (Fig. 2). No other seasons differed significantly, but a peak in winter is indicated in Figure 2. In males, gonadal volume increased dramatically from spring to a peak in summer, remained fairly high in fall, and declined in winter (Fig. 2).

Sebastes flavidus

Visceral fat volume in female *S. flavidus* increased from spring through fall, and then declined in winter (Fig. 1). Male *S. flavidus* exhibited a gradual increase in fat content between spring and fall, followed by a decline to minimal fat levels in winter (Fig. 1). Fat content of females exceeded that of males during their fall peaks, and the difference in fat content during their winter lows was not significant (Table 3).

Ovarian volume in *S. flavidus* showed a pattern similar to most of the rest of the species: an increase

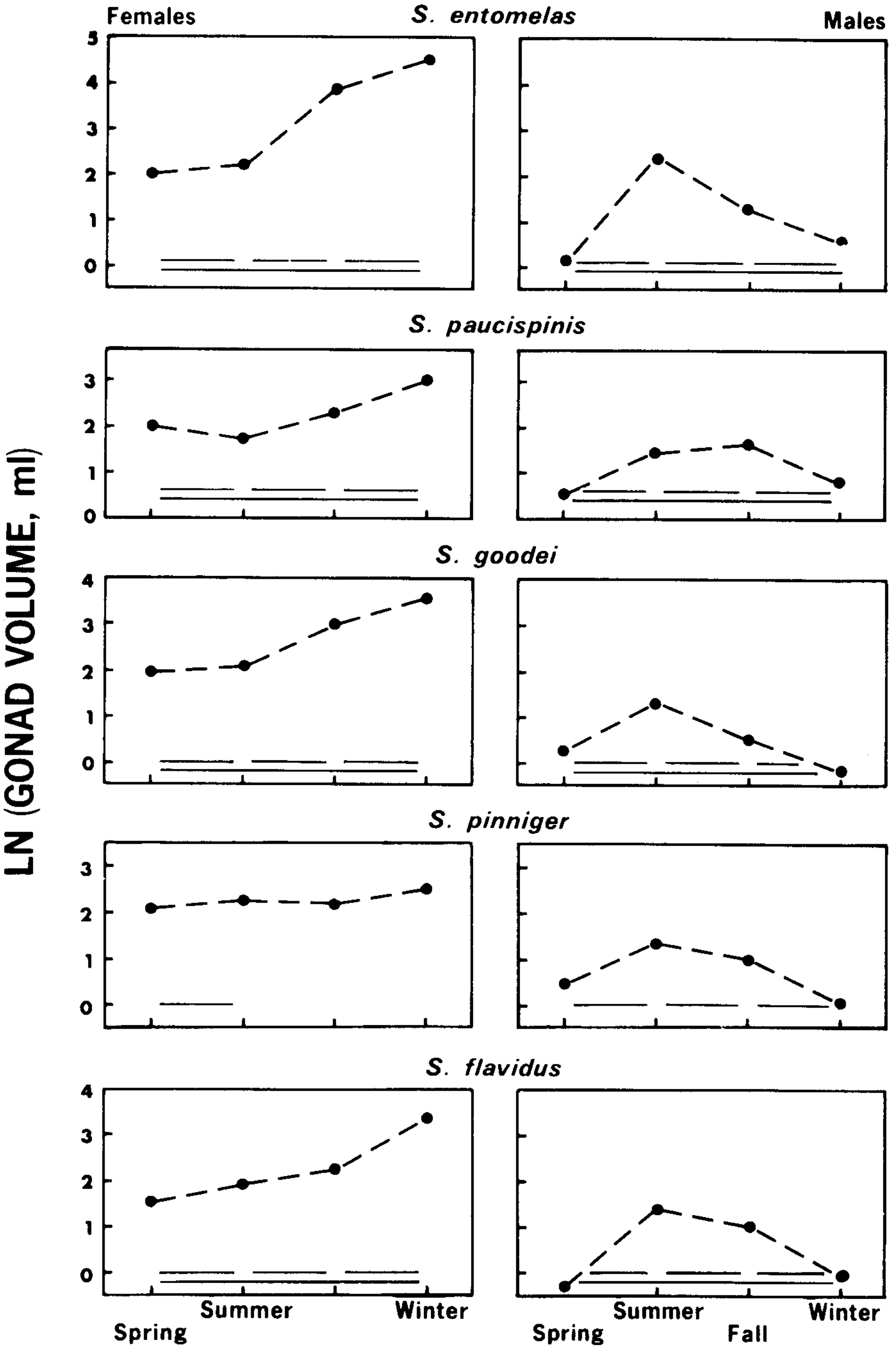

FIGURE 2. – Seasonal variation of gonad volume in adults of five species of *Sebastes* from northern and central California, as in Figure 1. Averages of ln (total length, mm) used in estimating gonadal volume are *S. entomelas* females, 6.14, and males, 6.06; *S. paucispinis* females, 6.24, and males, 6.17; *S. goodei* females, 6.09, and males, 5.88; *S. pinniger* females, 6.20, and males, 6.13; and *S. flavidus* females, 6.09, and males, 6.04. Seasons: spring (March-May 1981), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

from low volume in spring to peak volume in winter (Fig. 2). In males, the volume of testes increased from spring to a peak in summer, declined slightly in fall, and fell greatly in winter (Fig. 2).

Summary and Comparison of Adult Fat Cycles

In all species studied, visceral fat volume was high, if not at a peak, during fall. In males, fat content was usually high during summer as well. In male *S. entomelas*, *S. paucispinis*, and *S. flavidus*, summer and fall fat content did not differ significantly, and in male *S. goodei* the fat content in summer was actually greater than in fall. Summertime fat content was relatively high in female *S. entomelas*, *S. goodei*, and *S. flavidus*, but in females of all species the fat content increased to a peak in fall. Winter and spring were usually the seasons of low fat volume in both sexes. Little pattern existed in *S. pinniger*, except that fat volume appeared to reach a peak in fall.

Both the relative amplitude of fat cycles and peak fat volume differed among the species and sexes. In male and female *S. entomelas*, *S. goodei*, and *S. flavidus*, the fat volume of average-sized fish changed by about a factor of three during the year (Table 4). The amplitude of the fat cycle was lower in *S. paucispinis* and *S. pinniger*, where there was less than a twofold change in fat content between peak and low seasons (Table 4). Among females, *S. entomelas* and *S. flavidus* generally had higher peak fat volumes than the other species (Table 5). Among the other three species, peak fat content of females seemed to decrease from *S. pinniger* to *S. paucispinis* to *S. goodei* (Table 5). Females of *S. entomelas* and *S. flavidus*, then, possessed high-volume, high-amplitude fat cycles, while *S. pinniger* and *S. paucispinis* had low-volume, low-amplitude fat cycles, and *S. goodei* showed low volume and relatively high amplitude. The peak fat volume in male *S. entomelas* far exceeded that of the remaining species, most of which had relatively similar fat-length relationships during peak seasons (Table 5). Thus among males, only *S. entomelas* showed a high-volume, high-amplitude fat cycle. Males of *S. flavidus* and *S. goodei* possessed fat cycles of low volume and moderately high amplitude, and *S. paucispinis* and *S. pinniger* had cycles of low volume and low amplitude, like the females of these species.

TABLE 4.—Relative amplitude of fat cycles in five species of *Sebastes*. The ratio of estimated peak season: low season fat volume is presented for each species and sex, and is used as an index of cycle amplitude. Ratios are the antilogs of the differences between estimated ln (fat volume) at the average of ln (total length) in peak and low fat seasons (Fig. 1, Table 3).

Species	Amplitude	
	Females	Males
S. entomelas	3.50	3.10
S. paucispinis	1.83	1.44
S. goodei	3.20	2.91
S. pinniger	1.67	1.84
S. flavidus	3.61	2.64

Fat Cycles in Juveniles

Fat cycles were examined in juveniles of male and female *S. paucispinis*, and of female *S. pinniger* and *S. flavidus*, where seasonal sample sizes were large enough to permit analysis (Table 6). In *S. paucispinis*, juvenile females appeared to reach a peak in fat content during winter, but in juvenile males there were no significant differences among the seasonal regressions (Fig. 3). In *S. pinniger*, juvenile females

TABLE 5.—Comparisons of the peak-season regressions of ln (fat volume) on ln (total length) for different species of *Sebastes*. Comparisons were made by analysis of covariance. For significantly differing regressions ($P \leq 0.05$), the comparative fat volumes are indicated (based on the positions of the regressions, cf. Fig. 1, Table 1), unless intersecting lines made position difficult to interpret. NS denotes regressions that did not differ significantly.

	S. paucispinis	*S. goodei*	*S. pinniger*	*S. flavidus*
Females				
S. entomelas	*S.e.* > *S.pa.*	*S.e.* > *S.g.*	NS	NS
S. paucispinis		*S.pa.* > *S.g.*	NS	*S.pa.* < *S.f.*
S. goodei			*S.g.* < *S.pi.*	*S.g.* < *S.f.*
S. pinniger				*S.pi.* < *S.f.*
Males				
S. entomelas	*S.e.* > *S.pa.*	*S.e.* > *S.g.*	*S.e.* > *S.pi.*	*S.e.* > *S.f.*
S. paucispinis		intersection	*S.pa.* < *S.pi.*	intersection
S. goodei			NS	NS
S. pinniger				NS

possessed little fat in the spring, and higher levels in summer through winter (Fig. 3). Fat content in juveniles of female *S. flavidus* peaked in fall (Fig. 3).

TABLE 6.—Seasonal regressions of ln (visceral fat volume, mL) on ln (total length, mm) in juveniles of three species of *Sebastes* from northern and central California.

Species and sex	Season	Sample size	Intercept	Slope	*r*
S. paucispinis					
females	Spring	140	−19.637	3.510	0.325
	Summer	138	−26.793	4.669	0.455
	Fall	55	−23.626	4.189	0.419
	Winter	67	−29.508	5.205	0.719
males	Spring	92	−10.309	1.976	0.157
	Summer	86	−22.626	3.969	0.362
	Fall	10	−48.866	8.324	0.599
	Winter	21	−27.486	4.818	0.766
S. pinniger					
females	Spring	41	−21.012	3.655	0.402
	Summer	76	−21.794	3.859	0.624
	Fall	37	−36.539	6.383	0.875
	Winter	20	−18.568	3.345	0.651
S. flavidus					
females	Spring	21	−22.796	4.080	0.388
	Summer	70	−8.502	1.642	0.260
	Fall	53	−36.450	6.558	0.639
	Winter	19	−9.906	1.848	0.361

Thus, in three of the four groups analyzed, fat content of juveniles varied during the year. The timing of the apparent cycles was similar to that of adults. The amplitude of the fat cycle in juveniles of female *S. paucispinis* and *S. pinniger* (less than twofold change in fat volume) was similar to adult amplitude. In female *S. flavidus*, the amplitude of the fat cycle in juveniles (less than twofold change) was lower than in adults. As adults, *S. flavidus* showed high-amplitude fat cycles, while *S. paucispinis* and *S. pinniger* showed low-amplitude cycles.

DISCUSSION

Clear cycles of visceral fat volume and gonadal volume occurred in both sexes of *S. entomelas*, *S. paucispinis*, *S. goodei*, and *S. flavidus*. The fat cycles of male and female *S. pinniger* were less well-defined, as was the gonadal cycle of female *S. pinniger*. Many of the female *S. pinniger* we examined were relatively small adults. This may account, at least in part, for the small and ill-defined fat and gonad cycles, as the fat cycles of female *S. flavidus* increased in amplitude from juveniles to adults.

Visceral fat volume generally increased propor-

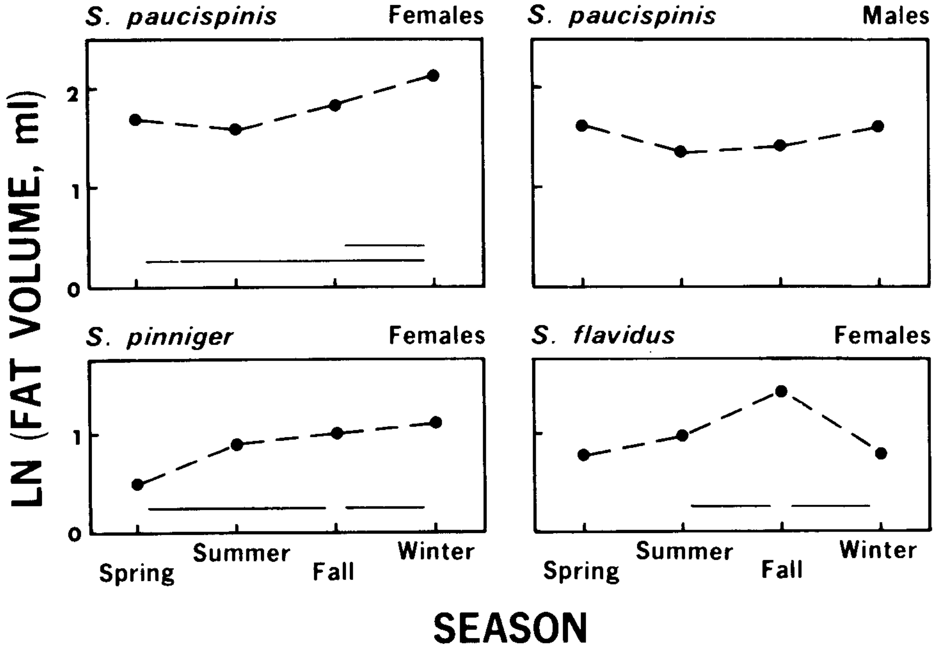

FIGURE 3.—Seasonal variation of visceral fat volume in the juveniles of five species of *Sebastes*, as in Figure 1. Averages of ln (total length, mm) used in estimating fat volume are *S. paucispinis* females, 6.08, and males, 6.04; *S. pinniger* females, 5.88; and *S. flavidus* females, 5.78. Seasons: spring (March-May 1980), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

tionately with fish volume, since most slopes of ln (fat volume) on ln (length) were near 3. Slopes smaller than 3 occurred in those seasons when fish of all sizes had little fat. Some slopes during seasons of high fat volume were significantly greater than 3, indicating that larger fish had disproportionately greater fat volume than smaller fish. This was particularly true of, but not limited to, the species and sexes with high-magnitude fat cycles (males and females of *S. entomelas* and females of *S. flavidus*). It would be interesting to discover whether larger females of *S. pinniger* have high-amplitude fat cycles, since the slopes of the fat regressions for female *S. pinniger* were relatively high.

The dependence of fat volume on fish size and season of collection, while applicable on average, does not apply to every individual. The scatter about the regressions of fat volume on length was large. Some of the scatter was probably due to errors in measurement, but a large part was real. We have observed large differences in the amount of visceral fat among fish of the same size and sex in the same collection. The reasons for such variation may be difficult to resolve, since it is difficult to know the history of individuals collected in the field.

However, our data were adequate in most species to detect seasonal changes on average. We wanted to compare the timing of fat cycles and gonad cycles, and thus learn something of the function of fat storage in rockfish. Our initial hypothesis was that stored fat would be used in reproduction, based on Roberts' (1979) observations.

The data for males do not support this hypothesis. Fat and gonad cycles were nearly coincident, with peaks in both cycles occurring in fall and/or summer and lows in winter/spring. Thus the energy for gonadal growth was probably derived from current ingestion, not from material previously stored as fat. Maximum somatic growth also coincides with the summertime growth of testes and fat deposits (e.g., Love and Westphal 1981), so all three processes may be competing for energy consumed during this time.

The situation is more complicated in females. Some fat was deposited between spring and summer in females of *S. entomelas*, *S. goodei*, and *S. flavidus*, and females of all species gained fat between summer and fall. Some gonadal growth took place between spring and summer in females of all species except *S. paucispinis*. In all but *S. pinniger*, however, ovarian volume increased steadily between summer and winter. The growth of ovaries through fall was due largely to vitellogenesis, while the greater growth of ovaries into winter was due primarily to embryogenesis and hydration of ova (Moser 1967). Additional vitellogenesis probably occurred during winter in the multiple spawners, *S. paucispinis* and *S. goodei* (Moser 1967; MacGregor 1970).

In females, then, fat deposition usually began in summer, perhaps slightly before the initiation of vitellogenesis, but continued into the main period of vitellogenesis between summer and fall. Thus, like males, females of these species deposited fat more or less concurrently with gonadal maturation and somatic growth. The depletion of visceral fats occurred between fall and spring in females of most species, during and after gestation. It is possible that fat reserves are used for the maturation of additional ova in multiple spawners or are involved in the nutrition of embryos (Boehlert and Yoklavich 1984), but as in males, reserves are not used in the initial development of gonads.

There were two main differences in the fat cycles of males and females: females usually had larger fat cycles than males, and the peak fat volume of females occurred in fall, while fat volume in males usually reached a plateau that spread through summer and fall. It is possible that courtship activity in males (Helvey 1982) draws energy from fat deposition between summer and fall, or that this activity draws time from feeding. As a result, females may continue to fatten after fat deposition ceases in males. It is also possible that females require more reserves in winter and they somehow are able to acquire these extra reserves.

The synchronous depletion of reserves in males and females, however, indicates a common function for such reserves. We suggest two possible functions:

First, some rockfish may migrate during the period of fat depletion. Love (1981) presented evidence for seasonal movements in *Sebastes paucispinis* and *S. entomelas* off southern California, but had no data on the extent or direction of movement. Females of *S. alutus* undertake seasonal migrations covering as much as 300 m of depth (summarized in Gunderson 1977). Lenarz (pers. obs.) found evidence of seasonal movement in female *S. jordani*. Several species of rockfish undertake little or no seasonal migration, including *S. flavidus* from shallow waters off Alaska (Carlson and Barr 1977). Since seasonal migrations in rockfish may not be long and seem to occur primarily in females, we suggest that other possibilities be ruled out before accepting migration as a major use of fat reserves.

Second, we suggest that fat reserves are used for maintenance during wintertime periods of reduced food availability. Fattening, as well as growth and initial gametogenesis, occurs during and shortly after the spring-summer upwelling period, and depletion occurs during and after a time of lower primary production (Bolin and Abbott 1963). Roberts (1979) noted that several species of inshore rockfish near Monterey consumed more food during the summer, when macroplankton (euphausiids) and juvenile rockfish were abundant. During the nonupwelling season, juvenile rockfish and macroplankton were less abundant, and adult rockfish consumed less food. Love and Westphal (1981) found less food in the stomachs of *S. serranoides* during the nonupwelling season near Morro Bay. Gunderson (1977) noted a "summer feeding season" in *S. alutus.* Hobson and Chess[7], however, found the gelatinous prey of *S. mystinus* to be more abundant during nonupwelling periods off northern California. There is only limited information on the seasonal food habits of the five species studied here. *Sebastes paucispinis* is largely piscivorous (Phillips 1964), while *S. entomelas, S. goodei, S. pinniger*, and *S. flavidus* feed on macroplankton and small fish (Phillips 1964; Pereyra et al. 1969; Brodeur 1982). Brodeur (1982) examined seasonal changes in the diets of *S. flavidus* and *S. pinniger*, and found that food consumption declined during winter in *S. pinniger*, but not in *S. flavidus.* However, Carlson and Barr (1977) found a pronounced decline in activity during winter in *S. flavidus* off Alaska, suggesting seasonal changes in feeding. This hypothesis can be examined with concurrent data on food consumption and fat volume. It is not mutually exclusive with other functions of fat reserves, since some fat could also be used for migration, nourishment of embryos, or maturation of additional ova in multiple spawners.

The wintertime use of reserves for maintenance, however, is consistent with the overall pattern of long life and repeated reproduction in rockfish (as discussed also by Gunderson [1977]). As suggested by Slobodkin (1962) and Calow (1977), summertime fat deposition may exact a cost in current reproduction (if more gametes could be packed into rockfish abdomens) or in future increases in gamete capacity (through additional growth), but may help to ensure survival.

An interesting result of our study was the difference in magnitude of fat cycles among species, which was particularly evident in females. These differences are correlated with both the frequency of spawning and geographical distributions of the species. Females of *S. entomelas* and *S. flavidus* had fat cycles of high amplitude and volume, probably spawn only once a year (Westrheim 1975; Echeverria footnote 5), and have northerly distributions (Phillips 1957, 1964; Gunderson and Sample 1980; Adams 1980). On the other hand, *S. paucispinis* and *S. goodei* had fat cycles of low amplitude and/or volume, spawn more than once a season, at least in southern California, and have southerly distributions (Phillips 1957, 1964; Gunderson and Sample 1980; Adams 1980). The case with *S. pinniger* is unclear. Females seemed to have low-amplitude fat cycles, but the small sample and small sizes of females in the samples make conclusions tenuous. Echeverria (footnote 5) has some evidence for multiple spawning in *S. pinniger.* If so, its northerly distribution would be inconsistent with the pattern seen in the other species. We will restrict our discussion to the remaining four species, although further studies of *S. pinniger* may be instrumental in evaluating the suggestions we make below.

The small fat cycles of multiple spawners are probably not caused by their potentially greater reproductive output, since fat deposition stops long before the maturation of additional batches of ova. It seems more likely that the magnitude of the fat cycle, frequency of spawning, and geographical distribution are all related. Boehlert and Kappenman (1980) suggested that year-round spawning in southern populations of *S. diploproa* served to increase reproductive output in response to annual variation in the survival of planktonic larvae. Multiple spawning in southern populations and species may also be a response to the more even seasonal distribution of upwelling in southern vs. northern areas of the northeastern Pacific (Bakun et al. 1974; Parrish et al. 1981; Smith 1978), as it affects planktonic larvae. However, the more restricted upwelling season in northern waters may also lead to larger and better defined seasonal variation in the food supply of adults. A more pronounced summertime pulse of food may enable northerly species like *S. entomelas* and *S. flavidus* to store large amounts of fat. Similarly, a more pronounced decline in food during winter may make the accumulation of such reserves necessary, and preclude the maturation of additional batches of ova. On the other hand, a more even seasonal distribution of food in the south may enable southerly species like *S. paucispinis* and *S. goodei* to produce additional batches of ova during winter, and may also reduce the need for wintertime reserves. These suggestions are speculative, but it should be possible to compare the seasonal variation of food consumption in species with northern vs. southern distributions.

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[7] Hobson, E. S., and J. R. Chess. 1981. Seasonal patterns in trophic relationships of the blue rockfish, *Sebastes mystinus.* [Abstr.] Proceedings of the 1981 Western Groundfish Conference.

In summary, we suggest that seasonal changes in the availability of food are rather important in the life histories of rockfish. The summer storage and winter use of fat reserves, in near synchrony with growth and decline of gonad volume, indicate a wintertime paucity of food that is compensated by the use of material that was stored at the expense of fecundity or growth. Further study of seasonal feeding, fat deposition, and reproductive cycles, categorized by size and sex, would be useful in evaluating this hypothesis. Further, geographical comparisons of these cycles may illuminate some causes of differences in the life histories of rockfishes.

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