

Variation of Growth with Latitude in Two Species of Rockfish (*Sebastes pinniger* and *S. diploproa*) from the Northeast Pacific Ocean

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ABSTRACT: Growth of two *Sebastes* species was measured as fish length versus age, determined from otoliths. *S. pinniger* and *S. diploproa* were collected extensively over their wide latitudinal ranges in the northeast Pacific Ocean. In both species, females grew faster and larger than males. Growth of *S. pinniger* did not vary with latitude. For *S. diploproa*, however, there was a cline of increasing growth with higher latitude. In the habitat of the adult fish, which are demersal on the continental shelf and upper slope, latitudinal variation in environmental factors, such as temperature and oxygen concentration, appears insufficient to account for the observed differences in growth. Thus two other possible causes of the growth cline are discussed. First, *S. diploproa* has been exploited by fisheries more in the north than in the south, possibly resulting in more available prey and thus increased growth in the north (short term density-dependent response). The second possible cause is a density-independent, evolutionary response at the population level characterized by differences in reproductive strategy. Reproductive success in the southern part of the range of this species is probably less predictable due to the effects of oceanographic currents on the survival of epipelagic larvae and prejuveniles; reproductive effort in the south would therefore be greater. The relative importance of the suggested mechanisms for growth differences requires further elucidation from population genetics and studies of density effects and fishing pressure.

INTRODUCTION

Marine fishes inhabiting wide latitudinal ranges frequently show distinct variations in biological characteristics and life history strategies. Maximum size, longevity, age distribution, fecundity, and growth rate may vary in response to environmental factors, either through direct physiological mechanisms or through evolutionary responses to long-term environmental gradients at the population level. Latitudinal variation in growth rate has been studied in only a few species. Leggett and Carscadden (1978) observed faster growth with increasing latitude in the anadromous American shad (*Alosa sapidissima*), but correlated this difference with varying reproductive and life history strategies at the population level. Chadwick (1976), on the other hand, observed no differences in growth rate in either of two species of tidepool cottids from collections 1120 km apart on the Pacific coast. The evidence for latitudinal variation in growth in the scorpaenid genus

Sebastes is conflicting; Westrheim (1973) observed more rapid growth in southern collections of *S. alutus*, whereas Love (1977) observed slower growth in *S. serranoides* collected in the warmer waters south of Point Conception as compared to those from cooler, northern waters. The present study compares growth of two species of *Sebastes* to analyze latitudinal variation in growth. The two species studied, *Sebastes diploproa* and *S. pinniger*, were chosen as representative of the genus; both have wide latitudinal ranges, from Baja California to southeastern Alaska (Hart, 1973). *S. pinniger* reaches maximum lengths of 76 cm and inhabits depths primarily from 91 to 183 m over hard bottoms (Miller and Gotshall, 1965; Hart, 1973). *S. diploproa* is smaller, reaching a maximum length of 46 cm, and occurs in deeper water (to 578 m) where it is associated with soft bottom (Hart, 1973). Age and growth have been analyzed for both species, but only for the following limited parts of the geographic ranges: California (Phillips, 1964), Oregon (Six and Horton, 1977) and British Columbia (Westrheim and Harling, 1975). These studies, taken as a whole, suggest that growth is faster in the southern parts of the range for both

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species. Conclusions drawn from different studies, however, may be misleading due to different collection methods and ageing methodologies. Therefore, in the present study we have sampled large numbers of individuals throughout the latitudinal range of each species.

MATERIALS AND METHODS

Both *Sebastes pinniger* and *S. diploproa* were collected in the 1977 Rockfish Survey undertaken by the Northwest and Alaska Fisheries Center (National Marine Fisheries Service) and several other cooperating agencies. Methods of sampling these species have been described (Gunderson and Sample, 1980). Sampling was conducted systematically from 34°09'N to 48°26'N latitude (Fig. 1) with trawling tracklines drawn perpendicular to the coast and spaced every 10 miles (every 5 miles in certain high-density areas). Along each trackline the following four depth intervals were sampled: 81-182 m, 183-273 m, 274-365 m, and 366-476 m. All sampling was with Nor'easter trawls with roller gear, 8.9 cm mesh in the body with a 3.2 cm cod end liner. All measurements taken were fork length to the nearest cm.

All otoliths were taken in the 1977 Rockfish Survey with the exception of 279 otoliths of *Sebastes pinniger* from California. In the southern part of its range (central and northern California), this species is generally not taken in trawls but enters the commercial longline fishery and the sport fishery (Miller and Gotshall, 1965). Otoliths collected by the California Department of Fish and Game from February 1977 to March 1978 were used in addition to a single collection from the Rockfish Survey to analyze growth for this species from California. Of the 279 otoliths from California, 171 were from males and 108 were from females; of the total, 173 were taken from commercial catches in the Eureka area and 106 were from the San Francisco sport catch.

Age was determined from whole otoliths, generally thought to be the best structure for age determination in *Sebastes* (Westrheim, 1973; Six and Horton, 1977; Kimura et al., 1979). Whole otoliths were read under reflected light at 10 magnifications on a dissecting microscope using the method of Westrheim (1973). No attempt was made to confirm the ages determined in this manner; it was assumed that each opaque-translucent ring pair constituted one year's growth. Annulus formation in young individuals has been demonstrated, however, by Kelly and Wolf (1959) for *S. marinus* and by Westrheim (1973) for *S. alutus*. The latter study also demonstrated the progression of a dominant year class of adults through the fishery over a

period of 6 years, further validating the use of otoliths for age determination.

Growth data for both species were fit to the von Bertalanffy growth equation. Least square estimates for the parameters L_{∞} , k , and t_0 were obtained using mean lengths at age weighted by the numbers of observations. Growth curves were compared using a predictive sample reuse procedure (Geisser and Eddy, 1979) modified for comparing growth curves (Kappelman, in prep.). This procedure chooses among alternative models with criteria based upon the lowest sums of squares of deviations within the alternative models. For comparing two populations, two alternative models are considered, model M_1 asserting that the two growth curves are the same, and model M_2 asserting they are different. With three populations, on the other hand, five alternative models are considered: model M_1 asserts that the three populations are represented by a single growth curve; M_2 , the first two populations are the same but differ from the third; M_3 , the second and third populations are the same but differ from the first; M_4 , the first and third populations are the same but differ from the second; and M_5 , all three populations are represented by separate growth curves. For

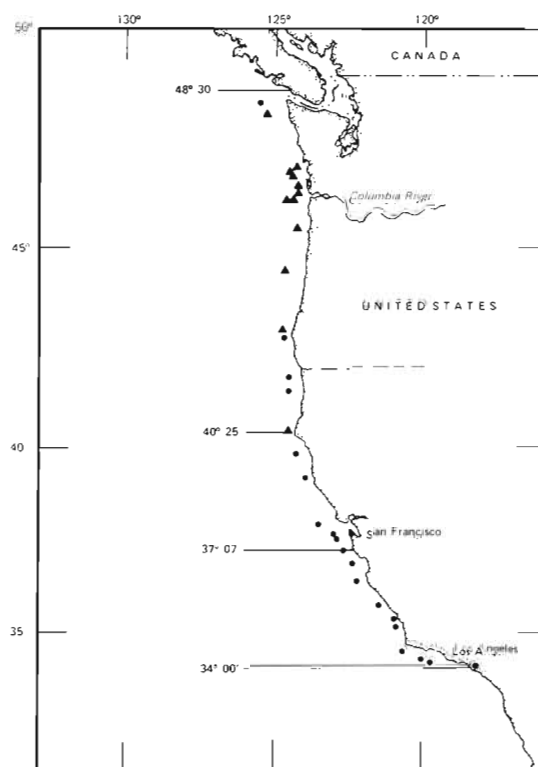


Fig. 1. *Sebastes diploproa* (circles) and *S. pinniger* (triangles). Geographic distribution of otolith collections from the 1977 Rockfish Survey. The boundaries for the three geographic areas for growth comparison of *S. diploproa* are indicated

every alternative model M_n , sums of squares of deviations D_n from a least squares fit of the relevant data are determined; the appropriate model is that with the lowest D_n (Kappenman, in prep.).

RESULTS

Sebastes diploproa

Otoliths were collected from 1075 males and 751 females from 34°06' to 48°06'N latitude. Based upon the distribution of samples, arbitrary latitudinal boundaries provided three geographic areas for growth comparison (34°00' to 37°06'N; 37°07' to 40°25'N; and 40°26' to 48°30'N; Fig. 1). Numbers of specimens, mean length, and standard deviation of mean length are given for each age by sex and geographic area in Table 1. For both sexes, mean sizes increased to the north, but this was primarily due to increased numbers of juveniles and fewer large specimens in the southern collections.

Growth curves for males and females show more rapid growth in the north (Fig. 2). Among the weighted sums of squares of deviations for the five alternative

models (Table 2), D_5 is clearly the lowest for both males and females. Thus the selected model is M_5 , three different growth curves, indicating a cline of increasing growth to the north (Fig. 2, Table 1). For comparison by sex, D_2 was lowest, suggesting acceptance of M_2 and different growth between sexes in all geographic areas (Table 2). Females and males show similar growth rates through ages 9 to 11, after which females grow more rapidly than males (Table 1).

Weighted least squares estimates of Bertalanffy parameters are presented in Table 3 for the present study and also from Phillips (1964) and Westrheim and Harling (1975). Parameter values, growth curves, and maximum ages from the northern geographic area compare favorably with those of Westrheim and Harling (1975); in the southern geographic area, however, the values reported in Phillips (1964) differ greatly. Westrheim and Harling (1975) determined age from otoliths (as in the present study), whereas Phillips (1964) used scales, fewer specimens, and back calculations. For slow growing, long-lived species such as *Sebastes diploproa*, scale annuli may become indistinct near the margin, making age determination of large, older individuals difficult. Westrheim and Harling (1973) compared scale and otolith age determina-

Table 1. *Sebastes diploproa*. Numbers of otoliths (N), mean lengths-at-age (L), and standard deviation of mean length-at-age (s) for males and females from three geographic areas

Age (years)	34°00' to 37°06'						37°07' to 40°25'						40°26' to 48°30'					
	Males			Females			Males			Females			Males			Females		
	N	L	s	N	L	s	N	L	s	N	L	s	N	L	s	N	L	s
1	10	8.7	0.7	6	9.3	0.8	0	-	-	0	-	-	0	-	-	0	-	-
2	23	10.8	1.0	26	10.3	1.0	0	-	-	0	-	-	1	16.0	0.0	0	-	-
3	36	12.7	1.1	33	12.9	1.3	2	15.5	2.1	1	16.0	0.0	9	16.2	0.4	9	17.1	0.8
4	19	14.4	1.3	11	13.6	1.3	2	18.0	0.0	6	16.5	0.6	8	18.5	1.5	13	17.8	1.2
5	7	17.3	1.7	5	14.4	1.3	9	18.6	1.5	14	18.9	1.3	17	20.2	1.3	11	20.3	1.4
6	19	17.0	1.9	9	16.7	1.9	18	20.3	1.5	18	19.8	1.2	10	21.0	0.7	10	21.8	1.0
7	15	18.5	2.3	10	19.9	2.8	17	21.4	1.4	15	21.3	0.7	10	21.6	0.8	9	24.1	2.0
8	14	20.8	2.1	9	21.6	1.9	17	22.1	1.9	9	22.1	0.9	4	24.0	0.8	7	24.9	1.3
9	5	22.8	1.5	9	22.3	0.9	18	23.0	1.6	15	24.0	1.1	15	26.1	1.3	5	25.4	1.7
10	17	23.1	1.1	13	22.6	1.1	14	23.4	1.7	14	25.1	1.0	15	26.2	1.2	13	27.1	1.0
11	19	23.1	1.1	15	24.0	1.3	18	24.4	1.0	10	25.4	1.3	10	26.9	1.5	9	27.4	1.5
12	17	24.4	1.3	15	24.7	1.7	21	24.8	1.6	8	26.5	2.0	19	26.6	1.3	5	27.4	1.1
13	33	24.9	1.2	12	25.8	1.7	26	25.7	1.0	6	26.2	1.7	17	27.7	1.4	5	29.8	1.6
14	50	25.1	1.3	26	26.2	1.2	24	26.3	1.5	4	27.8	1.0	20	28.3	1.7	5	30.0	1.6
15	43	26.0	1.4	32	27.2	1.6	35	26.5	1.5	8	28.9	1.6	16	28.4	2.0	13	29.6	1.9
16	28	26.1	1.0	33	27.4	1.5	25	27.1	1.1	7	29.1	1.2	21	29.2	1.7	5	32.0	1.2
17	25	26.7	1.1	45	28.2	1.4	29	27.3	1.4	9	30.0	1.2	29	30.1	1.6	8	32.6	1.3
18	19	26.8	1.4	25	28.4	1.2	18	28.3	1.5	11	29.7	1.1	15	30.2	1.5	17	33.6	3.2
19	12	27.2	2.2	23	29.4	1.5	14	28.6	1.3	6	29.8	1.8	10	30.0	2.0	5	31.4	1.8
20	8	28.0	1.2	18	29.9	1.7	7	29.0	1.6	6	30.0	1.7	15	31.5	2.1	6	34.3	2.2
21	8	27.8	2.1	11	30.6	0.9	6	28.8	1.0	4	31.0	1.2	12	31.5	1.7	8	34.9	2.2
22	2	27.5	2.1	7	30.4	1.0	6	30.3	1.5	2	30.5	2.1	4	32.5	0.6	9	34.3	1.9
23	1	27.0	-	3	30.7	0.6	5	31.4	0.9	2	34.5	2.1	12	31.6	1.2	3	35.3	1.5
24	0	-	-	2	31.0	1.4	3	32.6	0.6	0	-	0.0	5	32.6	1.5	4	34.8	1.0
25	0	-	-	1	33.0	0.0	3	31.0	1.0	2	32.5	0.7	8	31.9	1.2	3	35.0	2.0
26+	0	-	-	0	-	-	2	30.0	1.4	1	35.0	0.0	4	32.5	0.6	2	36.0	2.9

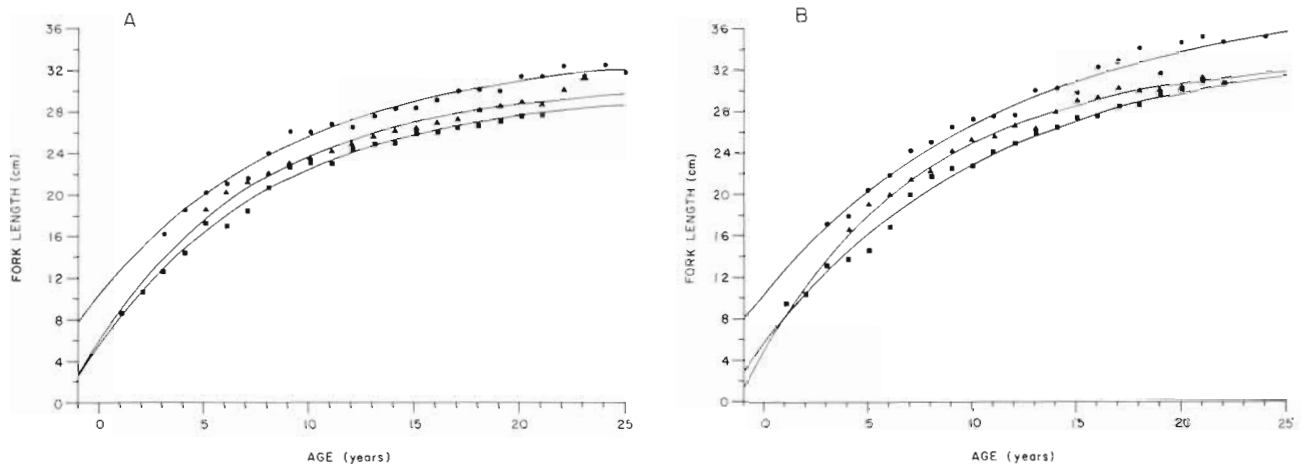


Fig. 2. *Sebastes diploproa*. Fitted growth curves and mean lengths-at-age from the three geographic areas (Fig. 1); only mean lengths represented by four or more observations are shown. A: Males; B: Females. Squares: southern geographic area; triangles: central geographic area; circles: northern geographic area

tions from the same specimens of *S. alutus*; ages determined from otoliths were greater than those from scales in 53 %, equal in 40 %, and less in 7 %. More importantly, the positive deviations of otolith ages increased with increasing age, reaching 8 years for an individual 21 years old (as determined by the otolith). If this is indeed the case in the data of Phillips (1964), the use of backcalculated values in determining growth could cause positive bias in the estimates of younger age groups as well as underestimating maximum ages (Maraldo and MacCrimmon, 1979).

Sebastes pinniger

Rockfish Survey and California Fish and Game collections provided otoliths from 817 males and 557 females. *Sebastes pinniger* has a more restricted geographic range of significant abundance than does *S. diploproa* (Gunderson and Sample, 1980) and the otolith collections were distributed accordingly. Two geographic areas were arbitrarily chosen based upon the numbers of otoliths; the southern area was bounded by 37°06' to 45°00'N latitude, the northern

Table 2. *Sebastes pinniger* and *S. diploproa*. Weighted sums of squares of deviations D_n for the alternative models M_n for growth comparisons. In two-way comparisons, the models are as follows: in M_1 the two growth curves are the same; in M_2 , they are different. For three-way comparisons, the models are represented by: M_1 , all populations characterized by the same growth curve; M_2 , the first two populations are the same but differ from the third; M_3 , the second and third populations are the same but differ from the first; M_4 , the first and third populations are the same but differ from the second; and M_5 , all three populations are represented by separate growth curves

Geographic comparisons			
<i>S. pinniger</i>			
	Males	Females	
D_1	80641.11	60850.58	
D_2	81670.28	78620.91	
<i>S. diploproa</i>			
	Males	Females	
D_1	245863.11	236511.82	
D_2	69043.96	70140.07	
D_3	132140.12	104965.25	
D_4	256451.21	249520.64	
D_5	39632.05	38256.91	
Comparisons by sex			
<i>S. pinniger</i>			
	37°06' to 45°00'	45°01' to 48°30'	
D_1	155585.54	207016.85	
D_2	68895.18	91396.02	
<i>S. diploproa</i>			
	34°00' to 37°06'	37°07' to 40°25'	40°26' to 48°30'
D_1	49141.17	53936.97	60856.98
D_2	20075.51	35095.92	22717.53

area by 45°01' to 48°30'N latitude. Age-length data for males and females in the two areas are presented in Table 4. Within sexes, mean lengths at age for older specimens are slightly greater in the north. For both males and females, however, the weighted sum of squares of deviations was lower for M_1 (Table 2), suggesting acceptance of a single growth curve and therefore lack of latitudinal differences in growth. As in *S. diploproa*, however, analysis of differences by sex suggests acceptance of M_2 , different growth curves by sex (Table 2); females grow faster than males (Table 4, Fig. 3). Growth between sexes is similar through age 11,

after which mean lengths of females are greater than those of males at a given age.

Weighted least squares estimates of Bertalanffy parameters for males and females of *Sebastes pinniger* (geographic areas combined) are presented in Table 5 with comparative values from Phillips (1964), Six and Horton (1977), and Westrheim and Harling (1975). Most of the individuals examined in the present study were collected in the area offshore from the Columbia River (Fig. 1), a geographic area similar to the areas of collections of Six and Horton (1977). Age determinations and resulting growth curves from the two studies

Table 3. *Sebastes diploproa*. Bertalanffy-parameter estimates. TL: total length; FL: fork length. Areas in the present study are (1) 34°00' to 37°06'N, (2) 37°07' to 40°25'N, (3) 40°26' to 48°30'N. N: number of individuals. The number in parentheses for Phillips (1964) represents the number of observations, including back calculations, taken from the 92 individuals used to fit the growth curve

Study Area	Phillips (1964)	Westrheim & Harling (1975)		Present study					
	California	British Columbia		1		2		3	
Sex	Combined	Males	Females	FL	Males	FL	FL	Females	FL
Measurement	TL	FL	FL	FL	FL	FL	FL	FL	FL
L_{∞} (cm)	41.8	32.7	36.8	30.04	30.58	33.84	34.33	32.95	38.91
k	0.123	0.14	0.10	0.117	0.129	0.105	0.091	0.125	0.084
t_0	-0.408	-0.9	-1.5	-1.76	-1.62	-3.46	-2.01	-1.30	-3.69
Max. age	16	28	28	23	28	29	25	28	30
N	92 (803)	260	245	430	339	306	399	178	174
Predicted length (cm) at age (years)	5: 20.3 10: 30.2 20: 38.4	18.4 25.6 30.9	17.6 25.1 32.5	16.4 22.5 27.7	17.6 23.7 28.7	19.9 25.6 31.0	16.2 22.8 29.7	18.0 24.9 30.7	20.2 26.6 33.6

Table 4. *Sebastes pinniger*. Numbers of otoliths (N), mean lengths-at-age (L), and standard deviation of length-at-age (s) for males and females from two geographic areas

Age (years)	N	37°06' to 45°00'			45°01' to 48°30'		
		Males	Females		Males	Females	
		N	L	s	N	L	s
3	0	—	—	—	0	—	—
4	3	25.8	2.3		8	27.3	1.9
5	6	30.5	4.0		8	31.1	3.0
6	10	31.9	2.3		8	32.2	2.9
7	6	36.6	2.4		8	35.8	3.1
8	7	41.6	2.6		7	39.8	3.0
9	27	44.1	2.0		17	43.2	3.3
10	37	46.0	2.4		18	46.7	2.8
11	25	47.7	2.7		14	49.5	2.3
12	27	48.4	3.4		22	51.7	2.4
13	29	48.5	3.2		25	52.1	3.1
14	29	50.3	1.7		27	53.9	2.5
15	12	50.5	2.4		17	55.4	1.7
16	13	51.7	2.7		4	55.7	1.9
17	10	51.7	2.5		8	54.6	2.4
18	4	51.5	1.8		6	56.7	1.9
19	2	52.5	0.7		1	58.6	—
20	1	48.0	—		2	59.5	3.1
21	0	—	—		0	—	—

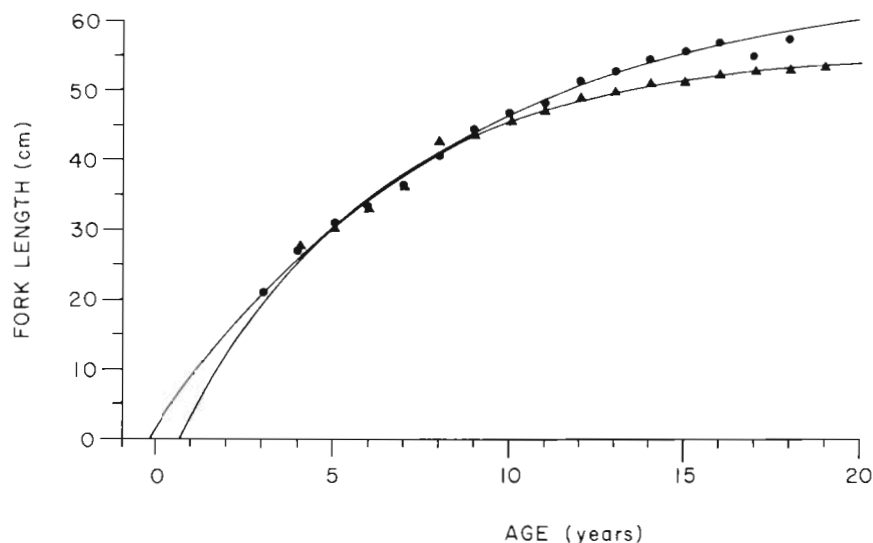


Fig. 3. *Sebastes pinniger*. Fitted growth curves and mean lengths-at-age for combined collections of males (triangles) and females (circles). Only mean lengths represented by four or more observations are shown

are similar (Table 5). The values of Westrheim and Harling (1975) suggest lower mean lengths at age, but the numbers of age determinations are relatively low. The data from Phillips (1964) are similar, considering that he measured total length rather than fork length and combined both sexes. Age determination with scales is probably appropriate for this species; Six and Horton (1977) showed a close correspondence of age determined from scales and otoliths from the same specimens but greater consistency between readers for otoliths than scales.

DISCUSSION

Westrheim and Harling (1975) studied growth of northern and southern collections of 8 species of *Sebastes* through comparison of predicted lengths at ages of 10 and 20 years. Individuals of *S. babcocki* and *S. zacentrus* had greater predicted lengths in British

Columbia than in Alaska, indicating faster growth in the south, whereas no difference was apparent for *S. aleutianus*. Westrheim and Harling (1975) compared their data from British Columbia with that of Phillips (1964) from California, and suggested faster growth in southern populations of 5 rockfish (*S. crameri*, *S. diploproa*, *S. entomelas*, *S. flavidus*, and *S. pinniger*). A similar latitudinal cline was demonstrated for *S. alutus* by Westrheim (1973).

Contrary to these comparisons, we observed no differences in growth with latitude for *Sebastes pinniger* and faster growth in the northern collections for *S. diploproa* (Figs 2 and 3, Table 2). These results suggest caution in comparing age and growth determined by different investigators, particularly in species for which age determination has not been validated. For both *S. diploproa* and *S. pinniger*, females grew faster than males (Fig. 3, Table 2); this is in agreement with past observations on the following rockfish: *S. alutus* (Westrheim, 1973), *S. marinus* (Kelly and Wolf, 1959),

Table 5. *Sebastes pinniger*. Bertalanffy-parameter estimates. Abbreviations as in Table 3

Study Area	Phillips (1964) California	Six and Horton (1977) Oregon		Westrheim & Harling (1975) British Columbia		Present study 37° 06' to 48° 30'	
Sex	Combined	Males	Females	Males	Females	Males	Females
Measurement	TL	FL	FL	FL	FL	FL	FL
L_{∞} (cm)	65.5	53.60	60.95	51.8	56.9	55.72	66.11
k	0.122	0.189	0.146	0.16	0.15	0.178	0.118
t_0	-0.402	0.681	0.537	0.5	0.9	0.595	-0.240
Max. age	18	20	21	26	26	20	20
N	143 (1285)	not stated		61	24	817	557
Predicted length (cm) at age:							
5:	31.6	29.9	29.2	26.6	26.1	30.3	30.5
10:	47.1	44.4	45.6	40.5	42.4	45.3	46.4
20:	60.1	52.2	57.4	49.5	53.7	54.0	60.0

S. pinniger, *S. flavidus*, and *S. melanops* (Six and Horton, 1977), among others. The greatest differences in growth between sexes is attained after the age and size of sexual maturity (Phillips, 1964; Gunderson et al., 1980).

We will consider three possible explanations for the observed trend in growth for *Sebastes diploproa*. The first is an immediate response at the individual level based upon the physiological effects of environmental parameters. The second is a short-term response at the population level based upon density-dependent regulation. The third is a long-term response but density-independent, since it involves genetic differences and evolutionary responses at the population level. We consider the evidence for each explanation below.

Analysis of physiological differences in growth must consider the immediate effects of physical factors which vary over the latitudinal range of the species. The depth of maximum biomass for *Sebastes diploproa* is approximately 300 m (Gunderson and Sample, 1980); over the latitudinal range of this species, the important parameters at this depth are temperature and dissolved oxygen. At 300 m, as one proceeds between 34°00' and 48°00'N latitude, mean temperature decreases from 7.3 ° to 6.2 °C, and mean dissolved oxygen increases from 1.40 to 1.85 ml l⁻¹; seasonal variations are approximately 0.3 °C and 0.1 ml l⁻¹ (Chingin and Halminski, 1974). Higher temperatures usually result in an increase in the rate of growth (Bertalanffy's *k*) but a decrease in maximum predicted size (*L*_∞) (Beverton and Holt, 1959). Mean size and maximum size of *S. diploproa* increase with depth and latitude in accordance with the decreased temperature (Boehlert, 1980). Reduced dissolved oxygen may decrease growth (Stewart et al., 1967). The interplay between temperature and dissolved oxygen may be important here, however, as levels of dissolved oxygen critical for growth are inversely related to temperature (Doudoroff and Shumway, 1970); unfortunately, the oxygen requirements of *S. diploproa* are unknown. In general, these physical differences would not appear sufficient to cause the observed latitudinal differences in growth in *S. diploproa*; indeed, based upon the direction of change, one would expect increased growth in the southern rather than the northern areas, as observed for *S. alutus* by Westrheim (1973).

Another factor which affects growth is food availability. *Sebastes diploproa* feeds almost exclusively on euphausiids (Phillips, 1964). Unfortunately no information is available on biomass and availability of euphausiids over the geographic range of *S. diploproa*; density-dependent mechanisms, however, may implicate food availability indirectly in the observed trend of growth. For *S. diploproa*, there has been no directed fishery in the southern part of its range since the early

1960's (Heimann, 1963), although it has been taken incidentally in the animal food fishery (Nitsos and Reed, 1965). Data from the 1977 Rockfish Survey (Gunderson and Sample, 1980) show the maximum biomass of *S. diploproa* in the two southernmost areas for growth analysis in the present study. In the northern part of its range no directed fishery exists for *S. diploproa*; it is, however, the species most closely associated with catches of *S. alutus* (Alverson and Westrheim, 1961), and stocks of *S. alutus* in the north-eastern Pacific have declined drastically due to over-fishing (Gunderson, 1977). Large-scale removals of *S. diploproa* as incidental catch (recorded as 'other rockfish') are likely. Although biomass data on northern *S. diploproa* previous to 1977 are unavailable, the length frequencies from the 1977 Rockfish Survey (Boehlert, 1980), as compared to those from Alverson et al. (1964), show a dramatic decrease in mean size and size distribution in recent data, indicative of probable stock reduction (Boehlert, 1980). The reduction of stocks of *S. alutus* has been suggested as a factor in the southward extension of the ranges of northern species of *Sebastes* and the walleye pollock, *Theragra chalcogramma* (Snytko and Federov, 1974). Density-dependent regulation of fish populations in the adult stage is generally restricted to changes in growth (Jones, 1973); for example, Margetts and Holt (1948) observed increased density and decreased individual growth in plaice (*Pleuronectes platessa*) during cessation of the fishery in 1939 to 1945, but decreased density and increased individual growth after fishing resumed. Some evidence therefore exists for the hypothesis that the increased growth in the northern part of the range of *S. diploproa* is the result of density-dependent regulation of growth.

The final explanation is based upon latitudinal variation in life-history strategy and thus requires the assumption of reproductive isolation of sub-populations of *Sebastes diploproa*. Many species with latitudinal variations in life history spawn in restricted areas; the variations may be related to population structure. Leggett and Carscadden (1978) observed faster growth, decreased relative fecundity, and increasing proportions of repeat spawners with increasing latitude in populations of the American shad *Alosa sapidissima*, which exist in reproductively isolated populations. Similarly, mean size of spawner in anadromous steelhead *Salmo gairdneri* increases with increasing latitude (Withler, 1966). Genetic differences and reproductive isolation have been suggested for some species of *Sebastes*. Three subpopulations of *S. alutus* (Gulf of Alaska, Prince William Sound, and Oregon-British Columbia) exist in the northern Pacific (Wishard et al., 1980); it appears that the latitudinal growth differences observed by Westrheim (1973) are

associated with subpopulation structure. Westrheim (1973) further noted bathymetric variations in growth rate in the same areas and later suggested reproductive differences between shallow and deep populations (Westrheim, 1975). Preliminary electrophoretic evidence suggests that two subpopulations of *S. piniger* may exist (Wishard et al., 1980), but no corresponding differences in growth rate were detected for this species. Tsuyuki et al. (1968) demonstrated two electrophoretic hemoglobin variants in *S. diploproa*, but could not associate these patterns with geographic or bathymetric distribution. The geographic extent of their samples, however, corresponded only to the northern, fastest growing segment of the population in the present study.

Although *Sebastes* species are ovoviviparous, larvae are pelagic (Ahlstrom 1961) and may have extended pelagic periods lasting up to a year (Boehlert, 1977; Moser and Ahlstrom, 1978). Although subpopulations may be mixed during the pelagic phase, it has been suggested that localized eddies of the California current may alter recruitment patterns of certain species (Love and Larsen, 1978). Furthermore, Gunderson (1972) demonstrated that *S. alutus* forms aggregations with different biological characteristics, and Carlson and Haight (1972) provided evidence for homing behavior in *S. flavidus*; it is thus plausible that even stocks mixed during the pelagic stage may return to separate reproductive populations later in the life history.

Habitats with differing environmental stability may select for reproductive strategies and, therefore, differential partitioning of energy to reproduction and growth. Where reproductive success is unpredictable from year to year, species may exhibit either iteroparity or increased fecundity, often at the expense of somatic growth (Murphy, 1968; Charnov and Schaffer, 1973; Schaffer and Elson, 1975). Variations in reproductive strategy are observed within species characterized by wide latitudinal or bathymetric distributions. We have already referred to the case of the American shad (Leggett and Carscadden, 1978) and the steelhead (Withler, 1966), both anadromous species with wide latitudinal ranges. The trend in principal parturition season for *Sebastes diploproa* is towards a shorter and later season as one proceeds northward (Boehlert, 1977), although some variations have been observed (Westrheim, 1975). In the population south of Point Conception, there is apparently year-round spawning (Boehlert, unpublished). Fecundity of *Sebastes* spp. is generally related to weight (Gunderson et al., 1980) and no latitudinal trends have been documented within species. Multiple spawning, however, which may increase realized yearly fecundity occurs in several southern species (Moser, 1967; MacGregor, 1970).

Increased reproductive effort in the southern part of the range of *S. diploproa* may, therefore, bear some relationship to the decreased somatic growth reported in the present study.

Serious consideration of this latter hypothesis requires some factor making reproductive success less predictable in the south than in the north. Physical conditions in the adult habitat show little variation, as discussed earlier. In the pelagic larval habitat, however, oceanographic conditions over the latitudinal range may affect survival and recruitment differentially. Parrish (1977) predicted that species spawning between Point Conception (34°16'N) and Cape Mendocino (40°25'N) would suffer large scale losses of epipelagic eggs and larvae due to initial offshore Ekman transport and subsequent southerly transport in the California current. Ekman transport in this region is generally offshore during the spawning season of this species but is variable from year to year (Bakun, 1975). North of Cape Mendocino, however, offshore Ekman transport is less pronounced (Bakun, 1975) and off Washington geostrophic flow may bring epipelagic eggs and larvae towards shore (Parrish, 1977). Thus if genetic differences and reproductive isolation exist for *Sebastes diploproa*, we would suggest that Cape Mendocino would be the breakpoint between northern and southern populations; this corresponds to the boundary between the central and northern populations in the present study. It is significant in this regard that model M_2 in the present study has the second lowest sum of squares (D_2) for both male and female geographic comparisons (Table 2); this model predicts that the southern and central populations are represented by a single growth curve but differ from the northern population in growth characteristics.

The alternative hypotheses posed above relate to different time scales of population response. The first is based upon the short term response to differential fishing mortality over the range of the species. Differences in growth are, therefore, a simple density-dependent mechanism. The second hypothesis is based upon density-independent, evolutionary responses at the population level; it follows theoretical predictions of live history patterns in response to environmental predictability (Murphy, 1968). Testing these alternative hypotheses will require a cessation of the fishery in the north and analysis of genetic population differences over the range. The first hypothesis would be supported if growth decreased in the north as density increased and if no genetic differences are apparent. If, on the other hand, increased density did not alter the growth pattern and genetic differences are observed, the latter hypothesis would be supported. Data available on growth in the present study and biomass in 1977 (Gunderson and Sample, 1980) will

provide comparative data for future studies as the stocks of *Sebastes alutus* and presumably *S. diploproa* are allowed to recover.

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