

NOTES

THE EFFECTS OF PHOTOPERIOD AND TEMPERATURE ON LABORATORY GROWTH OF JUVENILE *SEBASTES DIPLOPROA* AND A COMPARISON WITH GROWTH IN THE FIELD

Growth rates of fishes may act as sensitive indicators of environmental conditions. Variations in food supply, temperature, photoperiod, and other physical and biotic conditions may be reflected in the pattern of growth in a given species, yet the effect may vary depending upon the ontogenetic stage studied. Young stages, for example, generally tolerate and prefer higher temperatures than adults, both in the laboratory (Ferguson 1958; McCauley and Read 1973) and in the field (Brandt 1980); thermal optima for growth may similarly be higher. The present study examines the effects of temperature and photoperiod on growth rate in juveniles of the splitnose rockfish, *Sebastes diploproa*, in the laboratory and compares these growth rates with growth in the field. Adults of this species are benthic at depths of 200-500 m in the northeastern Pacific Ocean. *Sebastes* larvae are pelagic (Ahlstrom 1961), and prejuveniles of this species remain pelagic for about 1 yr, reaching maximum sizes near 55 mm standard length (SL) prior to migrating to the benthic habitat (Boehlert 1977). The thermal regime of the surface waters (13°-22° C) differs greatly from that in the adult habitat (6°-8° C; Reid et al. 1958), suggesting that temperature is an important factor in the life history of this species.

Materials and Methods

Prejuveniles were collected from under drifting kelp by dip net 8-18 km offshore from San Diego, Calif. (lat. 32°52' N, long. 117°20' W), and brought to the laboratory. Animals were initially maintained under ambient temperature and photoperiod, but these were changed at 0.5° C and 15 min/d, respectively, until reaching the two photoperiods and three temperatures of acclimation (12 light:12 dark, 16L:8D; 10°, 15°, and 20° C). Fish for the 12L:12D experiments were collected 17 March 1976 at 15.5° C; those for the 16L:8D experiments were collected 14 and 21 May 1976 at 17.7° and

17.6° C, respectively. When acclimation conditions were reached, standard lengths of all fish in each treatment were recorded. During the experiments fish were fed to satiation once daily on a mixture of Trout Chow,¹ ground squid, and frozen brine shrimp. An average of 26 fish were used for each experiment; the range of initial lengths was 30-55 mm SL.

Individual fish were not marked or tagged; individual growth rates were estimated by assuming that rank of individuals in length did not change during the experiment. This allowed determination of the size dependence of growth rate, subject to some unmeasured error if rank of individuals changed enough to affect estimated growth rate. These data were fit by photoperiod to quadratic response surface models using stepwise multiple regression (Nie et al. 1975) in the form

$$G = a + b_1L_i + b_2T + b_{11}L_i^2 + b_{22}T^2 + b_{12}L_iT$$

where G = growth rate (millimeters standard length per day), L_i = initial standard length (millimeters), T = temperature of acclimation (degrees Celsius), a = constant, and b_n = regression coefficients.

To compare the growth rates measured in the laboratory with growth of fish in the field, several specimens were collected for analysis of age using daily growth increments on the otoliths. Fish collected for age determination were taken to the laboratory alive where the otoliths were removed and stored dry in vials. Otoliths were processed for age determination as described in Taubert and Coble (1977). Briefly, otoliths (sagittae) were placed on slides with histological mounting medium and ground in sagittal sections. Small otoliths were ground on only one side whereas otoliths from fish >25 mm SL were removed from the slide, remounted, and ground on the other side. After the final grinding cover slips were placed over the otoliths. Each otolith was assigned a random number and read three times at least a week apart at 800 to 1,000 magnifications. If the range of three independent readings was not within 10% of the mean, the otolith readings were rejected.

Results

Mean laboratory growth rates were dependent upon temperature and photoperiod (Table 1). Comparison of mean daily growth rates, however, is confounded by the effects of initial length. At 16L:8D, growth rate was positively correlated with initial length at 10° C ($r = 0.78$) but negatively correlated at both 15° and 20° C ($r = -0.99$ in both cases, Figure 1A). At 12L:12D, growth rates were negatively correlated with initial length at 10° C ($r = -0.97$) and at 15° C ($r = -0.94$) but positively correlated with initial length at 20° C ($r = 0.42$, Figure 1B). In the latter experiment, however, the length range was not as complete as in the other experiments (Table 1).

The relationship of growth to temperature and initial length are more easily interpreted with the multiple regression models. Regression coeffi-

cients for the growth response models were all significant with the exception of the length squared term (Table 2). Effects of temperature were similar at both photoperiods; growth increased to some optimum temperature and then declined (Figure 2A, B), as indicated by the negative value of the regression coefficient for temperature squared, b_{22} (Table 2). The apparent temperatures of optimum growth increased slightly with length at 12L:12D but decreased with length at 16L:8D (Figure 2A, B). Initial length showed a clear relationship with growth at 12L:12D (Figure 2B). At all temperatures, growth decreased with increasing length; zero growth, observed in the 10° C experiment at the largest sizes (Table 1), is predicted by the model at sizes >50 mm SL within the range of temperatures studied. At 16L:8D, the growth response to initial length is more complex. At approximately 10.5° C the model predicts a

TABLE 1.—Length-frequency distributions at the start and end of the growth experiments for laboratory acclimated prejuvenile *Sebastes diploproa* at two photoperiods and three temperatures. N = number of fish in the experiment, \bar{X} = mean standard length (millimeters), Δ = change in the sum of lengths (millimeters) between start and end of each experiment, t = duration of the experiment in days.

SL (mm)	12L:12D						16L:8D					
	10°		15°		20°		10°		15°		20°	
	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End
30	1		4		2		1		2			
31	2		3		1		1		1		1	
32	2		4		2						1	
33	4		5		3							
34	4		4		2							3
35	4		4	1	6	1	3		3			
36	3		2		3	2		1	1			
37					3	2						
38	3				4	4		1				
39	2	3		1	1	3						
40	3	3		2		6						3
41	1	7	2		1	2		2	1			
42	2	4		7		2	1		1			1
43	1	6		4		2	1	1				1
44	1	3	1	5		1	3					
45				5		2	1			1		
46		6	1	1			4		2	1		3
47				2		1	2		2	2		2
48			1	1			1		2			4
49		1		1			1	1	2	1		1
50	1						1	2	2	2	2	2
51	2	3		1					2			3
52			1				2		1		2	3
53							1			1		3
54	1			1			2				1	1
55	1	2					2		1			2
56							1		2			1
57							2		1			
58							1		3			
59									2			
60							1		3			
N	38	38	32	32	28	28	20	20	20	20	20	20
\bar{X}	38.3	43.9	35.2	44.0	35.1	40.1	42.7	50.6	42.8	54.2	44.8	49.7
Δ	213		281		140		158		228		97	
t	54		54		53		53		54		51	
Growth (mm/d)	.105		.164		.093		.150		.211		.096	

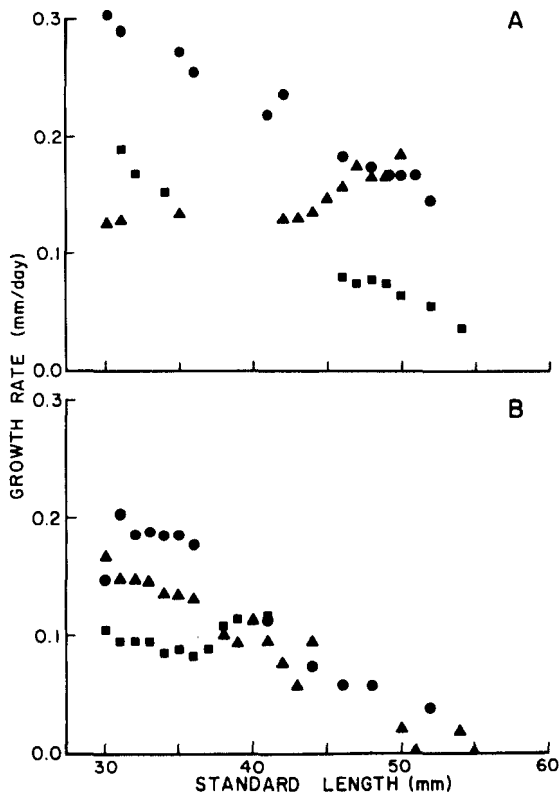


FIGURE 1.—Relationship of initial fish length with measured growth rates during A) 16L:8D experiments, B) 12L:12D experiments. Triangles represent values for fish acclimated to 10° C; dots, 15° C; squares, 20° C.

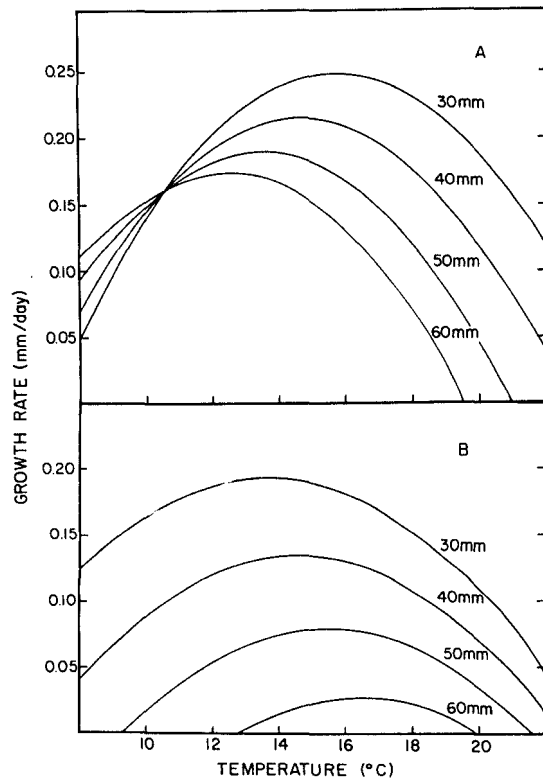


FIGURE 2.—Growth response surfaces for given isopleths of initial standard length as predicted by the multiple regression models. A) 16L:8D experiments, B) 12L:12D experiments.

nodal point where fish of all initial lengths are characterized by the same growth rate (Figure 2A). Below that temperature, growth increases with increasing length, whereas at higher temperatures, it decreases with increasing length. The response of growth to photoperiod indicates a generally positive relationship (Figure 2A, B), with faster growth under most conditions at 16L:8D. Growth with length at all temperatures at

TABLE 2.—Coefficients and related statistics for the growth response models for laboratory growth in *Sebastes diploproa*. Multiple correlation coefficients (R) were 0.919 and 0.933 for 12L:12D and 16L:8D, respectively.

Item	12L:12D (N = 98)			16L:8D (N = 60)		
	Value	SE	P	Value	SE	P
a	0.1378	0.0729	0.062	-0.8090	0.0919	0.001
b ₁	-0.0112	.0016	.001	.0080	.0018	.001
b ₂	.0459	.0073	.001	.1264	.0087	.001
b ₂₂	-.0021	.0002	.001	-.0033	.0003	.001
b ₁₂	.0004	.0001	.003	-.0007	.0001	.001

12L:12D and at higher temperatures at 16L:8D decreases with length, suggesting a temperature-dependent asymptote for growth. For low temperatures at 16L:8D, however, growth increases with length and no asymptote is apparent.

Growth of fish collected in the field was determined from daily growth increments. Otoliths from 53 specimens were processed as described. Due to broken or unclear otoliths, loss of material from the margin during grinding, or failure to meet the criterion of consistency in age from the three readings, 21 ages were determined. These 21 fish were collected in April (6), August (2), September (3), October (1), and December (9) from 1973 through 1978. Thus a variety of surface temperatures and thermal histories were experienced by these fish. Fish ranged from 9.0 to 42.7 mm SL; the age ranged from 43 to 205 d. The resultant pattern of growth in the field was linear over the size range studied (Figure 3). The growth rates for these specimens, averaged over the

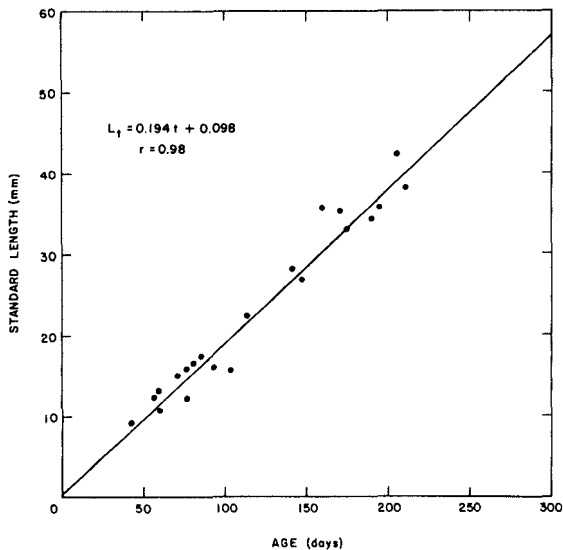


FIGURE 3.—Age at length for field-captured prejuvenile *Sebastes diploproa* as determined by analysis of daily growth increments on otoliths. L_t = length at time t (days).

lifetime of each fish, ranged from 0.154 to 0.225 mm SL/d, with the mean value indicated by the slope of the line, 0.194 mm SL/d. These rates were similar to predicted laboratory growth rates under a variety of temperature and initial length conditions at 16L:8D (Figure 2A) but only to the smallest fish between 10° and 18° C at 12L:12D (Figure 2B). *Sebastes diploproa* apparently grows more slowly in the field than pelagic juvenile *S. melanostomus* of similar size, the only other species of *Sebastes* whose growth has been estimated using daily growth increments (Moser and Ahlstrom 1978).

Discussion

Fish growth generally reaches a maximum at some optimum temperature and decreases at temperatures above and below this level (Brown 1957; Brett 1979), approaching zero near lethal temperatures. Upper lethal temperatures (critical thermal maxima) for prejuvenile *S. diploproa* range from 26° to 30° C, depending upon the temperature of acclimation (Boehlert 1981), and prejuveniles tolerate surface temperatures up to 23° C. The optimum temperature for growth of juvenile *S. diploproa* depends upon both photoperiod and fish length. The growth models suggest optimum temperatures for growth which increase

with length at 12L:12D from 13.8° C at 30 mm SL to 15.7° C at 50 mm SL (Figure 2B) and decrease with length at 16L:8D from 16.0° C at 30 mm to 13.8° C at 50 mm SL (Figure 2A). These temperatures clearly exceed those experienced by later benthic juveniles and adults.

Longer photoperiod enhanced growth at nearly all conditions of fish length and temperature (Table 1; Figures 1, 2). Increased growth with longer photoperiod has been observed in green sunfish (Gross et al. 1965), plaice and sole (Fonds 1979), and Baltic salmon parr (Lundqvist 1980). Brown (1946b), however, observed lower growth rate of brown trout in long photoperiods. As the fish in the present experiments were fed to satiation only once daily, it is reasonable to assume that rations under both photoperiods were similar. Surface prejuvenile *S. diploproa* acclimated to short photoperiods have greater standard metabolic rates than those acclimated to long photoperiods at the same acclimation temperatures (Boehlert 1978). Thus the enhanced growth in the longer photoperiod may be related to a greater scope for growth (Elliot 1976) due to lower standard metabolic rates.

The dependence of growth on fish size in the present study is interesting in relation to the life history of this species. Other investigators have observed both increases and decreases in the size range of fishes at the beginning and end of growth experiments. Brown (1946a) described the "size hierarchy effect," which apparently results from development of a peck order with larger fish dominant (Stringer and Hoar 1955). No dominance or peck order with respect to feeding was apparent in the experiments with *S. diploproa*, and in four of six experiments, growth rate decreased with increasing size (Figure 1), as is predicted by the growth models (Figure 2). Laboratory and field growth rates were similar for fish at approximately the same lengths, but it is uncertain whether the decreased growth apparent with increasing length observed in the laboratory occurs in the field. The largest specimen from the field successfully aged using daily growth increments on the otoliths was 42.7 mm SL, below the size at which significantly decreased growth rates occurred in the laboratory (Figure 1). If an asymptote does exist in the field, it fits well with the largest pelagic prejuvenile captured in the field (59 mm SL; Boehlert 1977) and with the maximum size after growth in the present study (60 mm SL, Table 1).

The parturition season for *S. diploproa* off California is February through July (Phillips 1964), with possible limited year-round spawning (Boehlert 1977). This results in poorly defined year classes and length-frequency distributions, yet a size threshold and distinct season exist for migration from the surface to the benthic habitat (Boehlert 1977, 1978). Zamakhaev (1964) suggested that size discrepancy within an age-group may be minimized through compensatory growth. The observed pattern of reduced growth at sizes >40 mm SL may serve as a variant on the phenomenon of compensatory growth, consolidating the 0-group fish at sizes near 50 mm SL prior to the migration, which occurs from May through September (Boehlert 1978). At the onset of migration, the oldest and largest fish would migrate first, as observed in sockeye salmon (Foerster 1937) and Atlantic salmon (Elson 1957). Smaller fish would continue rapid growth, and as they reached the size threshold, would also migrate.

Initiation of the surface-to-benthic migration of juvenile *S. diploproa* may be dependent upon photoperiod or rate of change of photoperiod subject to an endogenous program which depends upon a size threshold (Boehlert 1978, 1981). The temperature change between surface and benthic habitats is about 12° C, suggesting that temperature is an important consideration in the migration. Although there is no change in critical thermal maximum for juvenile *S. diploproa* acclimated to the same temperature but different photoperiods (Boehlert 1981), prejuveniles from the field are metabolically preadapted for the lower temperatures during the migratory season (Boehlert 1978). The size dependence of growth in the present experiments suggests a downward shift in the temperature of optimum growth with increasing size in 16L:8D but not in 12L:12D. Photoperiod may thus interact with size, resulting in an ontogenetic change in thermal requirements.

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GEORGE W. BOEHLERT

School of Oceanography, Oregon State University
Marine Science Center
Newport, OR 97365

A CORRELATION BETWEEN ANNUAL CATCHES OF DUNGENESS CRAB, *CANCER MAGISTER*, ALONG THE WEST COAST OF NORTH AMERICA AND MEAN ANNUAL SUNSPOT NUMBER

A recent paper by Driver (1978) described the prediction of shrimp landings off northwest England based on sunspot activity. Stimulated by this work, we examined the relationship between the Dungeness crab, *Cancer magister*, commercial fishery off the west coast of North America and mean annual sunspot number. The Dungeness

crab is commercially important and its fluctuating catch has made it the subject of numerous papers (Reed 1969; Peterson 1973; Botsford and Wickham 1975, 1978), some of which noted a distinct rhythm in annual catch. Moreover, Dungeness crab catch statistics are particularly favorable for this study, as it has been estimated that almost every legal crab within the species' range is taken during the commercial season (Pacific Marine Fisheries Commission 1965) and hence there was no need to factor fishing effort into the computations.

Catch statistics were provided by the Pacific Marine Fisheries Commission and comprise commercial landings made in Alaska, British Columbia, Washington, Oregon, and California from 1955 (the earliest year for which complete records were available) to 1980. We utilized the mean annual sunspot values in Waldmeier (1961, 1978) with additional data supplied by Adkins¹ and Eddy.² Data were plotted (Figure 1) and correlation coefficients and associated values generated by linear regression (Table 1) for two complete cycles, 1955-64 and 1965-75.

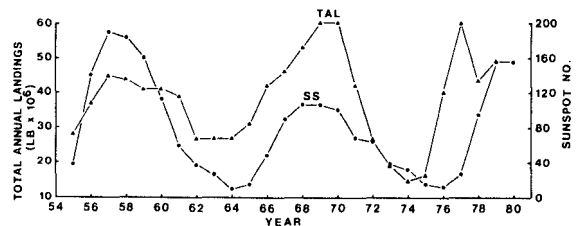


FIGURE 1.—Total annual landings of Dungeness crabs off the west coast of North America (TAL) and mean annual sunspot number (SS) for the period 1955 through 1980.

TABLE 1.—The correlation between commercial Dungeness crab catch and mean annual sunspot number off the west coast of North America.

Period	r	df	t-ratio	P
1955-64	0.90	1, 8	35.3	<0.001
1965-75	.87	1, 9	29.3	<.001

Dungeness crab catches and sunspot numbers both varied in approximately 11-yr cycles and the cycle periods for the two were strongly correlated

¹J. Adkins, Solar Observer, Mt. Wilson and Las Canpanis Observatory, 813 Santa Barbara Street, Pasadena, Calif., pers. commun. August 1980.

²J. Eddy, High Altitude Observatory, National Center for Atmospheric Research, Boulder, CO 80307, pers. commun. March 1981.