

AN ABSTRACT OF THE THESIS OF

Germán E. Pequeño for the degree of Doctor of Philosophy
in Fisheries presented on December 2, 1933

Title: Trophic Adaptations and Relationships of Rock-
fishes (Sebastes spp.) of Oregon

Redacted for Privacy

Abstract approved _____
Dr. Carl E. Bond

A comparative analysis of structures related to capture and processing of food, in 624 specimens belonging to 31 species of Sebastes of Oregon was made. The structures studied were the following: the tooth-bearing bones (premaxillary, dentary, vomer, palatine); the maxillary, angular, articular, parasphenoid and glossohyal bones; the lower limb of the first branchial arch and its gillrakers; the length of the intestine; number of pyloric caeca; and width of orbit.

The mean values calculated formed gradual clines with only minor discontinuities. Overlap of standard deviations and ranges was considerable. Gillrakers showed four types according to the relationship of the length to width, and there is a general relationship of the type to mouth size, and in some, to relative length of intestine. Number and size of spinulae on gillrakers

differ with gillraker type. Species with relatively long intestines have more pyloric caeca than those with short intestines. These are generally species that take a high proportion of crustaceans in the diet. Species with smaller relative eye size are generally planktivores, or are known to be diurnal in habit.

Although a few species have distinctive features or specializations that alone or in simple combination can distinguish them, the overlap in trophic adaptation of the somewhat generalized predators is great. There is a continuum of change from planktiphagous to ichthyophagous, so that the genus as a whole, should be capable of taking advantage of a wide spectrum of prey over a wide latitudinal and considerable bathymetric range. Overlaps in diet must be common, but there is probably sufficient difference in trophic adaptation so that each species would be successful in a particular niche if food were in short supply.

Trophic Adaptations and Relationships
of Rockfishes (Sebastes spp.) of Oregon.

by
Germán E. Pequeño

A THESIS
Submitted to
Oregon State University

in partial fulfillment of
the requirements for the
degree of
Doctor of Philosophy

completed December 2 ,1983
Commencement June ,1984

APPROVED:

Redacted for Privacy

Professor of Fisheries and Wildlife in charge of major

Redacted for Privacy

Head of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

Date thesis is presented December 7, 1983

Typed by Germán Pequeño for Germán Pequeño

ACKNOWLEDGMENTS

There is a long series of people who have directly or indirectly contributed to the realization of this thesis. I want to express my gratitude to all of them, but principally to my major Professor, Dr. Carl E. Bond, whose international reputation first led me to enter Oregon State University. Richard A. Tubb, Head, Department of Fisheries and Wildlife and William Q. Wick, Director, Oregon State University Sea Grant Program, were supportive of my ideas and goals. I am strongly convinced that they, as well as the members of my Graduate Committee represent the best of our academic ideals.

The members of my Graduate Committee have been dedicated, kind and effective in their mission to the best of my expectations. To Drs. Carl E. Bond, Howard F. Horton, Karl J. Nice, William G. Percy and Charles E. Warren my sincere acknowledgments and hopes that they can continue their high level of achievement for the benefit of our society.

Several persons were important in the preparation of this thesis: Alfred Soeldner, Director O.S.U. Scanning Electron Microscopy Facility; Lenora Bond and James Long, from the Dept. of Fisheries and Wildlife; William

H. Barss, Robert Demory and Neil Richmond, from the Oregon Dept. of Fish and Wildlife; and Luis Cid, from the Universidad de Concepcion, Chile (currently Graduate Student at Oregon State University).

I want to thank to the entire Department of Fisheries and Wildlife, for the excellent human environment they provided. This will be always appreciated by student, especially from abroad.

A Fellowship from the Organization of American States (OAS) provided support during my first two years at Oregon State University, and the Oregon State University Sea Grant Program and Agricultural Experiment Station made possible the conclusion of my program. To all of them my deepest and sincere appreciation.

I have to share with my wife, Gloria, any successful results. Her efforts helping me have been outstanding. Failures, undoubtedly, are my responsibility.

TABLE OF CONTENTS

Introduction	1
Methods and materials	6
Geographical origin of the sample	6
Size of the specimens	6
Measurements and counts	6
Preservation	11
Scanning electron microscopy procedures	13
Use of multivariate analysis techniques	15
Results	20
Study of selected bones	20
Premaxillary	20
Maxillary	30
Maxillary + premaxillary unit	35
Dentary-articular-angular unit	40
Vomer	43
Palatine	54
Pharyngeal bones	57
Parasphenoid	60
Glossohyal	66
First branchial arch	67
Study of the gillrakers	72

Length of the angular gillrakers	
and their form	75
Scanning electron microscopy analysis	96
Study of selected features involved in	
food-gathering and utilization	103
Orbital width	103
Intestine length	113
Pyloric caeca	119
Head length	122
Triangular co-ordinate analysis	126
Cluster analysis by multivariate statistics	130
Discussion	136
Bibliography	171
Appendix	181

Figure	LIST OF FIGURES	Page
1	External measurements on <u>Sebastes</u> spp. used in this study. A, on the head and B, on the complete body. Symbols in TABLE 3 (modified from Phillips, 1957)	8
2	Some food-gathering structures of <u>Sebastes</u> spp., with detail of selected parts. A, premaxillary; B, lower jaw; C, first branchial arch and D, gill-rakers. Symbols in TABLE 3.	10
3	Selected structures of the mouth of <u>Sebastes</u> spp., complementary to those shown in FIG. 2. A, vomer; B, palatine and C, infrapharyngeal. Symbols in TABLE 3.	12
4	Relative position of tooth-bearing structures in <u>Sebastes</u> spp. A, floor of the mouth and B, roof of the mouth. Symbols in TABLE 3	14
5	Gillrakers sites used for scanning electron microscopy analysis. A, upper view and B, lateral view. Symbols in TABLE 3.	15
6	Left maxillaries and premaxillaries of rockfishes, upper and lower respectively, in each case. A, <u>S. mystinus</u> (320 mm SL); B, <u>S. nebulosus</u> (294 mm SL); C, <u>S. nigrocinctus</u> (351 mm SL) and D, <u>S. ruberrimus</u> (580 mm SL).	23
7	Left maxillaries and premaxillaries of rockfishes. A, <u>S. entomelas</u> (432 mm SL); B, <u>S. wilsoni</u> (184 mm SL); C, <u>S. proriger</u> (285 mm SL); D, <u>S. flavidus</u> (465 mm SL); E, <u>S. zacentrus</u> (305 mm SL); F, <u>S. melanops</u> (445 mm SL) and G, <u>S. crameri</u> (394 mm SL).	24

8	Left maxillaries and premaxillaries of rockfishes. A, <u>S. reedi</u> (423 mm SL); B, <u>S. elongatus</u> (320 mm SL); C, <u>S. diploproa</u> (311 mm SL) and D, <u>S. pinniger</u> (490 mm SL).	25
9	Left maxillaries and premaxillaries of rockfishes. A, <u>S. brevispinis</u> (480 mm SL); B, <u>S. paucispinis</u> (645 mm SL); C, <u>S. chlorostictus</u> (390 mm SL) and D, <u>S. goodiei</u> (453 mm SL).	26
10	Three patterns of premaxillary dentition in <u>Sebastes</u> spp. A, <u>S. diploproa</u> (311 mm SL); B, <u>S. reedi</u> (493 mm SL) and C, <u>S. nigrocinctus</u> (351 mm SL).	28
11	Mean values, standard deviation and range of premaxillary process length as percent of standard length, in <u>Sebastes</u> spp. of Oregon.	29
12	Mean values, standard deviation and range of maximum maxillary width as percent of standard length, in <u>Sebastes</u> spp. of Oregon.	32
13	Mean values, standard deviation and range of the ratio maximum maxillary width/maxillary + premaxillary, in <u>Sebastes</u> spp. of Oregon	34
14	Mean values, standard deviation and range of maxillary + premaxillary as percent of standard length in <u>Sebastes</u> spp. of Oregon.	38
15	Selected regression lines for maxillary + premaxillary length vs standard length in <u>Sebastes</u> spp. of Oregon. Basic data on TABLE 4.	39
16	Articular bones of selected species of rockfishes, <u>Sebastes</u> spp., from Oregon.	43
17	Dentary bones of selected <u>Sebastes</u> spp. of Oregon, showing different patterns of dentition.	45

18	Mean values, standard deviation and range of preangular distance as percent of standard length in <u>Sebastes</u> spp. of Oregon.	46
19	Lower view of the vomer of <u>S. nebulosus</u>	51
20	Vomer bones of selected <u>Sebastes</u> spp.	53
21	Palatine bones of selected <u>Sebastes</u> spp.	56
22	Lower pharyngeal bones selected to show tooth-patches in several <u>Sebastes</u> spp.	61
23	Parasphenoid bones of several <u>Sebastes</u> spp.	65
24	Glossosnyal bones of selected <u>Sebastes</u> spp., with standard length for each case given in mm : A, <u>S. flavidus</u> (465); B, <u>S. entomelas</u> (432); C, <u>S. pinniger</u> (490); D, <u>S. ruberrimus</u> (580); E, <u>S. melanops</u> (445); F, <u>S. diploproa</u> (311); G, <u>S. mystinus</u> (320); H, <u>S. goodai</u> (453); I, <u>S. nigrocinctus</u> (351); J, <u>S. chlrostictus</u> (361); K, <u>S. elongatus</u> (320); L, <u>S. reedi</u> (423); M, <u>S. proriger</u> (255); N, <u>S. crameri</u> (394); O, <u>S. wilsoni</u> (184); P, <u>S. brevispinis</u> (480); Q, <u>S. paucispinis</u> (645) and R, <u>S. zacentrus</u> (305).	68
25	Mean values, standard deviation and range of length of the lower limb of the first branchial arch as percent of standard length, in <u>Sebastes</u> spp.	71
26	First left gill arches of <u>S. borealis</u> and <u>S. ruberrimus</u> , showing gillrakers of the I group type.	77
27	First left gill arch of <u>S. brevispinis</u> , showing gillrakers of II group type	80
28	First left gillarches of <u>S. mystinus</u> and <u>S. aleutianus</u> (both III gillrakers group type), compared with <u>S. melanops</u> (II group) and <u>S. pacocki</u> (I group).	81

29	First left gill arches of <u>S. entomelas</u> (III group type) and <u>S. flavidus</u> (IV group type).	82
30	Mean values, standard deviation and range for number of gillrakers by selected <u>Sebastes</u> spp. The lowest axis indicates number of species having a particular number of gillrakers.	85
31	Mean values, standard deviation and range for length of angular gillraker as percent of standard length in <u>Sebastes</u> spp.	91
32	Regression lines for angular gillraker length vs. standard length (mm), in selected <u>Sebastes</u> spp.	92
33	Mean values, standard deviation and range for the ratio angular gillraker/length of the lower limb of the first branchial arch, in <u>Sebastes</u> spp.	95
34	Tip and part of the body of the angular gillraker of the first branchial arch of <u>S. paucispinis</u> , 243 mm SL (x 35), under SEM.	99
35	Central-upper view of angular gillraker of <u>S. paucispinis</u> (x 35).	99
36	Centro-lateral view of angular gillraker of <u>S. paucispinis</u> (x 130).	100
37	Inner angular gillraker of <u>S. paucispinis</u> (x 30).	100
38	Tip of angular gillraker of the first branchial arch of <u>S. helvomaculatus</u> , 257 mm SL (x 35).	101
39	Central upper view of angular gillraker of <u>S. helvomaculatus</u> (x 35).	101
40	Centro-lateral view of angular gillraker of <u>S. helvomaculatus</u> (x 130).	102

41	Inner angular gillraker of <u>S. helvomaculatus</u> (x 30).	102
42	Tip of the angular gillraker of the first branchial arch of <u>S. diploproa</u> , 205 mm SL (x 35).	103
43	Central upper view of angular gillraker of <u>S. diploproa</u> (x 35).	103
44	Centro-lateral view of angular gillraker of <u>S. diploproa</u> (x 130).	104
45	Inner angular gillraker of <u>S. diploproa</u> (x 30).	104
46	Tip of the angular gillraker of the first branchial arch of <u>S. wilsoni</u> , 127 mm SL (x 35).	105
47	Central upper view of angular gillraker of <u>S. wilsoni</u> (x 35).	105
48	Centro-lateral view of angular gillraker of <u>S. wilsoni</u> (x 130).	105
49	Inner angular gillraker, near the root of the external gillraker of <u>S. wilsoni</u> (x 30).	106
50	Detail of the inner gillraker of <u>S. wilsoni</u> (x 120), to compare with FIG.50.	107
51	Mean values, range and standard deviation of orbital width as percent of standard length in <u>Sebastes</u> spp. Numbers at left indicate maximum depth of captures.	111
52	Mean values, range and standard deviation of values of the ratio orbital width/head length, in <u>Sebastes</u> spp.	112
53	Regression lines for orbital width vs standard length in selected <u>Sebastes</u> spp.	114
54	Ratio intestine length/standard length in <u>Sebastes</u> spp.	117
55	Regression lines for intestine length vs standard length in selected <u>Sebastes</u> spp.	118

56	Variation of the number of pyloric caeca in <u>Sebastes</u> spp.	123
57	Variation of the ratio head length/standard length in <u>Sebastes</u> spp.	124
58	Triangular co-ordinate analysis in several species of <u>Sebastes</u> , using structures linked to food-gathering process. Symbols in TABLE 3.	129
59	Dendrogram from cluster analysis	132
60	Dendrogram from cluster analysys	133
61	Dendrofram from cluster analysis	134
62.	Mean values for maxillary + premaxillary as percent of standard length in <u>Sebastes</u> spp. of Oregon, according to their angular gillraker length as percent of standard length. Dotted area enclose surface in which species with proportionally short intestine concentrate.	146
63	Scatter diagram showing relationships between mean values of length of angular gillraker and percent of standard length and intestine length as percent of standard length. Roman numbers and contours indicate groups according to gillrakers form.	143
64	Mean values for maxillary + premaxillary as percent of standard length in different <u>Sebastes</u> spp., according to their maximum recorded length. Dotted line enclose area in which typically short intestine species concentrate, meanwhile dashed line enclose those with proportionally long intestines.	154
65	Diagramatic description on the possible evolutive development of some rockfish (<u>Sebastes</u> spp.), of the North Eastern Pacific. More explanations in the text.	167

LIST OF TABLES

Table		Page
1	Summary of material used for this study, followed by size ranges in mm (* = not recorded in Oregon; X = not used in SEM analysis).	7
2	Abbreviations in the text	18
3	Regression equations, correlation coefficients and number of specimens analyzed for maxillary + premaxillary length vs standard length (mm), in <u>Sebastes</u> spp. of Oregon.	37
4	Regression equations, correlation coefficients and number of specimens analyzed for preangular distance vs standard length (mm), in <u>Sebastes</u> spp.	49
5	Regression equations, correlation coefficients and number of specimens analyzed for length of the lower limb of the first branchial arch vs standard length (mm), in <u>Sebastes</u> spp.	73
6	Different rockfishes, <u>Sebastes</u> spp., arranged alphabetically and by gillrakers form pattern groups.	74
7	Width as percent of length of gillrakers, in selected <u>Sebastes</u> spp. (n = 10, in each case).	78
8	Variation in the number of gillrakers in <u>Sebastes</u> spp. of Oregon. Detail about rows, in the text.	88
9	Regression equations, correlation coefficients and number of specimens analyzed for length of angular gillraker vs standard length (mm), in <u>Seoastes</u> spp.	93

10	Results of SEM analysis. °X°denotes presence of a given characteristic.	97
11	Regression equations, correlation coefficients and number of specimens studied for orbital width vs standard length, in <u>Sebastes</u> spp.	115
12	Regression equations, correlation coefficients and number of specimens studied for intestine length vs standard length, in <u>Sebastes</u> spp.	120
13	Regression equations, correlation coefficients and number of specimens studied for head length vs. standard length, in <u>Sebastes</u> spp.	126
14	Principal food items described in the diet of rockfishes, <u>Sebastes</u> spp., after several authors. Underlined figures represent the main one recorded in each case.	141
15	Mouth characteristics in selected species of <u>Sebastes</u> , with indication of orbital width, gillrakers and intestine types.	144
16	Examples of possible associations in <u>Sebastes</u> spp., after field observations by several authors.	162
17	Mechanisms allowing sympatry in selected species of <u>Sebastes</u> , according to different authors.	164

TROPHIC ADAPTATIONS AND RELATIONSHIPS
OF ROCKFISHES (SEBASTES SPP.) OF OREGON

INTRODUCTION

The rockfishes (Sebastes Cuvier, 1829, members of the family Scorpaenidae, are widely distributed in the North Pacific Ocean. Species are found on the west coast of temperate South America and in the Atlantic, although the number of species seems to be drastically reduced in the seas of the Southern Hemisphere. The highest number of species of Sebastes spp. live on the coastlines between Mexico and Japan. In the Eastern North Pacific around 61 to 69 species are recognized (Chen, 1975; Eschmeyer et al., 1983). On the coast of Oregon the number of species is around 30. The great number of species has drawn attention of ichthyologists to problems of speciation and comparative biology within the genus.

Although Ayres (1854) and a few other early ichthyologists placed the Eastern Pacific rockfishes into the genus Sebastes Cuvier 1829, Gill (1861, 1862, 1864) erected the genera Sebastodes, Sebastichthys, Sebastomus and Sebastosomus for their inclusion. Eigenmann and Beeson (1893) split the group further by adding the genera Acutomentum, Auctospina and Jordan and Evermann (1895) fragmented the group further by adding Rosicola, Eosebastes and Hispanicus; the same authors later (1898, 1927) added Sebastopyr and Sebastocarus.

The twelve genera were recognized by Jordan, Evermann and Clark (1930), but Schultz and De Lacy (1936) listed all the species under the single genus Sebastodes and Bailey et. al.(1970) placed Sebastodes into the synonymy of Sebastes. That action followed "recommendations of colleagues...(and conformed) with opinion of the last general monographer of these scorpaenids, the late K.M. Matsubara". Most investigators have followed this usage (Chen, 1975; Prince and Gotshall, 1976; Boehlert and Kappenman,1980). Subgeneric classification is not well defined. Early work (Cramer, 1895; Eigenmann and Beeson,1893) used cranial osteology in that classification, and Jordan and Evermann (1898) recognized 13 subgenera (Appendix 1). Modern investigators find considerable overlap in the nominal subgenera, but one, Petropodus, appears to be valid.

According to contemporary definitions (Briggs, 1955), the North Pacific Ocean is their "center of dispersal". Many species are similar in structure, in color pattern and some appear to be similar in ecology. Although some species are well known, the distribution, life history and ecology of others has not been adequately studied.

Rockfishes are all marine, mainly in habitats of the continental shelf, although some species are known to live over the continental slope. Some Oregon species are found as deep as 700 m. Some species are thought to live near the bottom (Phillips, 1957; Alverson et al., 1964; Lyubimova, 1964), but some appear to be pelagic forms (Pereyra et al., 1969; Dunn and Hitz, 1969). Rockfishes appear to utilize different habitats (Miller and Lea, 1972; Feder et al., 1974; Snytko and Fedorov, 1974; Gunderson and Sample, 1980; Love, 1980). Generally they overlap in latitudinal distribution as well as in depth. Geographical sympatry is a common factor in most of the species of Oregon, but that does not always mean identity of habitat. Bathymetric segregation of a pair of species was described in Californian waters (Larson, 1980).

The rockfishes are viviparous. Their larvae are about 4 to 5 mm when released. Larvae lead a pelagic existence and transform to benthic juvenile stages at varying sizes (Moser, 1967, 1972). Congregation under drifting objects and surface-to-benthic migration of juveniles have been described (Hitz, 1961, Boehlert, 1977).

Growth rate and maximum length of rockfishes may change - as well as longevity, age distribution and fecundity - according to latitude (Six and Horton, 1977; Boehlert and Kappenman, 1980). Behavior of rockfishes is not well known, but some studies showed diel movements or changes of feeding activity (Ebeling and Bray, 1977; Brodeur, 1983). The food of several species of rockfishes has been studied, mainly those common in

commercial fisheries. Brodeur (1983) gives new data, appearing principally carnivorous, eating some algae, maybe accidentally, but mainly crustaceans, mollusks, polychaetes and fishes.

The present study was designed to provide a basis for further study of rockfish ecology and systematics by examining their trophic adaptations, including (1) specific adaptations of orobranchial bones, teeth and digestive apparatus that could allow exploitation of different segments of food resources if these resources were limiting, (2) probable relationships and food habits that could be made evident by evaluation of the food-gathering and food-processing apparatus. A study based on similar assumptions was recently made in another speciose family -Embiotocidae - inhabiting the same North Eastern Pacificarea, with good results(De Martini, 1969).

The best defined subgenus appears to be Sebastomus Gill, 1964, one of the more compact groups within the genus. However the species show varying degrees of similarity, indicating that certain species may have closer affinity than other. In our concept, despite of a large effort to differentiate the species of Sebastes, the definition of subgroups remain very poorly understood and incipiently conceptualized.

Therefore, the Sebastes are insufficiently known to facilitate better study and management. But a starting point can be the study of a regional ensemble, as the one present in Oregon. This study is the first attempt to study the Sebastes of Oregon as a whole, based on a morphofunctional approach. From this standpoint I hope to contribute to a better knowledge of the natural history of the species according to their assumed roles in biological processes as deduced from the feeding apparatus.

I expect to describe morphological adaptations associated with feeding in the common rockfishes of Oregon and evaluate them as tools for determination of species. It will be desirable, whenever possible, to show probable relationships between trophic adaptations and intrageneric grouping, as well as relationships between these adaptations and foods habits and ecology of selected species.

METHODS AND MATERIALS

Geographical origin of the sample

Of the 37 species studied represented by 624 specimens, 33 were from Oregon. The few species from outside Oregon comprised 38 specimens (TABLE 1). The fishes are part of the O.S.U. Department of Fisheries and Wildlife collection or were landed by commercial, sport or scientific vessels. Some were captured on a cruise of the R/V "CHAPMAN" of the National Marine Fisheries Service.

Size of the specimens

Only large (mostly sexually mature) specimens were used in the study because of the assumption that juveniles might not have the feeding structures developed in definitive form. An effort was made to obtain the largest specimens available. The range of size of specimens by species studied are depicted together with the number of specimens used (TABLE 1).

Measurements and counts

The following measurements and counts were made (FIGS. 1A, B; 2A, B, C and D). Measurements: Standard length, head length, maximum horizontal orbital width,

TABLE 1. Summary of the material used for this study, followed by size ranges in mm (* = not recorded in Oregon; X = not used in SEM analysis).

Species		Number and size ranges (mm)	Sets of mouth bones	Gill arches	
				Wet	Dry
<u>aleutianus</u>		(9) 171-350		4	
<u>alutus</u>		(22) 141-230		4	
<u>babcocki</u>		(21) 179-360		4	
<u>borealis</u>		(25) 208-630		6	
<u>brevispinis</u>		(23) 176-510	6	5	3
<u>caurinus</u>		(10) 76-280		2	
<u>chlorostictus</u>	X	(17) 285-390	3	2	5
<u>ciliatus</u>	X	(23) 239-325		4	
<u>crameri</u>		(26) 148-394	6	10	6
<u>diploproa</u>		(24) 176-317	5	4	2
<u>elongatus</u>		(28) 143-318	4	2	4
<u>entomelas</u>		(21) 301-432	5	3	4
<u>flavidus</u>		(21) 203-565	6	4	6
<u>goodei</u>	X	(17) 320-453	3	2	4
<u>helvomaculatus</u>		(29) 160-257		6	
<u>jordani</u>		(30) 145-226		6	
<u>maliger</u>		(7) 353-404		4	
<u>melanops</u>		(24) 127-445	5	6	4
<u>melanostomus</u>	X	(2) 395-405		2	
<u>miniatus</u>		(1) 226			
<u>mystinus</u>		(16) 130-396	4	5	1
<u>nebulosus</u>		(4) 235-294	1	2	
<u>nigrocinctus</u>		(2) 250-351	1	2	
<u>paucispinis</u>		(23) 240-645	4	5	1
<u>pinniger</u>		(21) 226-490	6	5	3
<u>polyspinis</u>	*	(21) 138-325		4	
<u>proriger</u>		(23) 215-330	4	4	4
<u>rastrelliger</u>		(8) 179-465		2	
<u>reedi</u>		(23) 194-423	5	3	7
<u>rosenblatti</u>	*	(1) 164		1	
<u>ruberrimus</u>		(16) 180-499	4	6	3
<u>rufus</u>	X	(4) 311-354		2	
<u>saxicola</u>		(22) 162-266		4	
<u>serranoides</u>	*	(1) 155		1	
<u>variegatus</u>	*	(14) 176-205		4	
<u>wilsoni</u>		(20) 108-184	2	4	3
<u>zacentrus</u>		(25) 189-305	4	4	3

=====

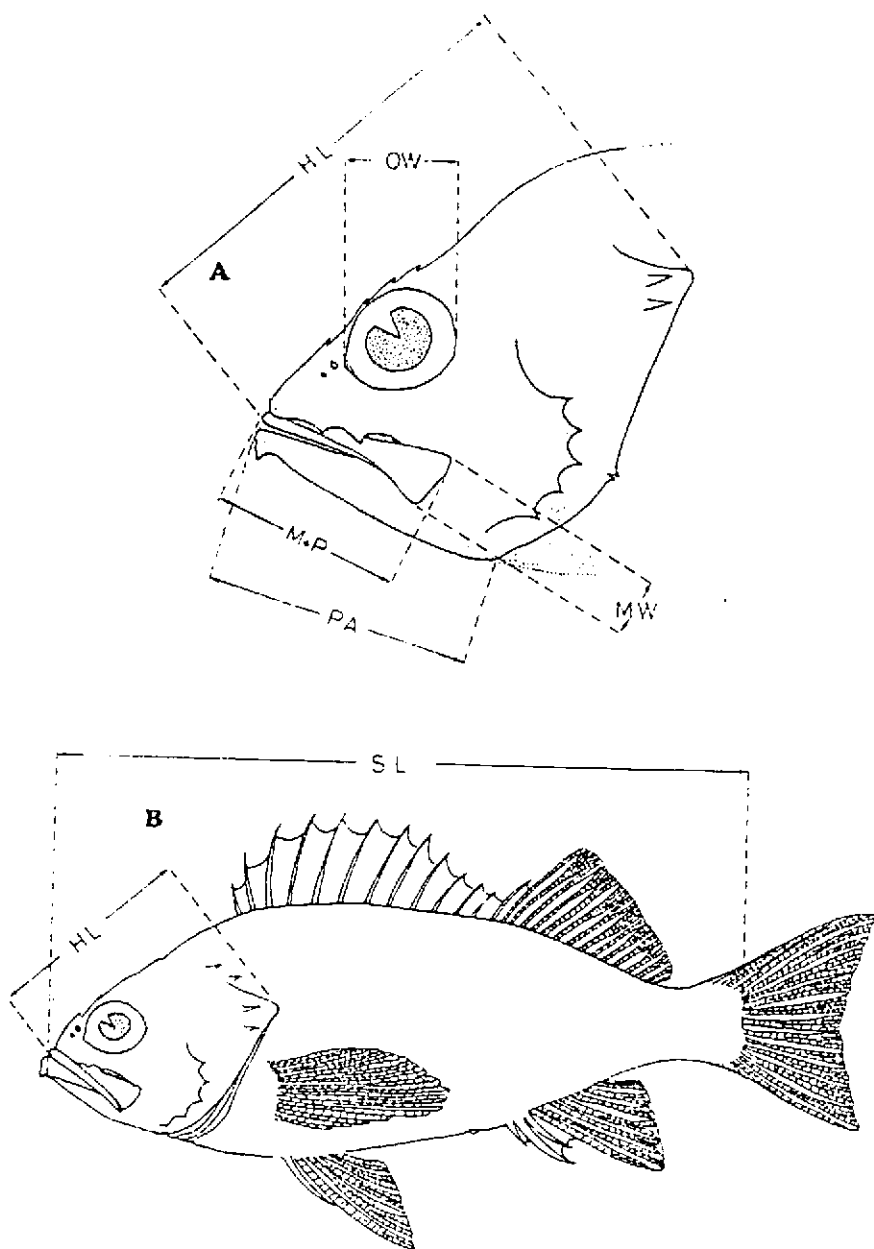


Fig. 1. External measurements on *Sebastes* spp. used in this study. A, on the head and B, on the complete body. Symbols in TABLE 3 (modified from Phillips, 1957).

maxillary plus premaxillary length (=upper jaw length), maximum maxillary width, length of the ascendent premaxillary process, length of the angular gillraker of the first branchial arch, length of the intestine from the pyloric valve to anal sphincter, preangular distance from the anterior end of the dentary to posterior end of the angular bone and length of the lower limb of the first branchial arch. Counts were made on pyloric caeca and number of gillrakers of the lower limb of the first branchial arch.

To measure the ascendent premaxillary process, a dissection was necessary. To facilitate measurement and counting on first gill arch, the arch was excised. The angular gillraker was measured from its base to the tip as shown in FIGS. 2D. A dial caliper was used for most measurements; a millimeter scale was used for measurements where accuracy to the nearest millimeter was required. Curve measurements were taken to study tooth-patch length on the premaxilla. Most of measurements and counts followed other authors (Phillips, 1957).

Abbreviations used in the text are explained in TABLE 2.

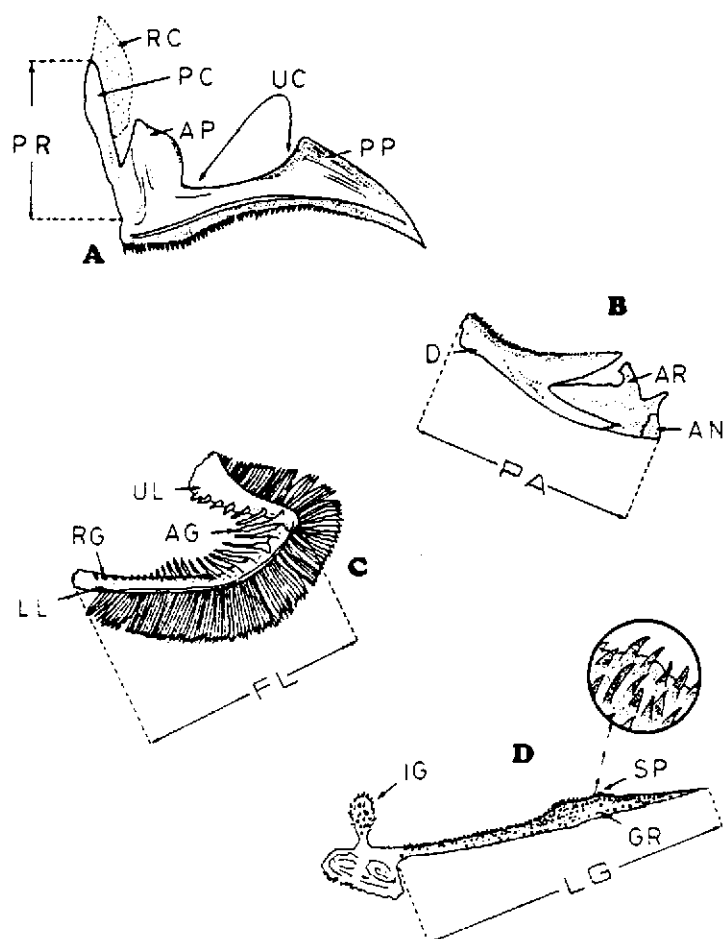


FIG. 2. Some food-gathering structures of *Sebastes* spp., with detail of selected parts. A, premaxillary; B, lower jaw; C, first branchial arch, and D, gillrakers. Symbols in TABLE 3.

Preservation

Specimens previously preserved in collections were in 40% isopropyl alcohol. New specimens were fixed for one week in 10% formaldehyde solution and then passed into isopropyl alcohol.

Selected bones of the mouth - maxillary, pre-maxillary, dentary, articular, angular, vomer, palatines, infrapharyngeals, glossohyal - were prepared from selected, larger specimens. The heads were cooked, then washed in running tepid water and submerged in a 10% solution of hydrogen peroxide; then they were dried at room temperature. Selected first gill arches from large specimens were preserved. Some were fixed directly in isopropyl alcohol and others - after soaking in a solution of 80% ethyl alcohol for 5 to 10 minutes - were dried as explained for bones. Dried arches were stored in plastic envelopes. Every set of bones, as well as each gill arch preserved was provided with data - species name, origin of sample, standard length. In short, 78 sets of mouth bones, 136 wet gill arches and 69 dry gill arches were prepared and preserved at O.S.U. Department of Fisheries and Wildlife for this and further studies (TABLE 1, FIGS. 3

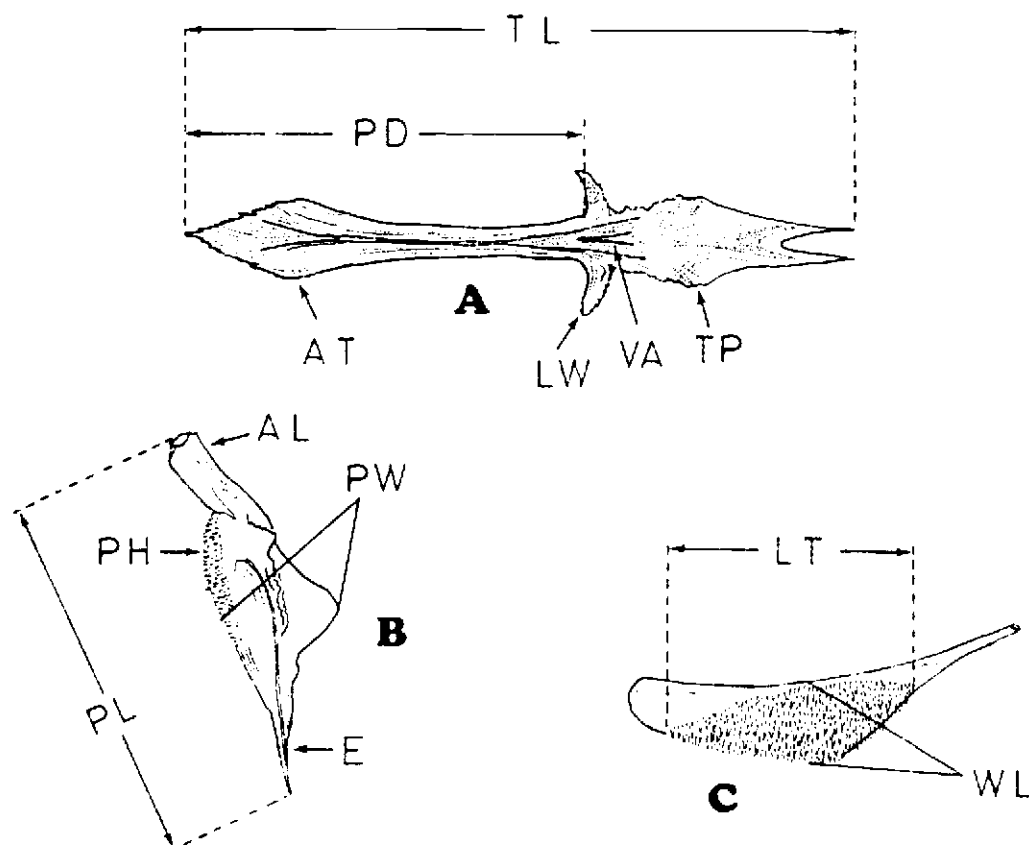


FIG. 3. Selected structures of the mouth of *Sebastes* spp. complementary to those shown in FIG. 2. A, parasphenoid, B, palatine, and C, infra-pharyngeal. Symbols in TABLE 3.

and 4).

Scanning electron microscope (SEM) procedures

All the gillrakers used were taken from previously preserved specimens in collections. The angular gillraker was separated from the gill arch together with the nearest inner gillraker (FIG. 5). Then they were processed as follows:

Step	Solution	Time (min.)
Soaked	H2O2 10%	2
Cleaning	KOH 10%	4
Soak	Destilled H2O	2
Dehydration I	CH3-CH2OH 50%	20
Dehydration II	id. 60%	15
Dehydration III	id. 80%	15 (12)
Dehydration IV	id. 100%	10 (8)

To facilitate removal of small particles of tissue, the vials were shaken vigorously twice during the treatment with KOH. Specimens were mounted with DUCO cement (DuPont Co., Wilmington, DE 19898) on an aluminum post. Coating was made with 60 : 40% Au/Pd alloy, with approximately 200 Angstrom thickness, by rotary vacuum evaporation in a VARIAN VE 10 vacuum evaporator (VARIAN Vacuum Division, 4940 El Camino

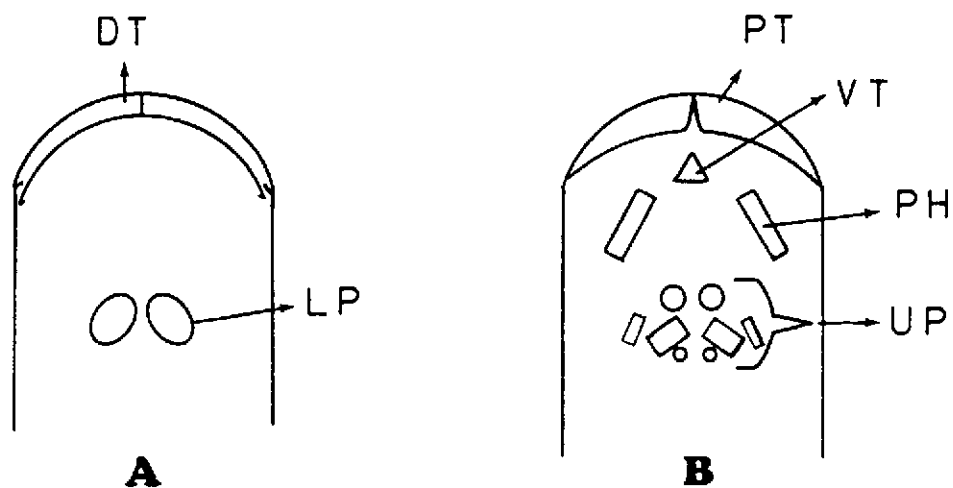


FIG. 4. Relative position of tooth-bearing structures in *Sebastes* spp. A, floor of the mouth and B, roof of the mouth. Symbols in TABLE 3.

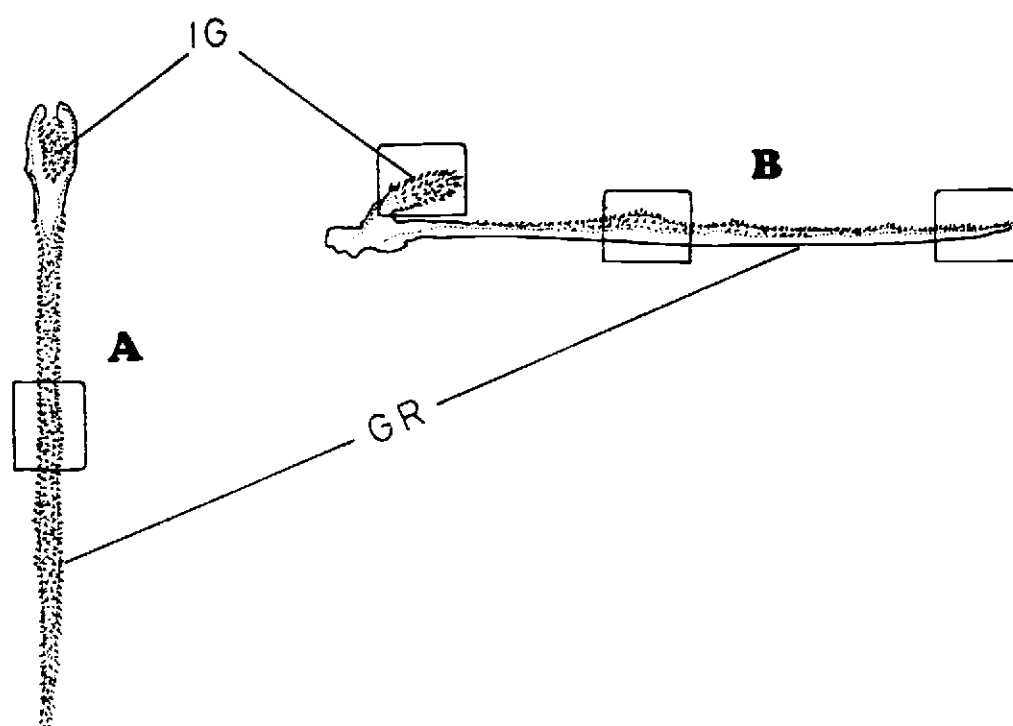


FIG. 5. Gillrakers sites used for scanning electron microscopy analysis. A, upper view and B, lateral view. Symbols in TABLE 3.

Real, Los Altos, CA 94022) at 1×10 Torr. All the gillrakers coated were preserved each in glass vials appropriately labeled.

The examination was made in an AMRAY 100 A scanning electron microscope, operated at 10 KV, secondary electron mode. The pictures were made on Polaroid type 55 positive/negative film (Polaroid Corp., Cambridge, Massachusetts 02139) in their original format. Each picture was preserved together with the negative in specially made paper envelopes provided by the O.S.U. Electron Microscopy Facility. Newer pictures were then prepared upon standard processes.

Use of multivariate analysis techniques

Multivariate analysis was used to study similarity of standardized values of characters, as a means to examine relationships of taxonomic units in a multidimensional space and to check the other techniques used in this study, all of which are based on phenetic similarity. The program CLUSTER was used here (Keniston, 1978). The data matrix was already transformed into percentage values and their standardization was performed by CLUSTER. The various similarity indices currently used have been summarized (Boesch, 1977). Aspects of clustering computations and

algorithms were also reviewed according to modern criteria (Gauch, 1982; Pimentel, 1979). The computations and clustering were performed in a CYBER computer. Two quantitative similarity coefficients were used : Bray-curtis and Canberra Metric (Boesch, Op. Cit.; Lance and Williams, 1966 and 1967). Both were expressed as dissimilarity measures.

TABLE 2. Abbreviations in the text.

AG	angular gillraker, that in the angle of the first gill arch
AL	anterior process, palatine
AN	angular bone
AP	articular process, premaxillary
AR	articular bone
AT	anterior transverse process, parasphenoid
D	dentary
DT	dentary teeth
E	posterior end, palatine
FL	length lower limb, first branchial arch
G	glossohyal
GA	gill arch or branchial arch
GF	gill filaments
GR	gillraker (= external gillraker)
HL	head length
IG	inner gillraker
IL	intestine length
LG	length angular gillraker
LL	lower limb, gill arch
LP	lower pharyngeal teeth
LT	tooth patch length, lower pharyngeals
LW	lateral process or wing, parasphenoid
MA	maxillary
M + P	maxillary plus premaxillary (= M + P length)
MW	maximum maxillary width
OW	maximum horizontal orbital width
PA	preangular distance
PR	length ascendent premaxillary process
PD	pre-lateral-process distance, parasphenoid
PH	palatine teeth
PL	palatine length
PM	premaxillary
PO	ascendent premaxillary process
PP	posterior process, premaxillary
PS	parasphenoid
PT	premaxillary teeth

TABLE 2 (cont.).

PW	palatine width
RC	rostral cartilage
RG	rudimentary gillrakers
SEM	scanning electron microscope
SL	standard length
SP	Spinulae, in gillrakers
TL	total length
TP	posterior transverse process, parasphenoid
UC	upper edge concavity, premaxillary
UL	upper limb, gill arch
UP	upper pharyngeal teeth
VA	ventral apophysis, parasphenoid
VO	vomer
VT	vomerine teeth
WL	teeth patch width, lower pharyngeals

RESULTS

Study of selected bones

The bones more or less directly responsible for capturing, holding and processing prey in most teleosts are the vomer and parasphenoid of the neurocranium, the mobile premaxillae and maxillae that form the secondary upper jaw, several bones of the splachnocranium, including the bones of the suspensorium (especially the palatines), the branchial apparatus (especially the pharyngobranchials), the hyoid apparatus and the mandible, a unit made up of the dentary, articular (= angular in recent literature) and angular (= retro-articular).

In the following paragraphs the function of these bones in opening, , protruding and closing the mouth will be covered. They will be treated separately and as units that operate together.

Premaxillary

It is the foremost bone in the upper jaw and has articulation with the maxillary by means of the rear portion of the articular process (FIG. 2A). It is the anteriormost bone of the oromandibular arch, which is the designation given to the bones surrounding the oral

cavity. These are premaxillary, maxillary, palatine, quadrate, articular and dentary, from dorsal to ventral positions. The right and the left premaxillaries are solidly attached to each other by means of connective tissue, mainly at the ascendent process level. There is an anterior ascendent process that has a close relation with the rostral cartilage, which moves with it when the mouth is protruded or retracted. The ascendent process is rather thin and pointed while the articular process is rather rounded and is located toward the middle of the bone.

The ascendent process differs slightly among the rockfishes. Evident differences are seen in the shape of the process, which is rather straight in S. entomelas, S. chlorostictus and S. nigrocinctus; is curved backward at the tip in S. mystinus, S. entomelas and S. crameri, and has a shallow sigmoid shape in S. reedi and S. diploproa.

The process angles forward - more than 2 degrees - in S. mystinus, S. nebulosus, S. zacentrus, S. melanops and S. pinniger; angles posteriorly in S. proriger, S. elongatus, S. brevispinis, S. paucispinis and S. goodei, and forms nearly a right angle - not more than 2 degrees - forward or back, in S. nigrocinctus, S. flavidus and S. entomelas.

The rostral cartilage is located beneath the ascendent process of the premaxilla in the Atherinomorpha and Actinopterygii. It slides in the groove of the ethmo-vomer block and enables the protrusion of the upper jaw in these fishes. In Actinopterygii it is firmly fused together with the ascendent process (Harder, 1975). All the rostral cartilages in Sebastes were observed to have a pair of parallel grooves as result of their relationship with the ascendent premaxillary processes. The rostral cartilages were not preserved.

Another important feature of the premaxilla is the concavity of the upper edge (FIGS. 6 to 9), which allow pivoting and sliding of the maxilla. The posterior premaxillary process acts as a stop point for the movements of the maxilla. In other words it prevents the bones of the upper jaw from sliding away from one another (Harder, Op. Cit.) and is instrumental in the operation of the mechanism for protrusion in all these species. The concavity has different shapes, according to species, but it is difficult to fit the shapes into categories. Some of them are rather deep and wide - S. flavidus, S. melanops, S. pinniger, S. elongatus, S. goodei - or wide but not deep, depending on the height of the articular and posterior processes - S. crameri,

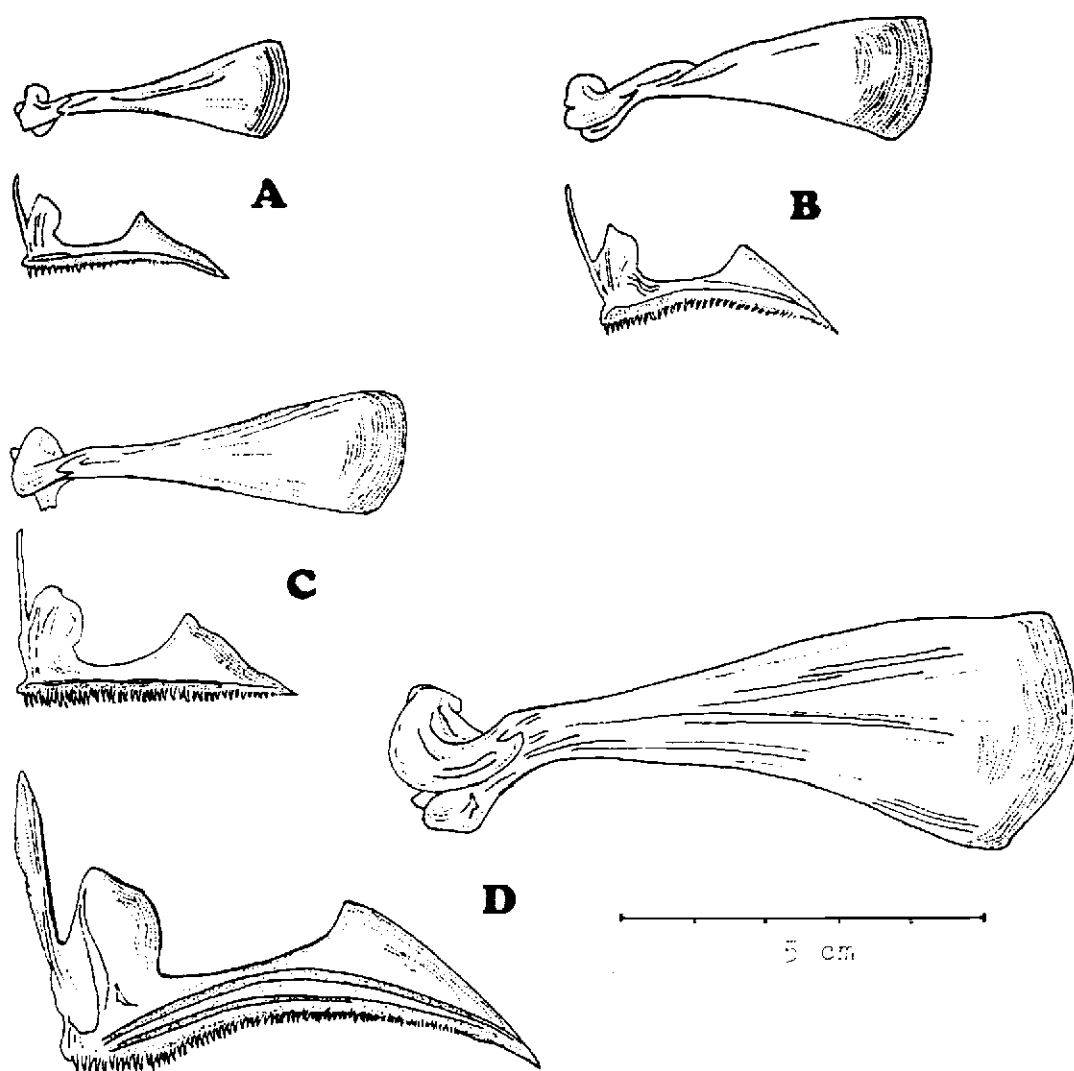


FIG. 6. Left maxillaries and premaxillaries of rockfishes upper and lower respectively, in each case. A, *S. mystinus* (320 mm SL); B, *S. nebulosus* (294 mm SL); C, *S. nigrocinctus* (351 mm SL) and D, *S. ruberrimus* (580 mm SL).

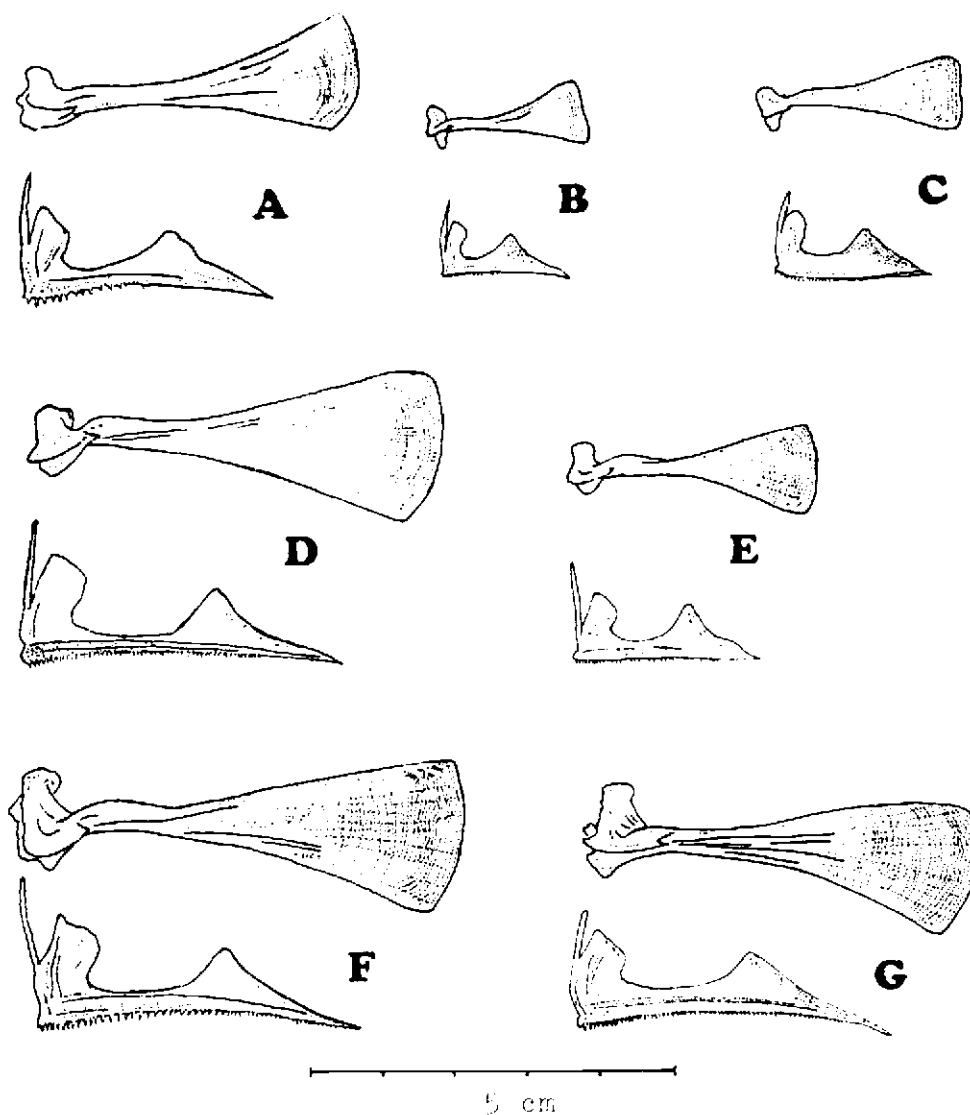


FIG. 7. Left maxillaries and premaxillaries of rockfishes. A, *S. entomelas* (432 mm SL); B, *S. wilsoni* (184 mm SL); C, *S. proriger* (295 mm SL); D, *S. flavidus* (465 mm SL); E, *S. zacentrus* (385 mm SL); F, *S. melanops* (445 mm SL) and G, *S. crameri* (394 mm SL).

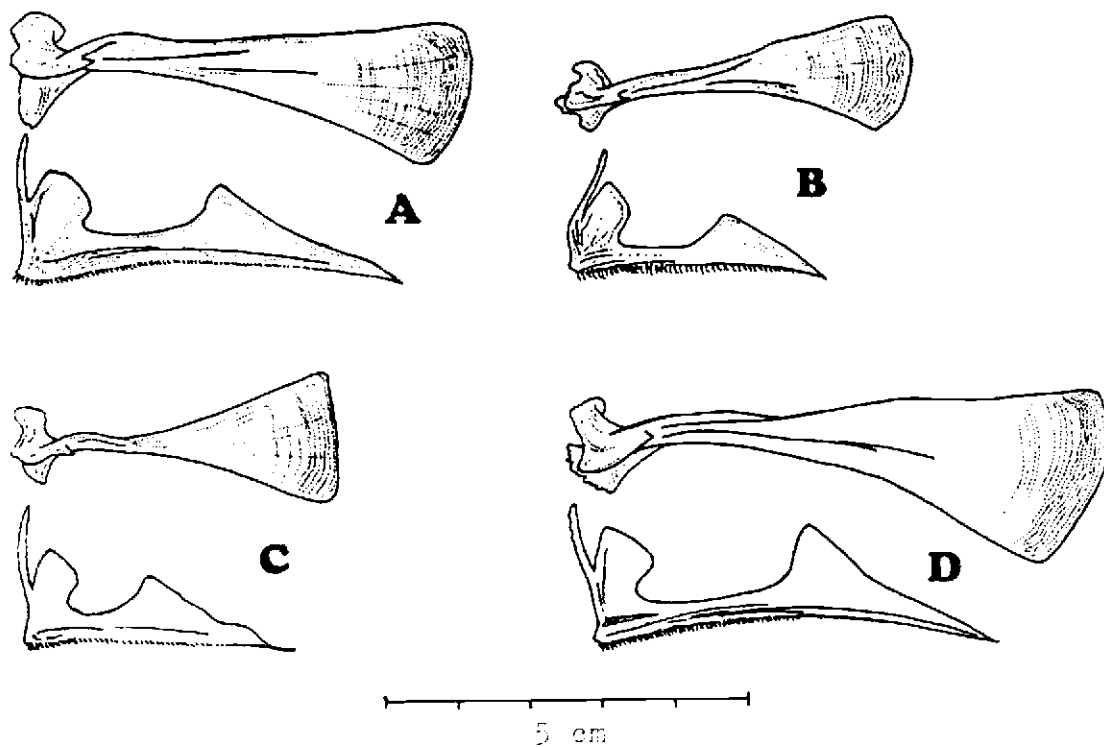


FIG. 8. Left maxillaries and premaxillaries of rockfishes. A, S. reedi (423 mm SL); B, S. elongatus (320 mm SL); C, S. diploproa (311 mm SL) and D, S. pinniger (490 mm SL).

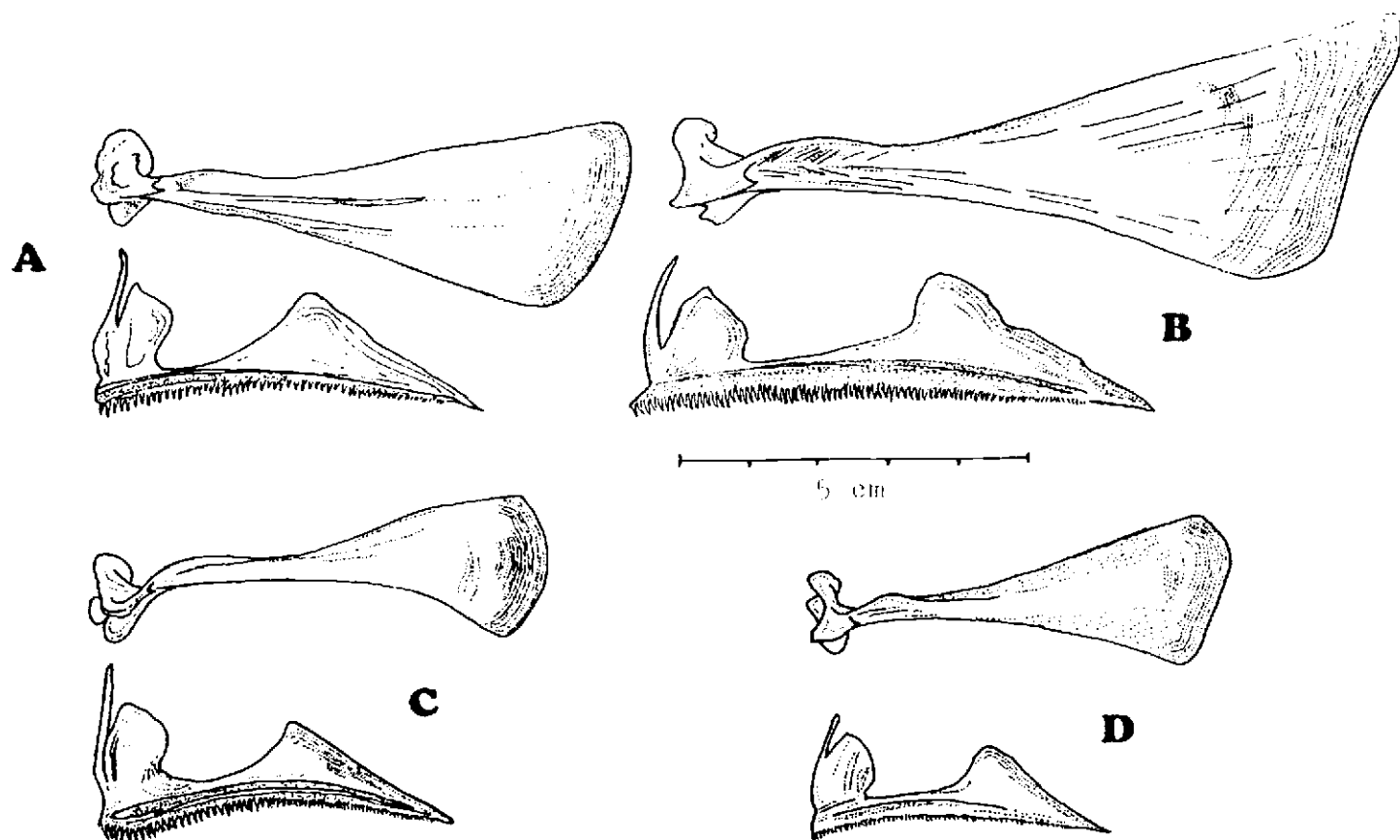


FIG. 2. Left maxillaries and premaxillaries of rockfishes. A, *S. brevispinis* (489 mm SL); B, *S. paucispinis* (645 mm SL); C, *S. chlorostictus* (390 mm SL) and D, *S. goodei* (453 mm SL).

S. reedi, S. ruberrimus - or deep, but narrower - S. mystinus, S. nebulosus, S. zacentrus - or possessing an inclined or curved edge - S. brevispinis, S. chlorostictus, S. paucispinis, S. entomelas, S. wilsoni and S. proriger.

The shape of the band of teeth on the premaxilla differs among the species. Many, including S. paucispinis, have a broad dentigerous area at the front of the bone, with an abrupt taper to a narrower band on the remainder of the bone. S. diploproa has a dentigerous process extending anteriorly (FIG. 10). Others have a gentle taper from the front to the back of the bone. Generally there are three main groups, according to the width of the tooth bands along the main shaft of the premaxilla. Those with a broad band include S. nigrocinctus, S. brevispinis, S. chlorostictus, S. flavidus, S. wilsoni, S. ruberrimus and S. nebulosus. Those with intermediate width are S. elongatus, S. pinniger, S. reedi, S. crameri, S. mystinus and S. melanops. Those with narrow bands are S. proriger, S. goodei, S. entomelas, S. zacentrus and S. diploproa.

The ascendent premaxillary process length was further studied in relation to its percentage of the standard length (FIG. 11). The complete sample has mean

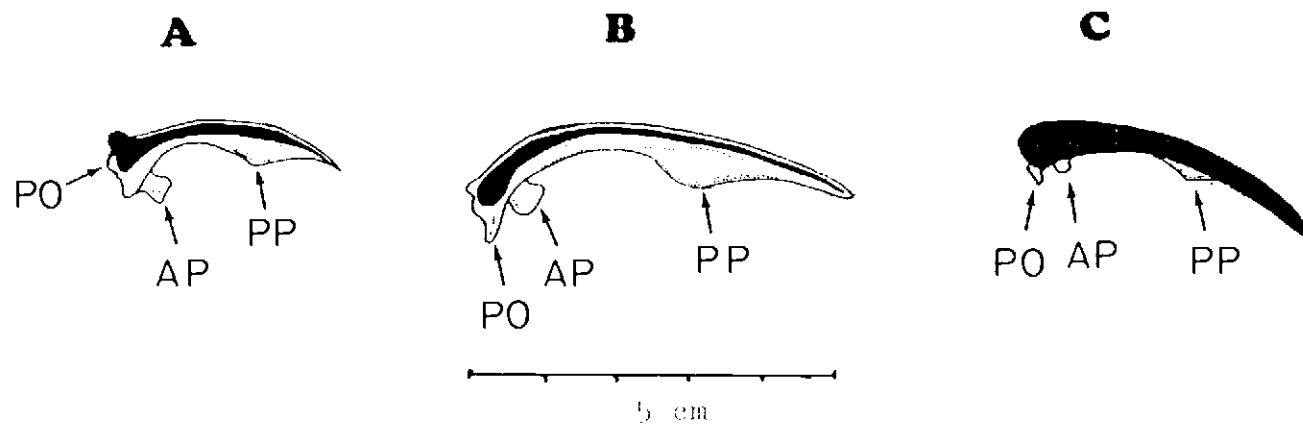


FIG. 10. Three patterns of premaxillary dentition in *Sebastes* spp. A, *S. diploproa* (311 mm SL); B, *S. reedi* (423 mm SL) and C, *S. nigrocinetus* (351 mm SL).

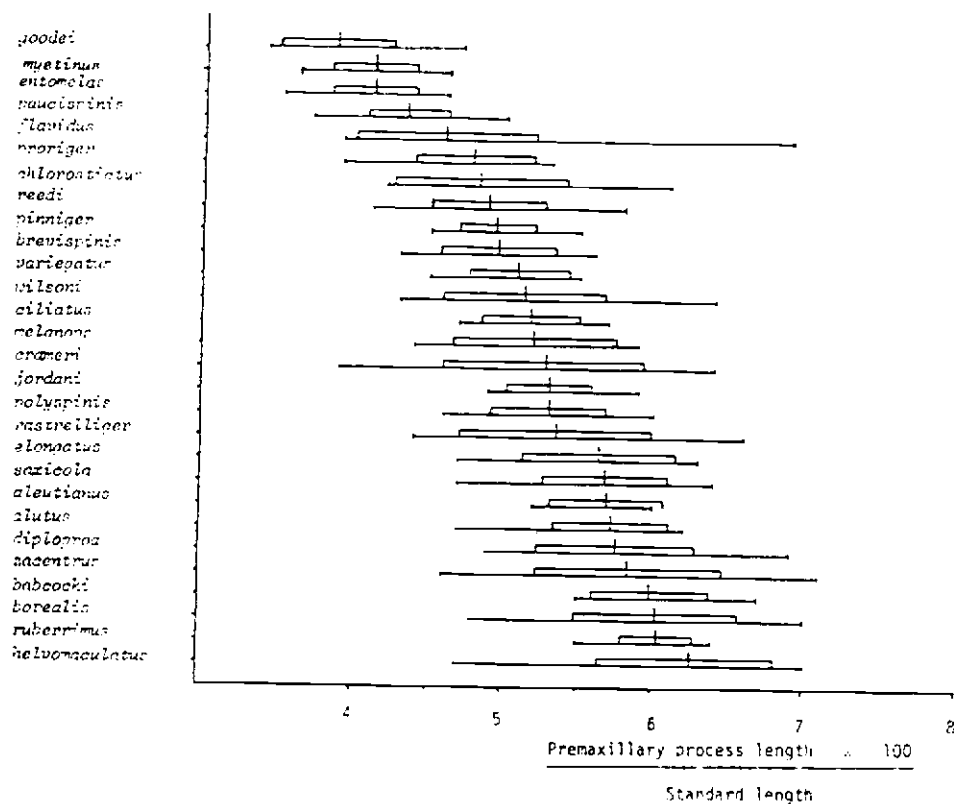


FIG. 11. Mean values, standard deviation and range of premaxillary process length as percent of standard length, in *Sebastes* spp. of Oregon.

values between 4.1 % and 6.3 % of the standard length which is, in general, a very narrow one. Ranges and standard deviations help to see that there is a gradation of the species according to their own values and they can be so ordered, showing that very few species do not overlap any of these values. S. goodei was found to have proportionally the shortest length, followed by S. mystinus, S. entomelas, S. paucispinis and S. flavidus. The gradient of values becomes steeper with S. proriger. S. chlorostictus, S. reedi, S. pinniger, S. brevispinis, S. variegatus, S. wilsoni, S. ciliatus, S. melanops, S. crameri, S. jordani, S. polyspinis and S. ratrelliger, showed only small differences in the mean. All the values fall between 4.8 and 5.4 %. Those with mean percentage values between 6 and 6.3 % are S. elongatus, S. saxicola, S. aleutianus, S. alutus, S. diploproa, S. zacentrus, S. babcocki, S. borealis, S. ruberrimus and S. helvomaculatus.

Maxillary

The bone is located dorso-caudally to the premaxilla and does not bear teeth in *Sebastes*. The activity of the maxilla is linked to that of the premaxilla, with which it articulates at its anterior

end. The caudal end of the premaxilla is attached to the lower jaw by means of ligaments, so that when the mouth is opened the maxilla is swung forward and downward. As it maintains its connection with the articular process of the premaxilla, it serves as a lever to protrude the premaxilla.

The shape of the maxilla varies according to species (FIGS. 6 to 9). The greatest differences are obvious in the form of the caudal end and the difference of curvature of the upper and lower edges of the bone. Some species show a rather vertical caudal end margin, as do S. proriger, S. diploproa and - to some extent - S. wilsoni. Most of the species tend to have a rounded caudal end of the maxilla as in S. nebulosus, S. chlorostictus, S. mystinus, S. ruberrimus, S. elongatus, S. reedi, S. melanops, S. crameri, S. flavidus and S. entomelas. Few species show an oblique caudal margin of the maxilla. Of these, S. paucispinis has the most oblique one; S. brevispinis and S. goodei are less oblique.

We have measured the width of the maxilla, calculated as percent value of their standard length of each fish (FIG. 12). Three species - jordani, entomelas and proriger - showed low mean values and their respective standard deviations do not overlap by

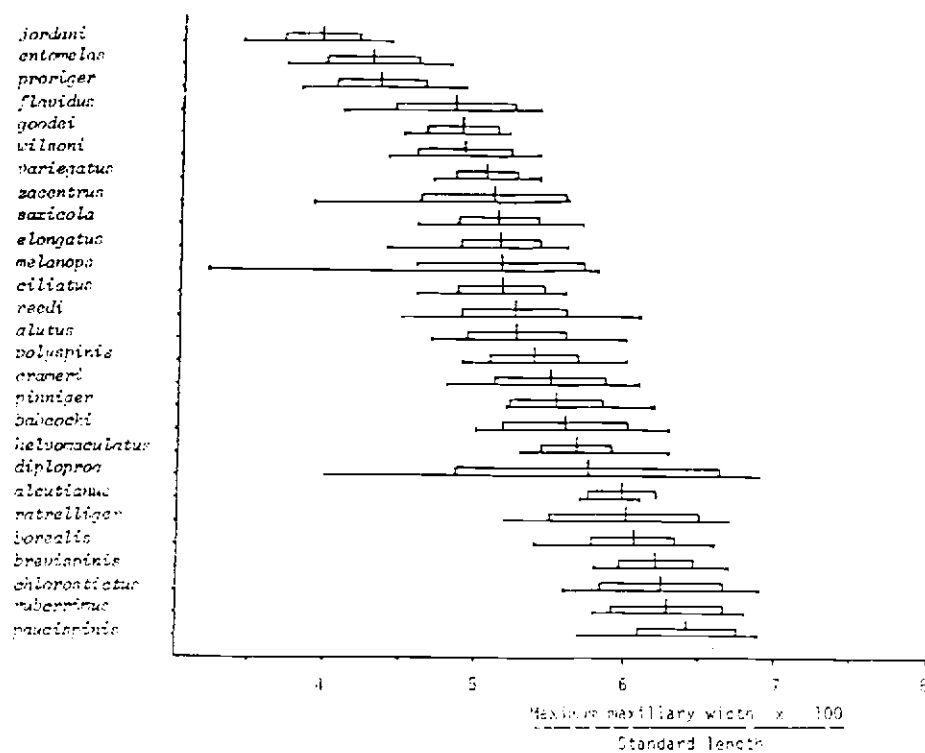


FIG. 12. Mean values, standard deviation and range of maximum maxillary width as percent of standard length, in *Sebastes* spp. of Oregon.

50% the nearest neighbor, S. flavidus, which has a mean value similar to S. wilsoni and S. goodei. S. variegatus seems to lead a large group in which the mean value of the analyzed character varies little (FIG. 12). Four species - melanops, elongatus, ciliatus, saxicola - have a high degree of overlap, the values of range for S. melanops being very wide. Very near are S. alutus and S. reedi, which almost overlap their mean, standard deviations, and ranges. S. pinniger and S. crameri have close means and standard deviations, but their reanges are quite different. From S. babcocki towards the highest value, the figure shows a gradient with some close values for neighbor species.

As the maxilla plays a functional role in close relation to the premaxilla, I measured the variations of the ratio of maximum maxillary width/maxillary + premaxillary length. In general, this analysis (FIG. 13) shows a gradient of the species mean values, with range values overlapping in all cases, most of standard deviations overlapped and some subgroups have very close mean values. There is some similarity in the order of the species compare to the same characteristic as percent of standard length (FIG. 12). We can see that S. jordani has the lowest mean in both cases and S. goodei and S. proriger mantained a similar

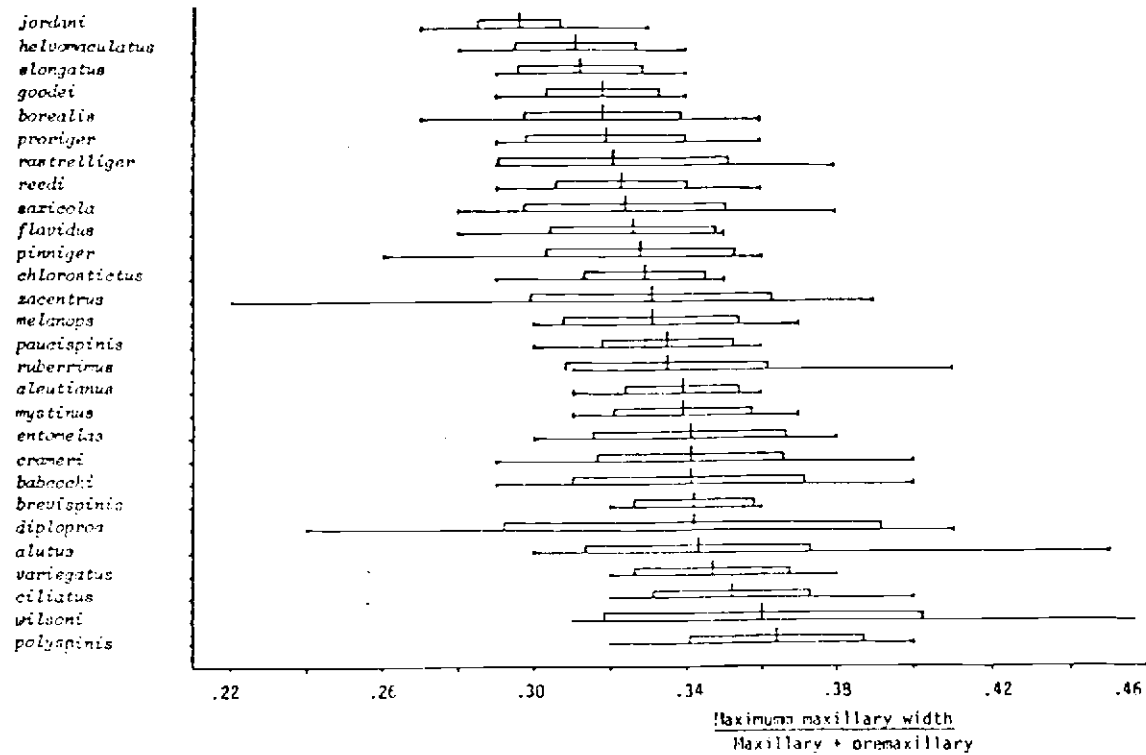


FIG. 13. Mean values, standard deviation and range of the ratio maximum maxillary width/maxil premaxillary, in *Sebastes* spp. in Oregon.

situation, but most of the species have different values. S. wilsoni is situated quite differently, as well as S. helvomaculatus, S. paucispinis and others. There are outstanding examples of variability in S. zacentrus, S. alutus and S. diploproa, whose range overlap all the other species.

The shape of the maxilla is also marked by different upper and lower edge forms. With slight variations, the upper one is almost straight in S. nigrocinctus, S. pinniger and S. elongatus. It is widely concave in S. entomelas, S. wilsoni and S. flavidus. A series of species showed an upper-anterior convex curvature, which gives a convex-concave sequence to this edge, as in S. zacentrus, S. diploproa, S. reedi, S. chlorostictus, S. brevispinis, S. paucispinis, S. mystinus and S. nebulosus. In some species the anterior convex form is so small or unclear that a general, also slight convex curvature is seen through all the edge, as is the case of S. crameri and S. ruberrimus (FIGS. 6 to 9).

Maxillary plus premaxillary unit.

Those dermal bones are the outer part of the upper jaw. The premaxillary is anterior - the only one bearing teeth - and shorter than the maxillary, which

in turn is toothless, excluded from the gape and acts as a lever for the protrusion of the former (Norman and Greenwood, 1975).

A study of this characteristic as percent of the standard length provides an appreciation of the wide range of mouth sizes in these species (FIG. 14). The range of mean values is from less than 13 to more than 19 percent, and there appear to be no discrete groupings, except that the species with the five lowest means are separated from the next higher mean by about 0.7 % and the species with the eight highest means are separated from the next lower mean by a similar value.

Regression equations and correlation coefficients for maxillary plus premaxillary length vs. standard length are shown in TABLE 4. Note that the correlation coefficients are all high, most over 0.900. Within the sizes range studied, some allometry in growth of the mouth was detected. The slopes of the selected regression lines shown in FIG. 15 show individual differences among the species and a tendency toward two groups with roughly parallel slopes. One group, including mystinus, entomelas and flavidus, showed little allometry. Others including the carnivorous borealis, ruberrimus and brevispinis showed a definite increase in mouth size with increasing length.

TABLE 3. Regression equations, correlation coefficients and number of specimens analyzed for maxillary plus premaxillary vs. standard length (mm) in Sebastes spp. of Oregon.

S p e c i e s	Y = a + bx	"r"	n
<u>aleutianus</u>	Y = 4.8903 + 0.1583X	0.992	9
<u>alutus</u>	Y = 1.8902 + 0.1429X	0.967	22
<u>babcocki</u>	Y = 2.8596 + 0.152X	0.972	21
<u>borealis</u>	Y = -1.3766 + 0.1952X	0.985	25
<u>brevispinis</u>	Y = 1.4872 + 0.178X	0.950	22
<u>chlorostictus</u>	Y = -3.7444 + 0.2008X	0.946	17
<u>ciliatus</u>	Y = 1.3792 + 0.1417X	0.894	23
<u>crameri</u>	Y = 0.5521 + 0.1598X	0.988	24
<u>diploproa</u>	Y = 5.6765 + 0.146X	0.978	24
<u>elongatus</u>	Y = 0.9768 + 0.161X	0.983	28
<u>entomelas</u>	Y = 1.6187 + 0.1218X	0.954	21
<u>flavidus</u>	Y = 7.0528 + 0.13X	0.969	21
<u>goodei</u>	Y = -10.3240 + 0.1793X	0.950	17
<u>helvomaculatus</u>	Y = -5.9810 + 0.21X	0.951	29
<u>jordani</u>	Y = 2.134 + 0.1214X	0.962	30
<u>melanops</u>	Y = 4.772 + 0.1449X	0.948	22
<u>mystinus</u>	Y = 3.9037 + 0.1163X	0.988	16
<u>paucispinis</u>	Y = 1.3153 + 0.189X	0.987	23
<u>pinniger</u>	Y = 11.7085 + 0.1399X	0.861	21
<u>polyspinis</u>	Y = 8.6547 + 0.1116X	0.924	20
<u>proriger</u>	Y = 3.5076 + 0.1224X	0.913	23
<u>reedi</u>	Y = -2.3582 + 0.17X	0.985	23
<u>ruberrimus</u>	Y = 0.1264 + 0.1817X	0.988	15
<u>saxicola</u>	Y = 2.6255 + 0.1465X	0.920	22
<u>variegatus</u>	Y = 3.5162 + 0.1268X	0.840	14
<u>wilsoni</u>	Y = -4.9598 + 0.172X	0.863	20
<u>zacentrus</u>	Y = 9.60 + 0.1125X	0.894	25

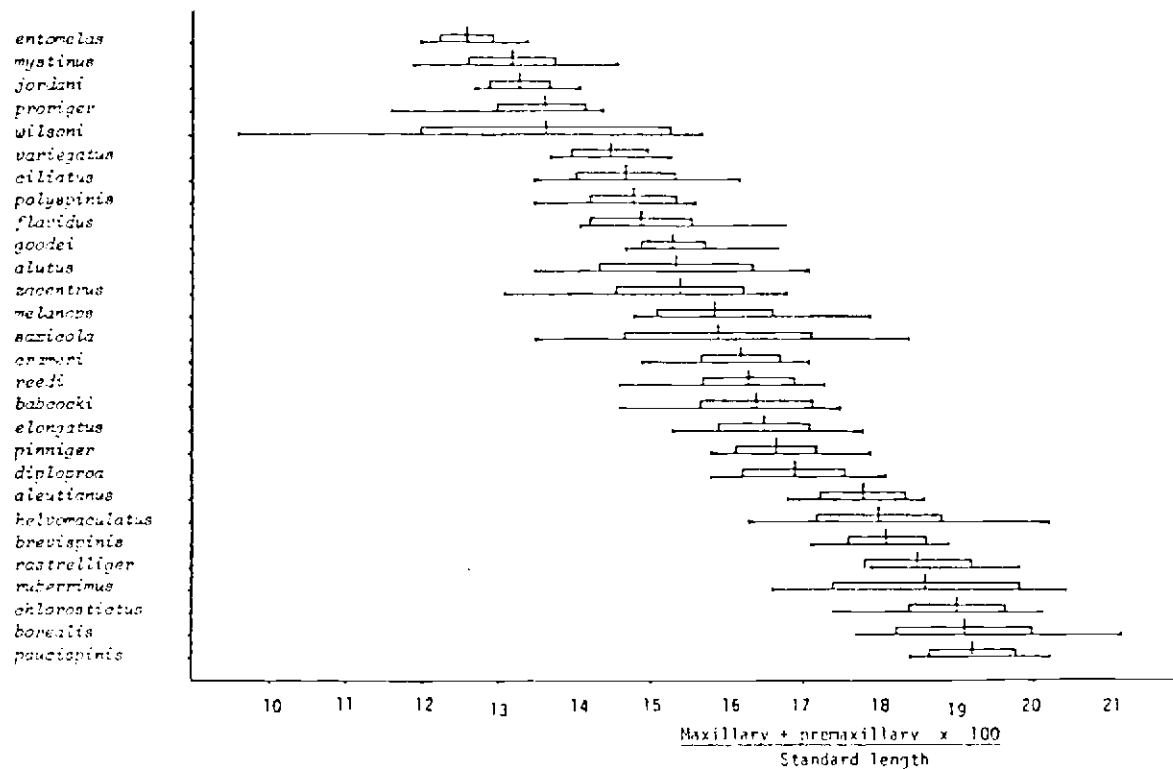


FIG. 14. Mean values, standard deviation and range of maxillary + premaxillary as percent of standard length in Sebastes spp. of Oregon.

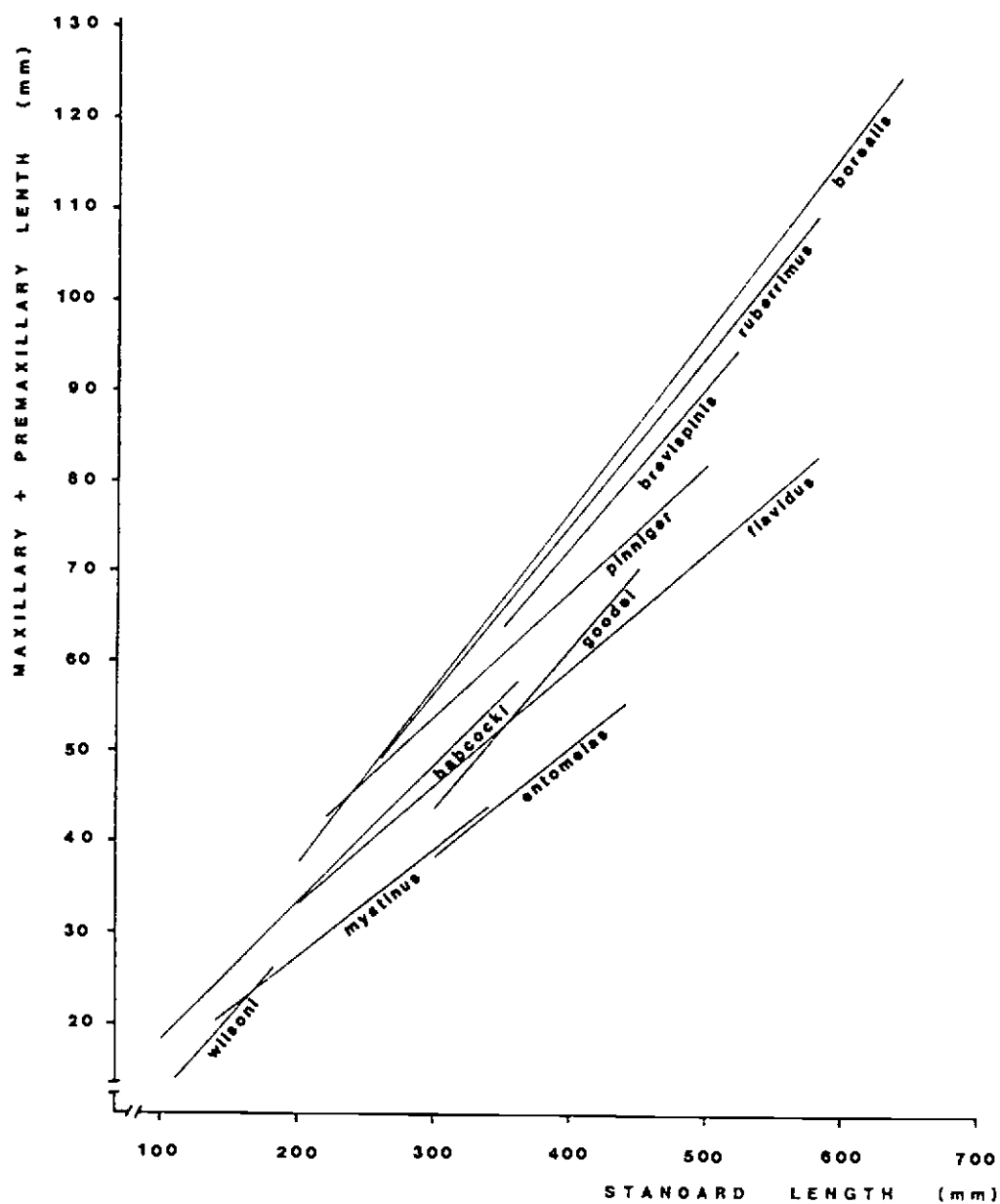


FIG. 15. Selected regression lines for maxillary pre-maxillary length vs. standard length in *Sebastes* spp. of Oregon. Basic data on TABLE 4.

Preangular length (= dentary-articular-angular unit)

As the maxillary-premaxillary unit plays a role in forming the upper jaw, the dentary, articular and angular bones forms the lower jaw or mandible. The dentary is the most important tooth-bearing element - and the only one in Sebastes - in the lower jaw of the Teleostei. It bears a lateral line canal also. The naming of the lower jaw bones differ in literature according to different authors causing some confusion. I will follow Goodrich (1930) in terminology and use "dentary" for the tooth-bearing bone, "articular" for the bone that connects the dentary to the quadrate, and "angular" for the small bone at the postero-ventral angle of the articular (in recent literature these are called respectively "dentary", "angular" and "retroarticular").

In bony fishes the development of the mandible at embryo stages starts with a mandibular cartilage - the Meckel's cartilage - which partly disappears and partly remains buried deep within the jaw structure. The posterior portion, which articulates by a socket with the upper jaw, ossifies as the articular bone. Thus the lower jaw consists chiefly of dermal bones. The three mentioned elements may curve inward

ventrally to appear also on the lower part of the inner surface of the jaw (Romer, 1955). The left and the right sides of the lower jaw join at the center line of the body (the mandibular symphysis). Each half of the lower jaw is a simple lever whose center of rotation is located in the quadrato-articular-joint, which is a kind of hinge joint, and permits full freedom of rotation in only one plane (Harder, 1975).

The lower jaw is opened the more the protrusion of the lower jaw. This was verified in the laboratory with juvenile specimens of S. paucispinis, S. elongatus and adults of S. melanops, S. goodei and S. chlorostictus. That agrees also with some observations in primitive fishes (Alexander, 1967) and also with Edwards (1926, vide: Harder, Op. Cit.) in that pulling downward of the lower jaw causes the upper jaw to move forward. There are no muscles that pull directly on the upper jaw. All that suggests that in some fishes there is rotation of the maxilla along its axis, which is caused in part by depression of the lower jaw. Maxillary rotation causes the premaxillary process of the maxilla to press against the articular process of the premaxilla, which forces the premaxilla to protrude anteriorly.

Of the trio of lower jaw bones, the articular in comparison to the dentary and the angular, is most

easily studied. The articular is flat, like a roof tile, but the dentary is strongly curved, the angular is very small and retains a comparatively large amount of connective and muscular tissue. That makes observation and photography of the bone edges difficult. I measured the length and height of the articular in several species using available dried material (TABLE 1). There were three types according to the index

$$\frac{\text{Height} \times 100}{\text{Length}}$$

Length

The types were those larger than 50%; approximately equal to 50% and smaller than 50%. S. mystinus, showed the highest value (@ 85.3%) followed by S. elongatus (73.7%), S. nigrocinctus (67.4 %), S. nebulosus (65.8%), S. ruberrimus (63.2%), S. pinniger (61.9%), S. chlorostictus (61.6%), S. crameri (59.2%), S. diploproa (59%), S. wilsoni (58%), S. brevispinis (57.4%), S. reedi (55.4%), S. melanops (55.2%) and S. entomelas (51.1%). Probably the last one can be together with S. proriger (50%) in the second group. With an index below 50% were S. zacentrus (48.5%), S. goodei (47.2%), S. flavidus (45.8%) and S. paucispinis (44.6%) (FIG. 16).

The dentition of the dentary differs according to

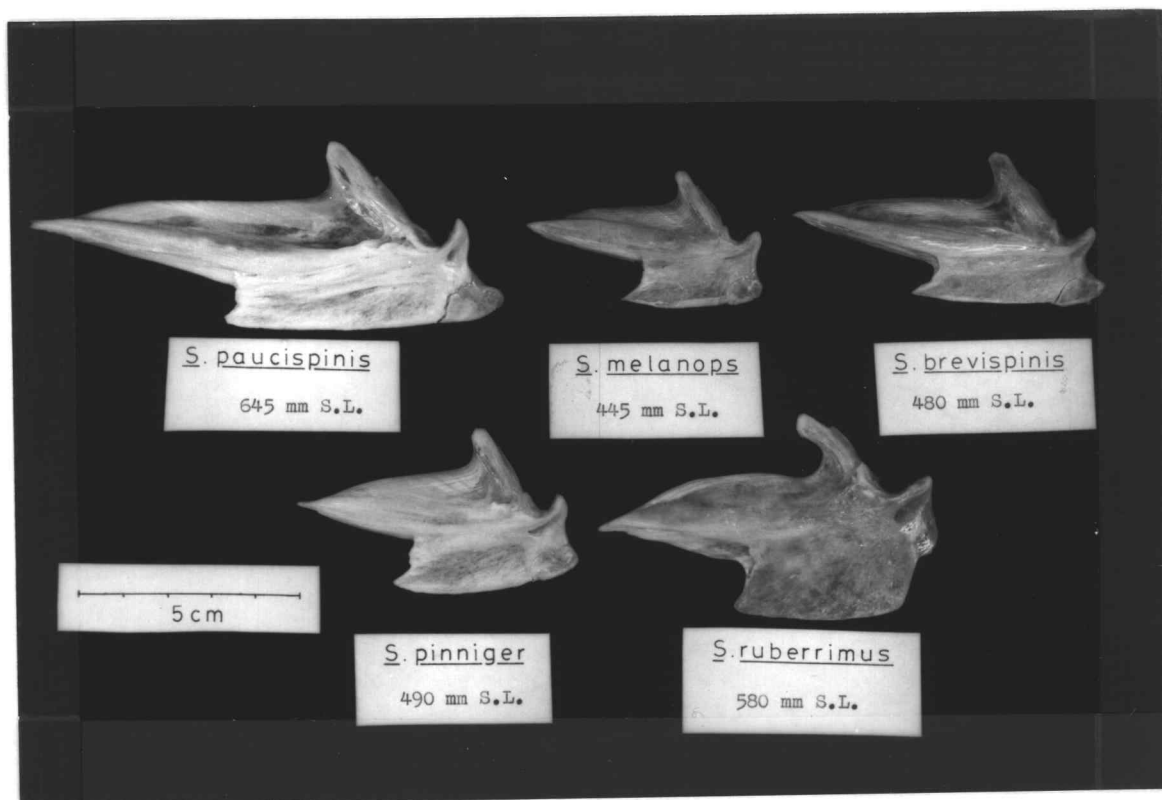


FIG. 16. Articular bones of selected species of rockfishes, Sebastes spp. from Oregon.

species. Some species have a relatively wide tooth band and a relatively wide dentary, e.g. S. nigrocinctus, S. ruberrimus, S. nebulosus and S. chlorostictus. Another group has a more slender, comparatively long dentary, with a narrow tooth band, as shown by S. paucispinis, S. goodei, S. flavidus, S. entomelas, S. wilsoni and S. brevispinis. The latter has a strong symphyseal knob and teeth directed inwards. Species with latively short dentary and rather narrow teeth bands are S. mystinus, S. pinniger and S. diploproa. A form of dentary of intermediate length, with narrow tooth bands, is present in S. melanops, S. crameri, S. elongatus, S. proriger, S. zacentrus and S. reedi.

Although a general classification by width of dentary tooth bands is possible, most species have particular features that contradict the system. For instance, S. reedi has greatly increased width of the tooth band anteriorly and a strong symphyseal knob. Others such as crameri, pinniger, diploproa, melanops, and brevispinis have a similar knob, but with individual differences. Typical forms without knobs are shown in FIG. 17.

These three bones as a unit were measured as a percentage of standard length (FIG. 18). As in other characteristics, S. entomelas showed the lowest value

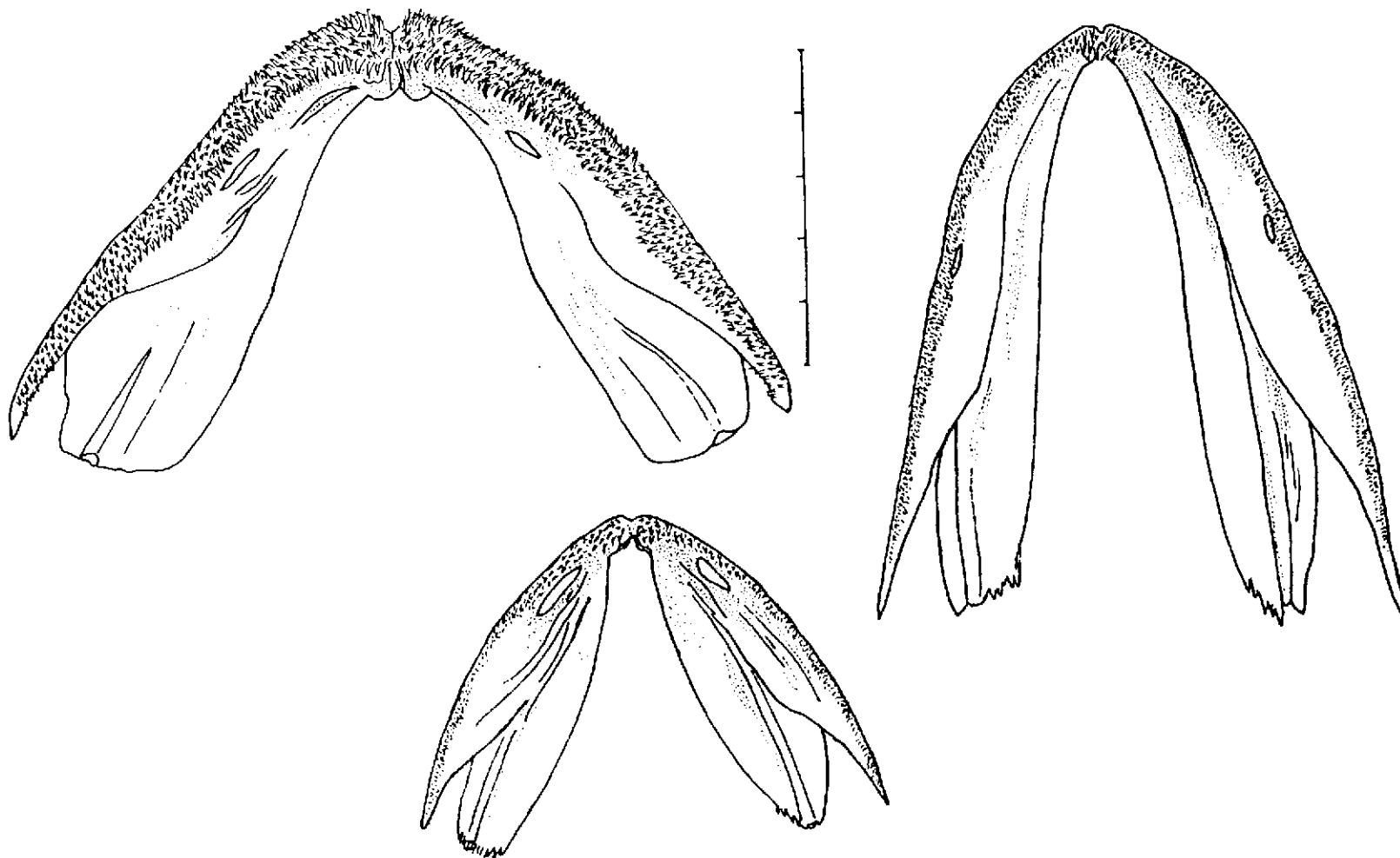


FIG. 17. Dentary bones of selected Sebastes spp. of Oregon.

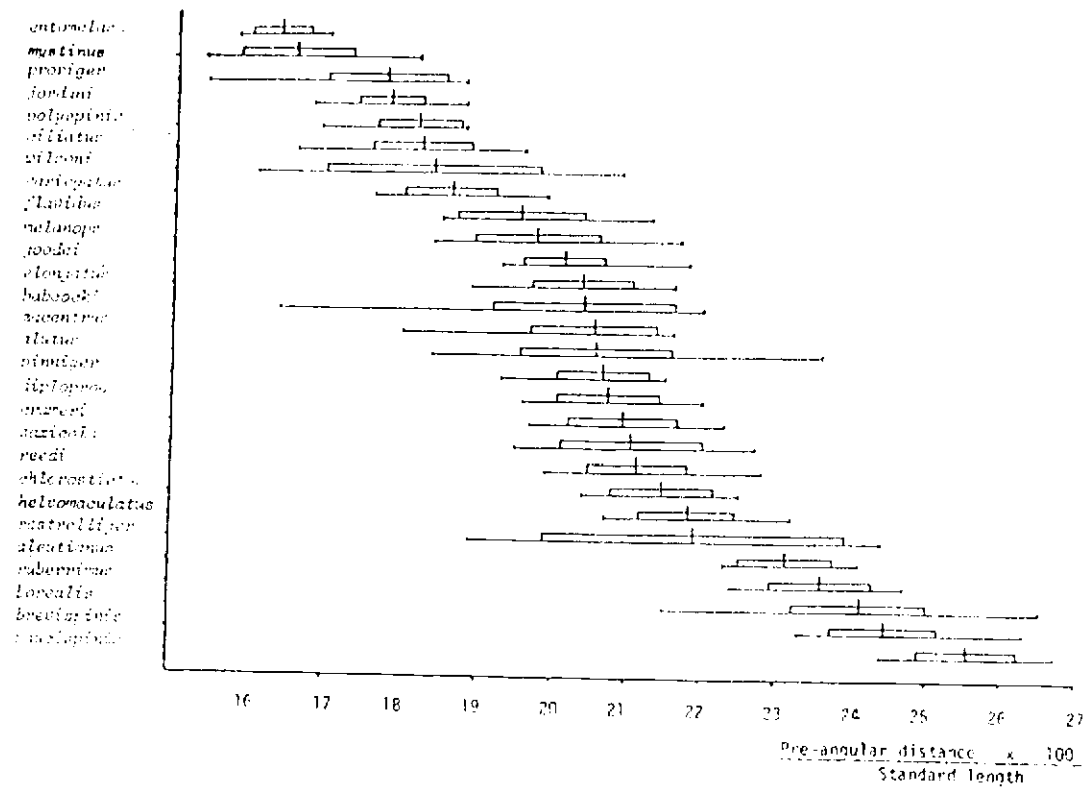


FIG. 18. Mean values, standard deviation and ranges of pre-angular distance as percent of standard length, in *Sebastes* spp. of Oregon.

and S. paucispinis the highest, being both more or less differentiated from the rest of the species. The overlap in mean values is very low, although in several cases, there is overlap in standard deviations and ranges. S. proriger and S. jordani, with low values, had close means. Some species have a rather restricted range for the preangular distance as percent of the standard length, but other like S. wilsoni, S. babcocki, S. alutus and S. borealis are quite variable; but the slope of values is rather shallow than sharp and there is no overlap of ranges between the nine having the lowest values and the five having the highest values.

Some grouping are apparent according to this graphic, which shows S. entomelas alone (16.5%), followed by S. proriger, S. jordani, S. polyspinis, S. ciliatus, S. wilsoni and S. variegatus (17.8 to 18.7%). A third group with S. flavidus, S. melanops and S. goodei is followed by several species: S. elongatus, S. babcocki, S. zacentrus, S. alutus, S. pinniger, S. diplproa, S. crameri, S. saxicola and S. reedi (19.6 to 21.2%). S. chlorostictus, S. helvomaculatus and S. rastrelliger seem to form a fourth group (21.5 to 22%), and from here (23%) to the highest value, the mean averages - no matter the degree of standard deviation

and range overlappings - are spread in such a way that no grouping will be attempted for them.

I have analyzed the preangular distance vs standard length and calculated "r" values (TABLE 4). If the regression lines are drawn, they are similar to those in FIG. 15. S. paucispinis has the longest lower jaw in relation to standard length, followed by brevispinis, ruberrimus and borealis. S. paucispinis and S. brevispinis show the strongest allometry. S. entomelas has the shortest relative length of lower jaw, but is not much different from mystinus, which shows slightly less allometry. Several of the medium-sized species have similar slopes, intermediate to the extremes.

Vomer

Although the vomer was primitively a paired structure, both parts are solidly fused together as a median bone in Sebastes. It is located at the base of the base of the nasal region, beneath the ethmoid and in front of the parasphenoid, another dermal bone. In Sebastes the vomerine teeth are in the midline of the roof of the oral cavity (FIG 4B).

It is difficult to maintain the teeth in place after dissection or - more difficult - after

TABLE 4. Regression equations, correlation coefficients and number of specimens analyzed for preangular distance vs. standard length (mm) in Sebastes spp. of Oregon.

Species	Y = a + bx	"r"	n
<u>aleutianus</u>	Y = 0.1694 + 0.2306X	0.993	9
<u>alutus</u>	Y = 1.6286 + 0.1964X	0.980	22
<u>babcocki</u>	Y = 4.6252 + 0.1844X	0.962	21
<u>borealis</u>	Y = 7.4735 + 0.2154X	0.991	25
<u>brevispinis</u>	Y = -0.3228 + 0.2470X	0.932	22
<u>chlorostictus</u>	Y = 3.7327 + 0.2036X	0.937	17
<u>ciliatus</u>	Y = -0.27 + 0.1832X	0.931	23
<u>crameri</u>	Y = -1.1977 + 0.2137X	0.986	24
<u>diploproa</u>	Y = 7.38 + 0.1779X	0.986	24
<u>elongatus</u>	Y = -0.9793 + 0.2076X	0.990	28
<u>entomelas</u>	Y = -5.9755 + 0.1805X	0.976	21
<u>flavidus</u>	Y = 6.0755 + 0.1795X	0.967	21
<u>goodei</u>	Y = 5.0502 + 0.1884X	0.923	17
<u>helvomaculatus</u>	Y = -5.3349 + 0.2449X	0.978	29
<u>jordani</u>	Y = 0.995 + 0.1721X	0.980	30
<u>melanops</u>	Y = 7.8759 + 0.1751X	0.961	23
<u>mystinus</u>	Y = 1.6745 + 0.1585X	0.989	16
<u>paucispinis</u>	Y = 2.6954 + 0.2496X	0.989	23
<u>pinniger</u>	Y = 9.8255 + 0.1820X	0.978	21
<u>polyspinis</u>	Y = 6.7153 + 0.1539X	0.949	20
<u>proriger</u>	Y = 5.6213 + 0.1553X	0.923	23
<u>reedi</u>	Y = -1.0715 + 0.2138X	0.982	23
<u>ruberrimus</u>	Y = 5.3066 + 0.2226X	0.991	15
<u>saxicola</u>	Y = 3.6189 + 0.1925X	0.970	22
<u>variegatus</u>	Y = 7.7012 + 0.1459X	0.859	14
<u>wilsoni</u>	Y = 2.3403 + 0.1677X	0.869	20
<u>zacentrus</u>	Y = 12.642 + 0.1525X	0.892	25

=====

preparation of the bones for dry preservation, because dehydration affects flexibility and they become fragile and deciduous. Most of the vomers have lost many, if not all their teeth in preservation.

The bone has a main body and tail. The surface of the bone exposed to the oral cavity is tooth-bearing (FIG. 19) while the rest of the bone lies under the mucous membrane of the roof of the mouth. The tail fits - with great detail - into the parasphenoid articulation, allowing no independent movement (except those possible by flexibility of the ensemble). The index

$$\frac{\text{Width} \times 100}{\text{Length}}$$

Length

is variable in the Sebastes examined (FIG. 20). Three groups were distinguished, based in one to three specimens of each species: (1) 63% to 50%, e.g., S. pinniger, 63.3%, S. ruberrimus, 60%, S. crameri, 53.3%, S. wilsoni, 52.4%, S. entomelas, 50% and S. nebulosus, 50%. (2) From about 49% to 40%, i.e., S. flavidus, 48.5%, S. reedi, 47.2%, S. goodei, 46.3%, S. elongatus, 45.7%, S. nigrocinctus, 43.9%, and S. chlorostictus, 43.6%, and (3) 39% and less, i.e., S. brevispinis, 39.6%, S. melanops, 39.5%, S. zacentrus,

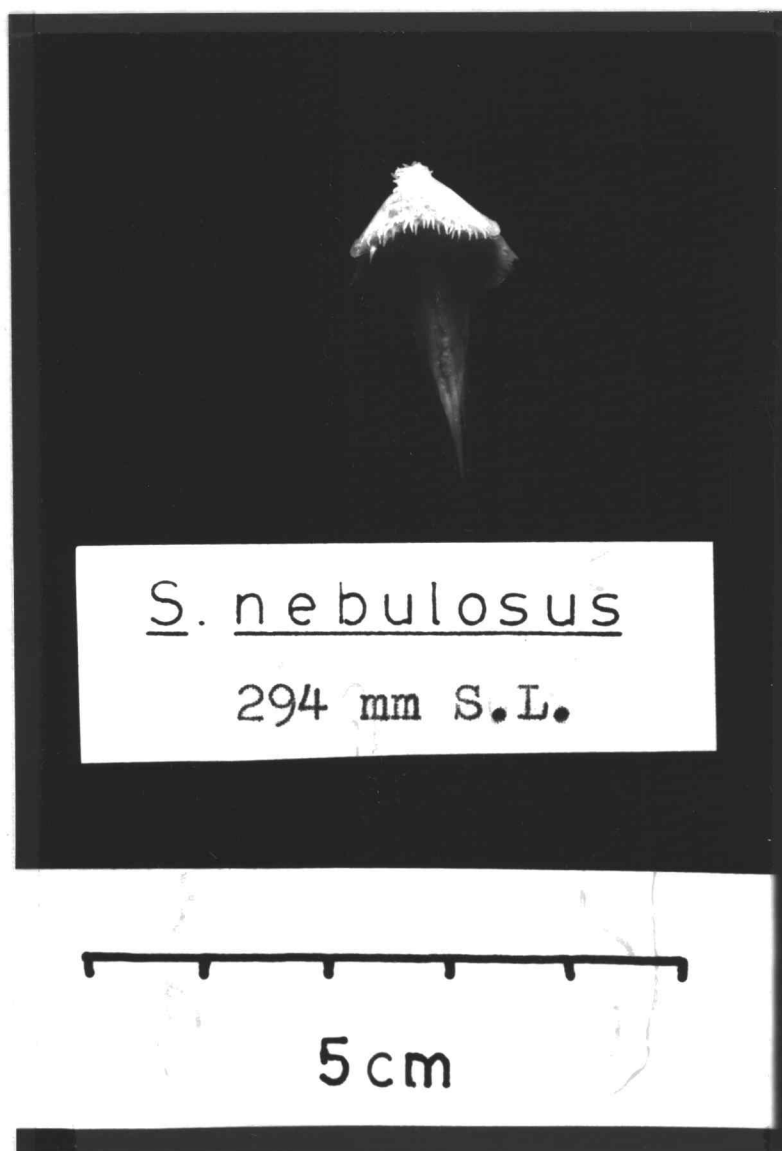


FIG. 19. Lower view of the vomer of S. nebulosus.

39.5%, S. proriger, 38.9% and S. diploproa, 34.2%.

The variation of the toothed surface varies according to species, but some structural similarities are seen in the shape of the surface. Some species have a patch of teeth that project anteriorly. This is very clear in S. nebulosus (FIG. 20), and also in S. chlorostictus, S. wilsoni, S. melanops and S. brevispinis, and to a lesser degree, in S. elongatus, S. nigrocinctus and S. zacentrus. Other species have a boomerang-like surface form, with variation in the angle and in the width of the symphysis. Examples are S. goodei, S. ruberrimus, S. pinniger, S. mystinus, S. paucispinis and S. entomelas. Other species that tend to have a rather triangular margin are S. diploproa, S. crameri and S. reedi. Other species, such as S. flavidus and S. proriger are in between the two groups described.

Location of the vomer suggests that vomerine teeth are used mainly for retention of prey within the oral cavity. The vomer opposes the toothless, but mobile tongue, which can force prey against the roof of the oral cavity. The tongue and its supporting bone, the glossohyal, will be covered in a later section.

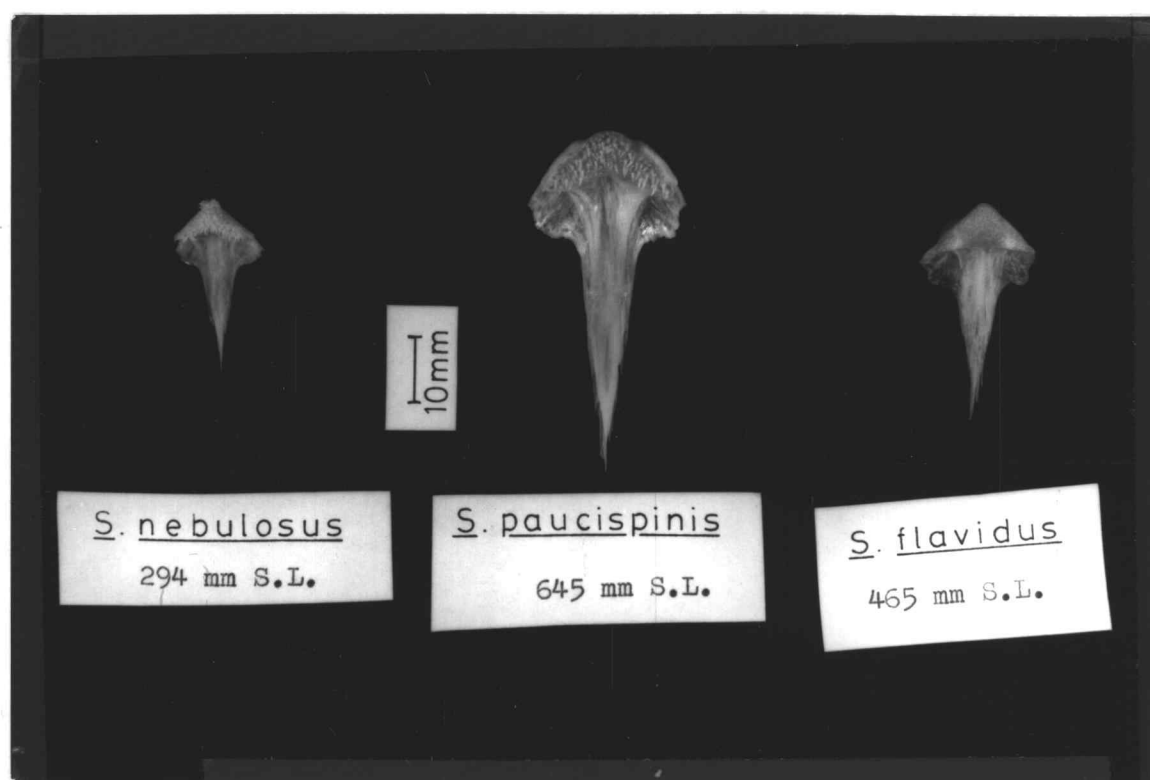


FIG. 20. Vomer bones of selected species of Sebastes.

Palatine

The palatine is the most anterior portion of the palatoquadrate or primary upper jaw. It lies laterally against the ethmo-vomer block and is posteriorly attached to the pterygoid, ventrocaudally to the ectopterygoid and dorsolaterally to the entopterygoid (Harder, 1975).

The palatine of most bony fishes, is a dermal bone, formed below the palatoquadrate cartilage by the coalescing of tooth bases, effectively supporting the autopalatine, which is part of the visceral cranium, one of the elements of the so-called oromandibular arch. In intermediate and higher teleosts a prong from the upper portion of the forward end of the palatine extends laterally over the anterior (median) part of the maxillary. Because of the suspensorium acts as a single movable unit, the tip of this palatine prong swings upward when the lower portion of the two suspensoria are spread apart, which happens whenever the oral cavity is laterally expanded. Since the palatine prong extends over the anterior end of the maxilla, its movement affects both the premaxilla and the maxilla. Thus the palatine becomes a component of the complex mechanism for moving the front of the upper jaw (Gosline, 1973). There is not a toothed counterpart

to the vomer and palatine in the floor of the mouth. I assume these bones work in opposition to the tongue in securing the prey.

The length and width of the palatine (FIG. 3B) were measured and the index

$$\frac{\text{Maximum width} \times 100}{\text{Length}}$$

allowed me to recognize different patterns of palatine forms. Three main groups are recognized: (1) slender, from the lowest possible percentage, to about 30%; (2) medium, from about 31% to about 39% and (3) stout, over 40%. After measuring from one to three specimens by species, they were grouped as follows. In the first group, S. paucispinis (28%), S. proriger (27.9%) and S. brevispinis (30%). The second group included S. zacentrus (32%), S. entomelas (32.4%), S. wilsoni (33.3%), S. flavidus (35%), S. diploproa (35.7%), S. elongatus (37.5%), S. mystinus (37.7%) and S. goodei (38.9%). Finally, in a third group, were S. nebulosus (40.5%), S. crameri (41%), S. melanops (41.2%), S. nigrocinctus (41.2%), S. ruberrimus (43.1%), S. reedi (43.8%), S. chlorostictus (44.7%) and S. pinniger (45.2%) (FIG. 21).

The tooth band can be, as seen in the premaxilla



FIG. 21. Palatine bones of selected Sebastes spp.

and maxilla: wide, intermediate and narrow, using principally the surface of the lower face of the lateral wing border. Dentition is different according to species. The main difference among species is based in the width of the band of teeth, which can be located on the edge itself or can be extended toward the internal wall in such a way that teeth are facing the center of the oral cavity. These teeth are easily removed.

Pharyngeal bones

These are dermal elements associated with the gill arches and bear the pharyngeal teeth. The upper pharyngeal teeth are located on the pharyngobranchials. The lower ones on the ceratobranchials (Harder, 1975). The dentigerous plates are formed on endochondral bones.

In Sebastes there are four pairs of upper pharyngeals. Generally the two anterior ones are closer to each other than the second or third or posterior. The fourth is located latero-external in respect to these other three, and will be not discussed here. The form of these dermal plates changes from species to species, but they show a general pattern. They do not show rows of teeth, but a rather random distribution of

them.

Because of modification of the fourth arch, the upper dentigerous plates are developed in the second, third (two dentigerous plates) and fifth pharyngobranchials. The second has a general narrow and transverse - in relation to food passage - tooth band that tends to be well fitted with the inner plate of the third arch, which is the largest in tooth-bearing surface in the group. The plate of the second arch looks like the most conservative in form, while the inner plate of the third seems to be more variable among species. In S. ruberrimus it is triangular with broad base. In S. nigrocinctus has an oval form and in S. brevispinis it is wide anteriorly and narrow posteriorly. All the other forms tend to change among these patterns, with a trend in S. flavidus to a rhomboidal form. All of them have teeth on the surface, generally numerous, and never borne on plates. The last or posterior dentigerous plate is generally intermediate in toothed surface but, like the plate of the second arch, is relatively conservative in form, being generally rounded or slightly enlarged as in S. brevispinis. In some species like S. pinniger and S. ruberrimus showed a tendency to have a waist.

The three plates studied form a unit which fits,

in great measure, the shape of the unique lower pharyngeal. The fourth - do not discussed here - seems to fit with the posterior end of the lower pharyngeals.

Lower pharyngeal dentigerous plates are developed on the ceratobranchial bones. They have always an elongate form, with tendency to a triangular surface in some species like S. nigrocinctus. But a main central area is general to them and gradually narrower towards both extremes. It was possible to measure (FIG. 3C) the length and width of this area - in one to three specimens for a species - and express the result as,

$$\frac{\text{Width} \times 100}{\text{Length}}$$

The lower the index the more elongate and slender the toothed surface. We visualize three possible groups or patterns: a first one, with narrow, elongate patch, index less than 20%; a second, intermediate, with index between 28% and 30%, and a third with a wide and relatively short teeth patch and index higher than 30%. The first group include species like S. brevispinis (20.3%), S. reedi (22.5%), S. zacentrus (23.1%), S. goodei (23.8%), S. proriger (25%), S. crameri (27.2%), S. flavidus (27.3%) and S. wilsoni (27.4%). The second group contained S. pinniger (28%),

S. mystinus (28.6%), S. paucispinis (28.8%), S. entomelas (29.1%), S. diploproa (30%) and S. chlorostictus (30.4%). In the third group were S. melanops (39.8%), S. nigrocinctus (33.3%), S. ruberrimus (34.4%), S. elongatus (35.3%) and S. nebulosus (50%). Although our figures are from bones from few specimens, they show the trend corroborated when more bones are seen (FIG. 22).

In all the species mentioned - and pictured in relation to pharyngeal teeth - are cardiform; each tooth is pointed and more or less curved. The upper pharyngeals, as the lower ones, easily lose teeth after drying.

Parasphenoid

The parasphenoid is a dermal bone, basal in the neurocranium. It laterally covers the basisphenoid and part of the basioccipital as well, and extends from the later to the vomer and forms a large part of the roof of the orobranchial cavity (Harder, 1975). It also integrates a bony unit: vomer-parasphenoid-basioccipital, also known as keel bone. Some authors name only the parasphenoid as keelbone (Gregory, 1933). This can be the situation of those elements of the head that provide rigid structural support for the cranium and

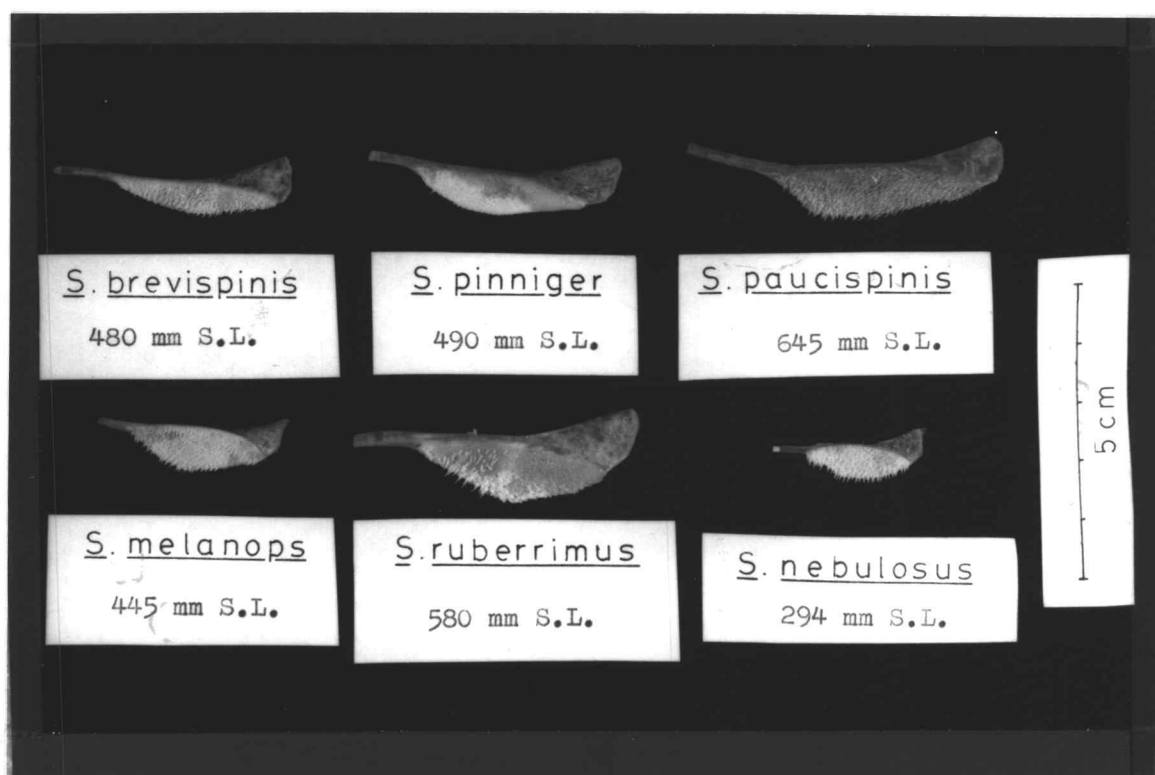


FIG. 22. Lower pharyngeal bones selected to show tooth-patches in several *Sebastes* spp.

form relatively large stiff units (Gosline, 1973).

Observations on selected parasphenoids of *Sebastes* are warranted because used in food intake by the more primitive fishes, in which it normally bears teeth. As is the case with certain other dermal components, parasphenoids lose their original special function in higher teleosts, but continue to exist as member of this complex (Gosline, Op.Cit.).

This bone tend to develop an anterior transverse process supporting the basitrabecular process of the basisphenoid region, an another more posterior lateral process - or wing - supporting the outer wall of the trigemino facialis chamber (Goodrich, 1930). These wings are easy to visualize at the lower posterior area of the interorbital foramen in their articulation with the ventral processes of the prootics (FIG. 3A). The morphology of the parasphenoid is rather complex. For example, the mode of attachment with the vomer is through a longitudinal, very narrow groove in the lower surface. All the parasphenoids have slender bifurcated caudal ends. Some species have an upwards curvature towards the caudal end in such a way that all the bone is curved from the level of the wing processes to the basioccipital connection. Species with this characteristic are: *S. entomelas*, *S. diploproa*, *S.*

reedi, S. wilsoni, S. flavidus, S. goodei, S. mystinus, S. crameri and S. proriger. A practically flat lower surface is seen in S. ruberrimus, S. nebulosus and S. paucispinis. A very slight elevation of the posterior or caudal end is seen in S. melanops, S. elongatus, S. zacentrus and S. nigrocinctus, a group that can be considered intermediate for purposes of comparisons.

In order to show possible patterns, more informative than the bone curvature, I calculated the index

$$\frac{\text{Pre-lateral process distance} \times 100}{\text{Total parasphenoid length}}$$

in one to four specimens of each species using available dry material. The larger the index the longer the length or proportion of the pre-process distance or, the shorter the post-process distance of the bone. In some way the lateral process is more forward or more backward according to each species. We do not see clear separation of groups although it is easy to show differences in the bones themselves. But a gradient according to the value of the index, calculated as few lines above, can give us at least a reference on the possible interspecific variation. We have the following order in our sample: S. diploproa (67.2%), S. goodei (66.3%), S. paucispinis (66.1%), S. entomelas (65.3%),

S. pinniger (63.5%), S. zacentrus (62.3%), S. brevispinis (61.9%), S. wilsoni (61.5%), S. crameri (60.9%), S. chlorostictus (60.7%), S. nigrocinctus (60.6%), S. elongatus (60.3%), S. flavidus (59.8%), S. proriger (59.6%), S. reedi (58.9%), S. melanops (57.4%) and S. mystinus (52.5%) (FIG. 23).

The form of the wings of the lateral process and their curvature up and forward, change according to each species, as well as the relationship between length and width of the post-lateral process part of the bone.

In the ventral surface of the bone, facing the orobranchial cavity, we have anteriorly the "V" shaped groove to articulate with the vomer. Toward the center of the bone, a longitudinal keel which may be wide and flat as in S. ruberrimus, S. melanops, S. goodei, S. brevispinis and S. paucispinis, or rather slender, with more or less sharp edges like shown by S. diploproa, S. zacentrus, S. chlorostictus, S. nebulosus and S. nigrocinctus. Other species in the study have neither raised or flat ventral keels.

At the level of the lateral process, the keel tends to bifurcate, backwards on the bone, giving origin to a more or less deep groove between both new arms, which finally forms the caudal extremes of the



FIG. 23. Parasphenoid bones of selected *Sebastes* spp.

parasphenoid. In the area of the very beginning of the bifurcation, below the lateral process, or a little before, these two new arms or branches of the projected keel are enlarged to form the ventral apophysis of the parasphenoid. These are sometimes so flat that no evidence for them is clear at all - S. ruberrimus, S. paucispinis, S. melanops - but the following species showed the apophysis very well : S. entomelas, S. crameri, S. elongatus, S. nigrocinctus and S. nebulosus, especially the latter two, in which the edges tend to be sharp, bearing in our specimens, fine serration-like formations. This shape of the apophysis deserves interest for further observations.

Glossohyal

The glossohyal is an endochondral bone of the visceral cranium, situated in the anteriormost part of the hyoid arch. It is known as the bone of the tongue and, as such, assumes medial position, holding the sides of the hyoid arch together (Harder, 1975).

This bone is a tooth-bearing structure in some fishes. Mostly these are phylogenetically more primitive than the socrapaenids. But here the toothless bone still plays a role in the tongue movement. The part of the tongue that contains the glossohyal is

anteriorly free from the floor of the mouth. The soft tissue of the tongue differs in form at the anterior end. This can be expected to have some relation to the shape of the glossohyal which is covered by those tissues.

We find outstanding differences in the glossohyal from species to species (FIG. 24). The principal variable characteristic is the width of the anterior end of the bone, which gives the idea of a spatula - as seen clearly in S. entomelas, S. flavidus, S. melanops, S. diploproa, S. pinniger, S. mystinus and S. ruberrimus - or a simple stick-like structure as showed by S. paucispinis, S. zacentrus and S. brevispinis. Other species showed an intermediate form, with a kind of waist, in some cases such as S. entomelas, S. proriger, S. flavidus, S. melanops, S. pinniger and others. The waist tends to be more evident the wider the anterior end of the glossohyal is. The spatula-like form appears abruptly truncated anteriorly in species like S. reedi, S. nigrocinctus and S. goodei, while in others it is well rounded, as seen in S. entomelas, S. diploproa and S. ruberrimus.

First branchial arch

Constituentsofthe visceral cranium, composed of

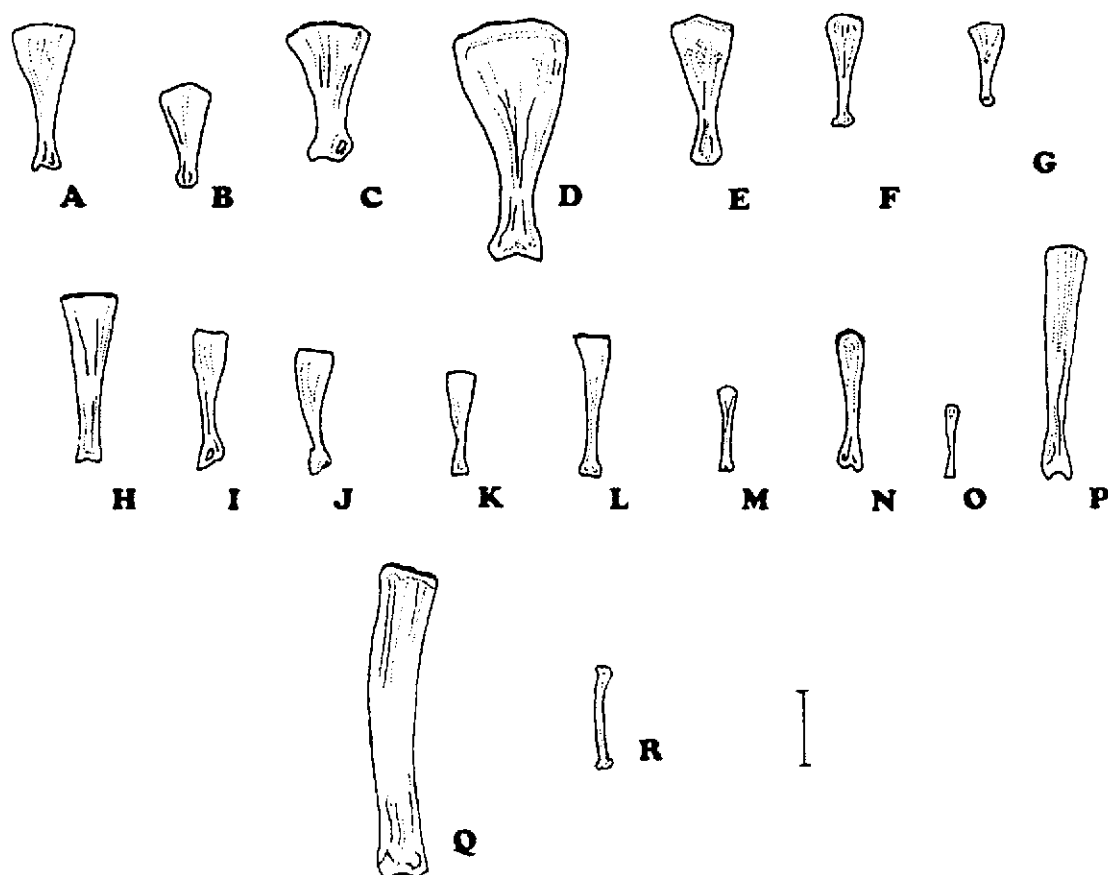


FIG. 24. Glossosnyal bones of selected *Sebastes* spp. from Oregon. Standard length for each case given in mm, in parenthesis. A, *S. flavidus* (465); B, *S. entomelas* (432); C, *S. pinniger* (440); D, *S. ruberrimus* (580); E, *S. melanops* (445); F, *S. diploproa* (311); G, *S. mystinus* (320); H, *S. roodei* (453); I, *S. nigrocinctus* (351); J, *S. chlorostictus* (361); K, *S. elongatus* (320); L, *S. reedi* (423); M, *S. proriger* (255); N, *S. crameri* (394); O, *S. wilsoni* (184); P, *S. brevispinis* (490); Q, *S. paucispinis* (645) and *S. S. zacentrus* (305).

endochondral bone, are located in the branchial region. They are bar-like bony elements: the pharyngo-, epi-, cerato- and hypobranchial. These elements bear gill filaments and gillrakers. The first branchial arch is the outermost of the group and bears gill filaments - in close contact with the pseudobranchiae located on the gill cover - and gillrakers (FIG. 2C). Between this arch and the gill cover there is an important water passage during the breathing process. In this process particles of food or other material can escape or pass by way of the pharyngeal openings and perhaps clogging or injuring the delicate gill filaments. This danger is lessened by special structures known as gillrakers which take the form of a double row of stiff appendages on the inner margin of each hoop-like gill arch (Norman and Greenwood, 1975). The external row of gillrakers of one arch joins the points of the inner row of gillrakers of the precedent arch, in such a way that all together form a filter basket structure, which can be opened or contracted according to needs of the fish.

The first gill arch, because of its strategic position to capture food particles, has the most specialized morphology required by the particular food habits of each species. Because of that I have studied the lower limb of this arch, which makes up more than

the 50% of the complete structure, because of the role I believe gravity must play in developing filtering structures. Because of this force, any heavy particles should go to the lower side of the arch. This lower limb is composed of the hypobranchial and the ceratobranchial, both gillraker-bearing bones.

We will attempt to show the existence of a gradient of differential lengths of the lower limb, according to species. I measured the lower limb as a percent of the standard length of the fish. Mean values, standard deviations and ranges for most common Oregonian species and some from adjacent areas can be seen in a gradient (FIG. 25).

As in other cases, S. entomelas leads the sample with the lowest mean. Although generally adjacent species overlap each other in this gradient. In the complete series of species there is a group of similar ratios in the center of the gradient. S. alutus, S. helvomaculatus, S. reedi, S. brevispinis and S. babcocki, are outstandingly similar for this characteristic. At the beginning we can visualize several - S. entomelas, S. proriger, S. variegatus and S. wilsoni - in which the gradient is steeper. Although S. jordani overlaps very much with S. wilsoni, does not overlap with S. entomelas, or with S. polyspinis or S.

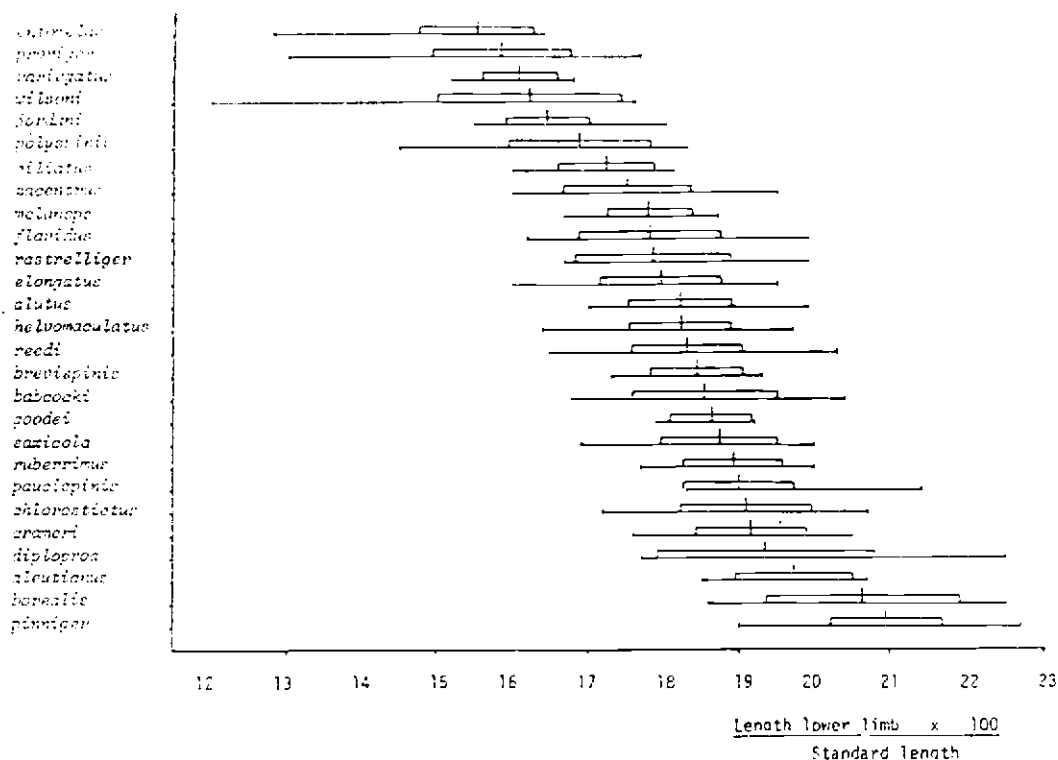


FIG. 25. Mean values, standard deviation and ranges of length of the lower limb of the first branchial arch as percent of standard length, in *Sebastes* spp.

ciliatus. At the highest value end, the ratio of S. proriger is close to that of S. borealis, which is separate from the rest. A series of species lies in between, but the degree of overlap does not allow separation of distinct groups.

In studying the length of the lower limb of the first branchial arch in its relationship with the standard length, I find a compact group of regression lines, with high correlation coefficients (TABLE 5). This analysis shows that S. pinniger has the steepest slope and S. polyspinis shows the least allometry.

S. pinniger, as well as S. borealis, S. paucispinis, S. brevispinis and S. flavidus, showed a clear trend to spread the "fan", to differentiate among themselves toward larger sizes. This is more evident because these species grow to larger sizes than the others, with lengths in excess of 450 mm. The species in the bulk of the sample have lengths between 150 and 350 mm.

Study of the gillrakers

The function of gillrakers is related to their morphology features for which results will be given on shape, number, presence of teeth or spinulae and length. In Sebastes the gillrakers in the outer row on

TABLE 5. Regression equations, correlation coefficients and number of specimens analyzed for length of the lower limb of the first branchial arch vs. standard length (mm) in Sebastes spp. of Oregon.

S p e c i e s	Y = a + bx	"r"	n
<u>aleutianus</u>	Y = -2.5085 + 0.2077X	0.988	9
<u>alutus</u>	Y = 0.7818 + 0.1776X	0.989	22
<u>babcocki</u>	Y = 6.2219 + 0.1588X	0.976	21
<u>borealis</u>	Y = 1.6649 + 0.2019X	0.980	25
<u>brevispinis</u>	Y = 14.4998 + 0.1518X	0.919	22
<u>chlorostictus</u>	Y = -1.0687 + 0.195X	0.917	17
<u>ciliatus</u>	Y = 0.4570 + 0.1705X	0.929	23
<u>crameri</u>	Y = 1.7776 + 0.1853X	0.982	24
<u>diploproa</u>	Y = 11.1762 + 0.1472X	0.925	24
<u>elongatus</u>	Y = -5.2906 + 0.2045X	0.994	27
<u>entomelas</u>	Y = -10.0118 + 0.1829X	0.932	21
<u>flavidus</u>	Y = 9.9379 + 0.1520X	0.954	21
<u>goodei</u>	Y = 16.8880 + 0.1432X	0.934	17
<u>helvomaculatus</u>	Y = 3.0527 + 0.1669X	0.945	29
<u>jordani</u>	Y = -0.0858 + 0.1649X	0.952	30
<u>melanops</u>	Y = 2.0403 + 0.1721X	0.976	23
<u>mystinus</u>	Y = 2.7361 + 0.1424x	0.979	16
<u>paucispinis</u>	Y = -2.7307 + 0.1958X	0.979	23
<u>pinniger</u>	Y = -6.3924 + 0.2257X	0.982	21
<u>polyspinis</u>	Y = 16.0075 + 0.1036X	0.912	20
<u>proriger</u>	Y = 2.9465 + 0.1466X	0.873	23
<u>reedi</u>	Y = -1.2549 + 0.1864X	0.977	23
<u>ruberrimus</u>	Y = -2.7106 + 0.1960X	0.988	15
<u>saxicola</u>	Y = 5.5125 + 0.1602X	0.970	22
<u>variegatus</u>	Y = 5.7817 + 0.1306X	0.865	14
<u>wilsoni</u>	Y = -1.7330 + 0.1747X	0.918	20
<u>zacentrus</u>	Y = 10.2000 + 0.1304X	0.945	25

TABLE 6. Different rockfishes, Sebastes spp. of Oregon, arranged alphabetically and by gillraker form pattern groups.

Short and stout	Intermediate short	Intermediate long	Long and slender
		<u>aleutianus</u>	<u>alutus</u>
<u>babcocki</u>			
<u>borealis</u>	<u>brevispinis</u>		
	<u>caurinus</u>		
<u>chlorostictus</u>	<u>ciliatus</u>	<u>crameri</u>	
		<u>diploproa</u>	
	<u>elongatus</u>	<u>entomelas</u>	<u>flavidus</u>
		<u>goodei</u>	
	<u>helvomaculatus</u>		<u>jordani</u>
	<u>maliger</u>		
	<u>melanops</u>	<u>melanostomus</u>	
<u>nebulosus</u>		<u>mystinus</u>	
<u>nigrocinctus</u>			<u>pinniger</u>
<u>paucispinis</u>			<u>polyspinis</u>
			<u>proriger</u>
<u>rastrelliger</u>		<u>reedi</u>	
	<u>rosenblatti</u>		
<u>ruberrimus</u>		<u>rufus</u>	
		<u>serranoides</u>	<u>saxicola</u>
			<u>variegatus</u>
			<u>wilsoni</u>
			<u>zacentrus</u>

the first gill arch are always longer than those of the inner row.

Gillrakers differ from species to species, even though they can be very similar in some. Each gillraker of the external row has an inner surface (towards the orobranchial cavity) which in this genus develops a variable number of spinulae. In very compressed gillrakers the spinulae can appear on the inner edge and on the upper and lower surfaces. I have seen no apparent order in the distribution of the spinulae.

Length of the angular gillrakers and their form.

I have studied the form of the complete body of the gillrakers, considered individually and as a group. the gillrakers appeared so different in form that at least three groups - one with two subgroups - can be made. I have ordered the species alphabetically and then located them in their respective groups as a mean to facilitate further analysis (TABLE 6). One group has relatively short and stout external gillrakers, while other has long and slender ones, that is they are narrow in relation to their own length, they are not long in relation to standard length in all species; an intermediate category can be considered with two possible patterns. We designate them as "intermediate

short" and "intermediate long". Some additional measurements were made in order to present this classification (FIG. 2C, D) although I have calculated some relationship for the length of the angular gillraker as a proportion of the lower limb of the first branchial arch (FIG. 26), which will be analyzed in following pages.

Ten gillrakers were measured starting from the angular gillraker towards the anterior end of the lower limb of the first branchial arch, and their length and maximum width were recorded. The width as percent of the length was calculated for four species, each one typical representative of our four pattern forms of gillrakers. The results of this rapid analysis are expected to support the idea of the four different patterns, which otherwise, can be directly observed (TABLE 7).

As representatives of the first group we have S. ruberrimus and S. borealis (FIG 26), although the later has comparatively longer gillrakers than the former, is has to be recognized that all thay are very stout and their decrease in length from the angle towards the front of the limb is not so abrupt as seen in other groups. S. paucispinis is very similar to S. borealis and the tips of its gillrakers - as well as in the

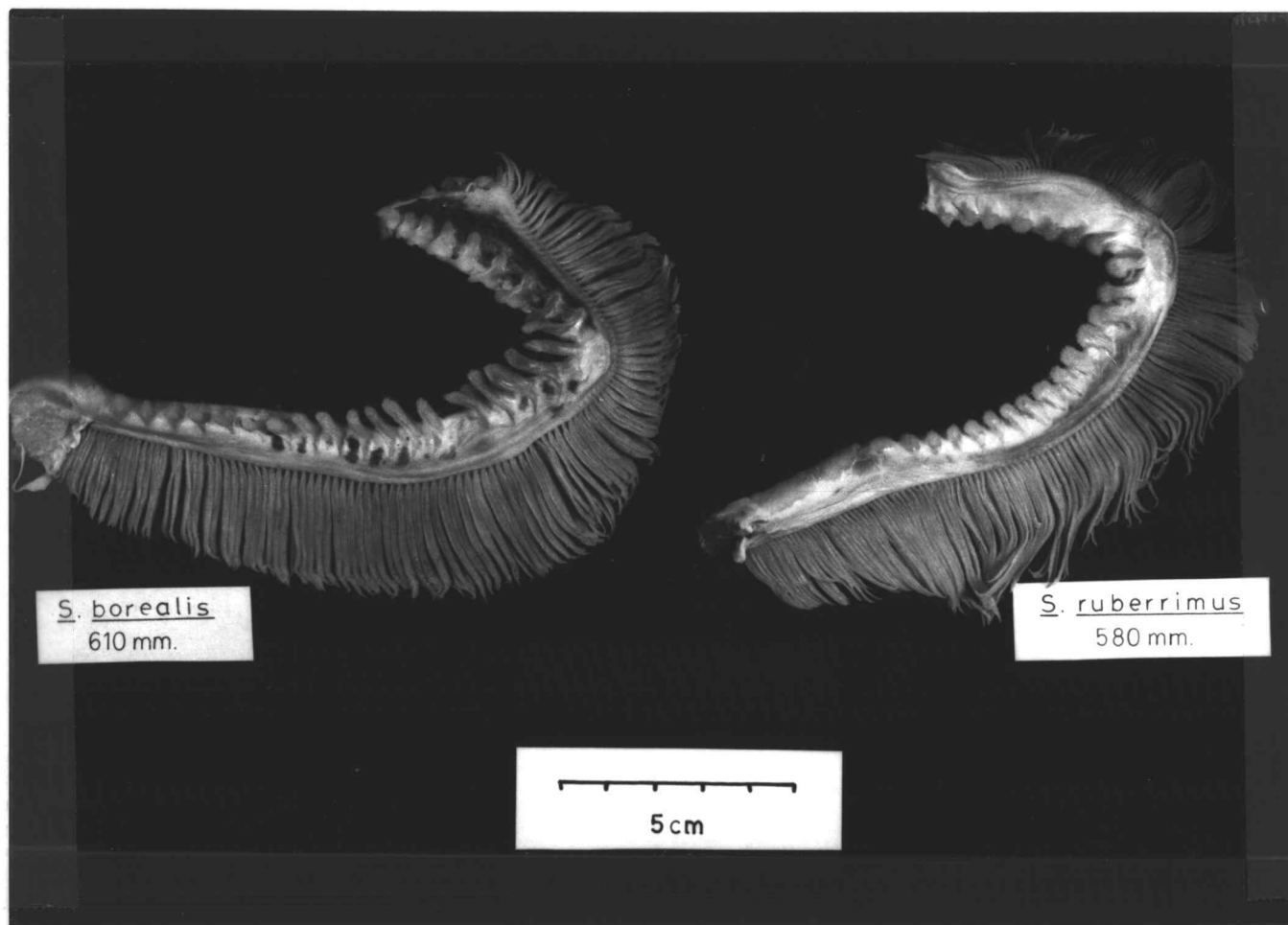


FIG. 26. Left gill arches of S. borealis and S. ruberrimus, showing gillrakers of the I group type.

TABLE 7. Width as percent of length of gillrakers in selected Sebastes spp. (n = 10, in each case).

Species	Range	X	S.D.
<u>S. ruberrimus</u>	32.50 - 49.04	42.13	6.095
<u>S. elongatus</u>	7.65 - 9.20	8.28	0.486
<u>S. crameri</u>	3.60 - 7.69	5.70	1.243
<u>S. saxicola</u>	2.38 - 3.81	2.99	0.467

other two - have strong, visible spinulae. The rakers of S. rastrelliger are so short that inner gillrakers reach them near the angle, in which their form tends to be rounded. S. nebulosus has a little more elongated gillrakers, and some of them are slightly undulated in their spinulated edge. S. nigrocinctus has the peculiarity of well rounded tips, with the inner gillrakers tending toward a pyramidal shape. S. chlorostictus also has rounded tips.

The intermediate short gillrakers group has eight species. The proportions of the ratios are maintained throughout size range of the fishes studied. These species have gillrakers with different configurations. S. brevispinis has acute tips but S. helvomaculatus shows button-like tips and S. melanops has fine rounded tips. S. elongatus has an uneven inner edge and its inner gillrakers are rather triangular in form. S. brevispinis has undulated inner edge, not too evident in some specimens. S. maliger has very little undulation, but the inner gillrakers are bifid (FIGS. 27 AND 28).

The intermediate long gillrakers group (FIGS. 28 and 29) has also particular differences, such as rather rounded tips in S. crameri and S. melanostomus or relatively acute tip with undulations in the inner edge

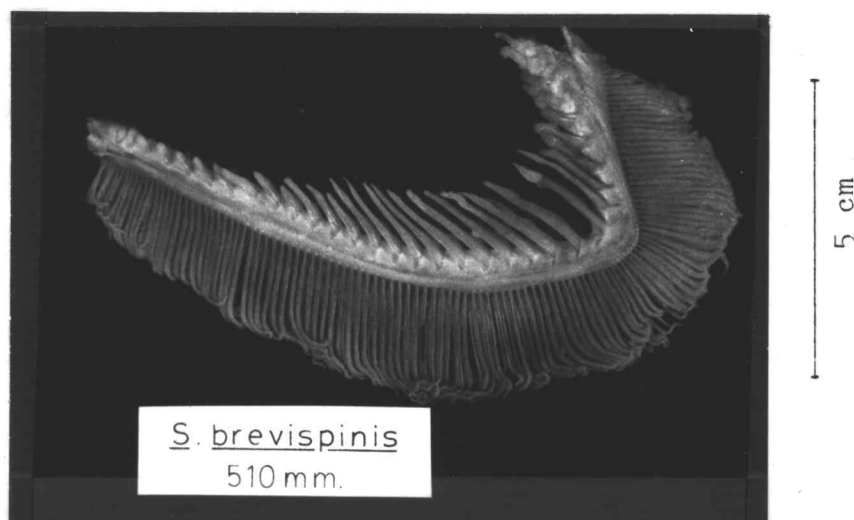


FIG. 27. First left gill arch of *S. brevispinis* showing gillrakers of the second group type.

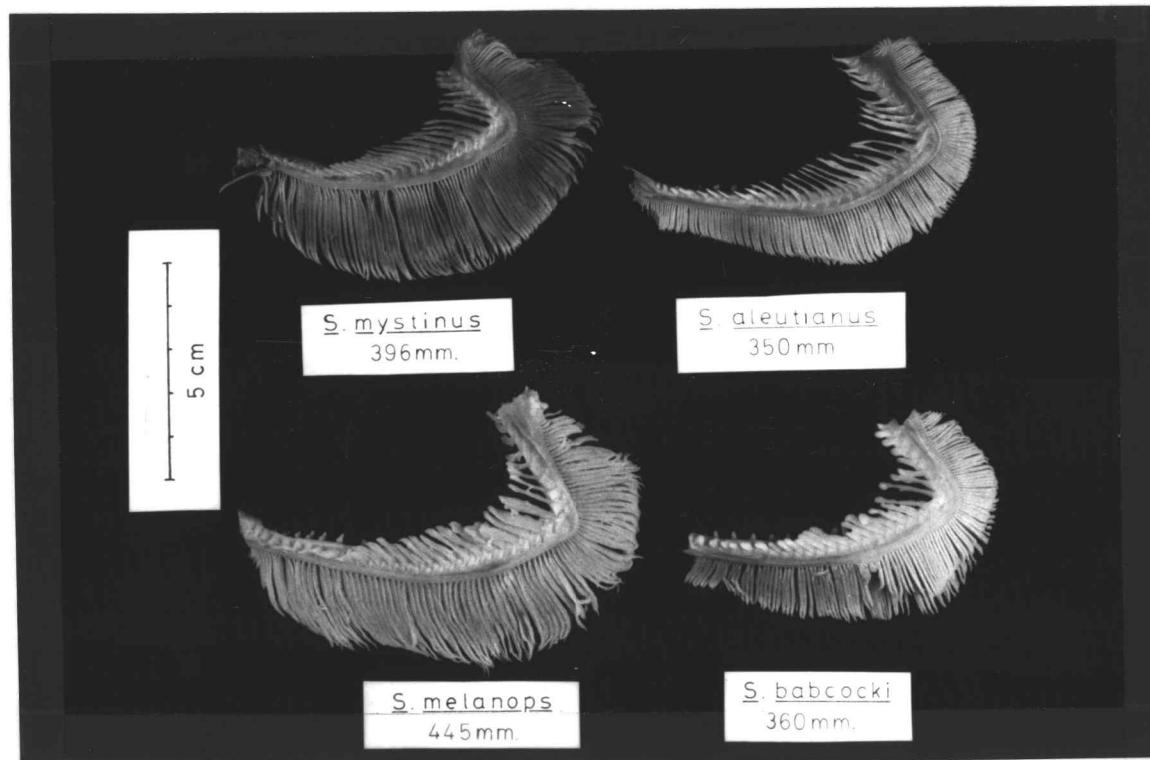


FIG. 28. First left gill arches of S. mystinus and S. aleutianus (both III gill-rakers group type), compared with S. melanops (II group) and S. babcocki (I group).

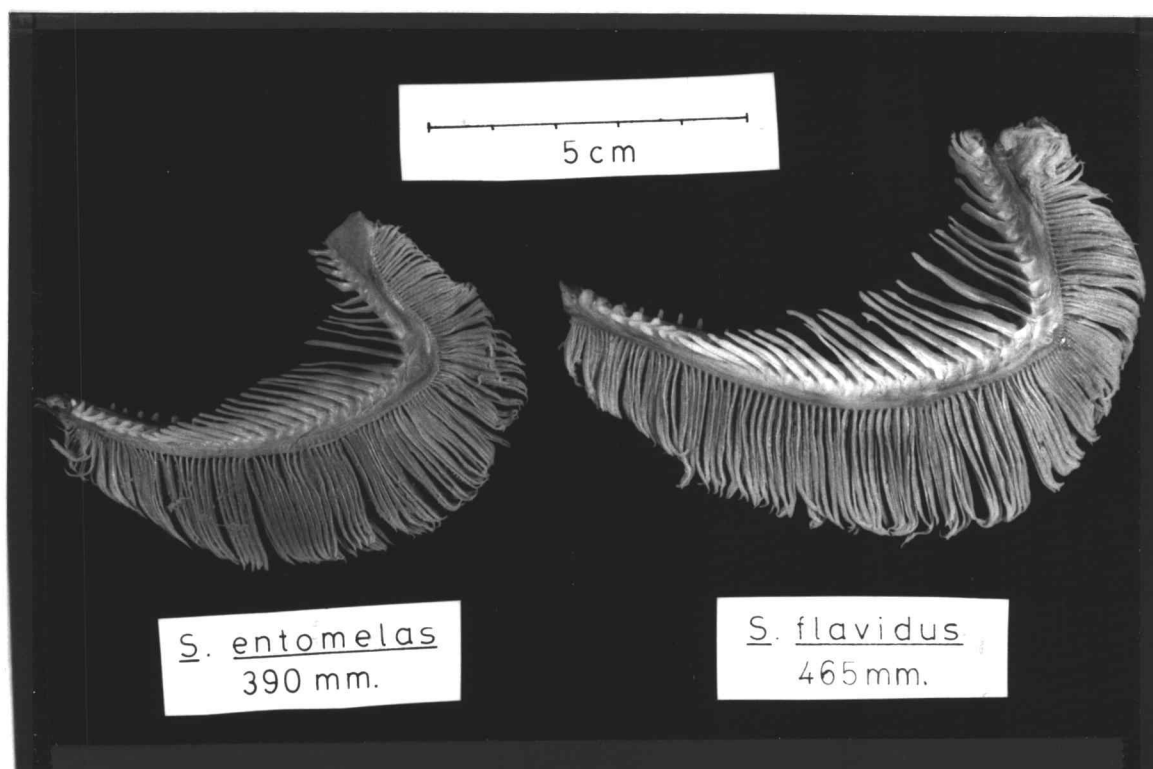


FIG. 29. First left gill arches of S. entomelas (III group type) and S. flavidus (IV group type).

bearing spinulae. These undulations make the surface of the spinulated area larger. Most of the species in this group - S. diploproa, S. goodei, S. reedi and S. rufus - have this kind of undulated edge.

A comparatively larger group of our sample is the fourth, with long and slender gillrakers. Most of them are very similar in shape, but fine differences are seen with magnification. Some species have stridulae on the inner edge - S. flavidus and S. wilsoni - and others such as S. zacentrus have softly rounded tips. The group with slender gillrakers tends to have a higher mean number of these structures. Species with comparatively robust gillrakers tend to have a lower mean number of them.

The lower gillrakers on the first arch tend to be modified. In specimens with short stout gillrakers the lower ones are often fused into one or more flat plates. In species with long gillrakers there is no fusion, but the lower 5 to 7 rakers are progressively displaced in origin from the anterior edge of the arch to a lateral position (FIGS. 26 to 29). At this point the inner gillrakers are as long as the exterior ones. The inner and outer rakers in this region interdigitate and form what appears to be an effective filter.

An analysis of the gillrakers number on the lower

limb of the first gill arch was made, resulting an extended gradient of values (FIG. 30). The lowest mean number is shown by S. rastrelliger (15.38), including a very flat plate of two or three fused gillrakers with nothing clear to distinguish numerically. S. ruberrimus (19.88), with a similar plate, S. borealis (20.4), S. nebulosus (20.5) and S. paucispinis (20.7) followed. All these plus S. babcocki (21.5), S. chlorostictus (22.6) and S. nigrocinctus (21.5) comprise the group of species with about short and stout gillrakers formerly studied. S. chlorostictus is the only member of the stout-raker group with a mean number of lower limb gillrakers higher than 22. Of the group with intermediate-short-rakers, S. elongatus, S. caurinus and S. helvomaculatus have mean numbers of lower limb gillrakers of 22 or fewer.

The highest mean number of gillrakers is shown by S. jordani (31.7). This is well separated from the next highest, S. pinniger (29.0), as in my sample there was an overlap in the ranges at 31 (one specimen each) but the standard deviations were well separated. Those species, plus S. wilsoni (26.7), S. proriger (27.1), S. variegatus (26.6) and S. polyspinis (26.2) typified the group with slender gillrakers. Other members of the group have mean numbers less than 26, with one, S.

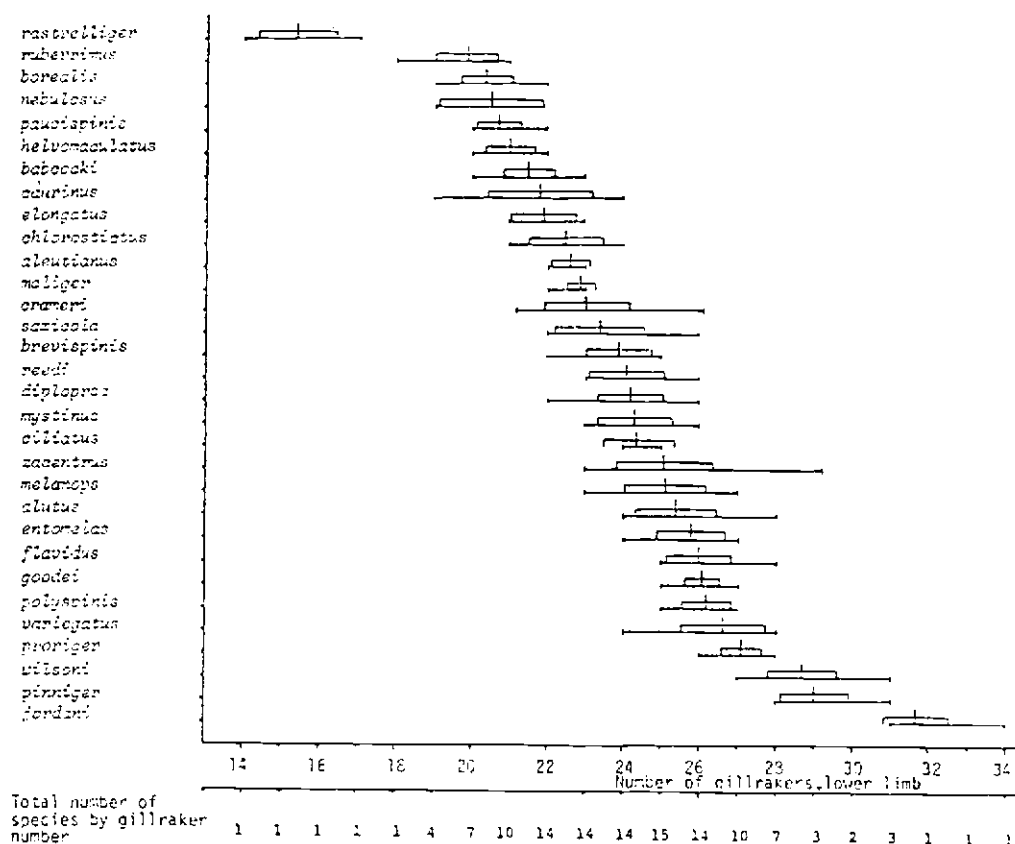


FIG. 30. Mean values, standard deviation and ranges for number of gillrakers by selected *Sebastes* spp. The lowest axis indicates number of species having a particular number of gillrakers.

saxicola close to the middle of the distribution. It is easy to recognize that, in general, those species from our intermediate and robust pattern - short and long - fall principally toward the center of the slope. Most have means between 22 and 26. S. brevispinis, S. reedi, S. diploproa, S. mystinus and S. ciliatus have means very close to each other and close to 24 which is the median of all values observed. S. goodei (26.06) has the highest mean of the intermediate group and overlaps the group with long and slender gillrakers. In turn S. zacentrus and S. saxicola appear among those with intermediate gillraker form. Towards both extremes values the mean for each species tend to be more distant from the respective neighbors. The lowest number of gillrakers counted in all the sample was 12 + 1 , in one specimen of S. rastrelliger, while the highest was 34, in two specimens of S. jordani.

In relation to the number of gillrakers we have calculated the coefficient of variation "V", which is equal to

$$\frac{100 \text{ SD}}{\bar{X}}$$

This coefficient can be useful in corroboration and/or further analysis started with the dispersion measurements (Chen, 1971). Simpson and Roe (1939)

mentioned that values between 4 and 10 and 5 or 6 are good average values. Much lower values usually indicate that the sample was not adequate to show the variability and much higher values usually indicate that the sample was not pure, for instance, that it included animals of decidedly different ages, developmental stages, or of different minor taxonomic divisions. One case of our sample is over 6 - S. rastrelliger - and we recognize the number of specimens was relatively low and one specimen, at least, was too small compared to large adult ones used. Two species were under two: S. maliger and S. proriger. The first was relatively poor with only seven specimens and the second was the lowest standard deviation of the sample, with a rather high mean average number of gillrakers and, although is the most numerous in individuals, size variation in standard length was not so notable - 215 to 330 mm - and the "V" coefficient reflects only a numerical shift. All other species have rather acceptable coefficients of variation (TABLE 8).

The number of gillrakers can be observed as a whole, making a count of how many species have a given number of such structures (FIG. 30, lowest scale). It is again a gradient based in the range number recorded for each species. There is a high number of species

TABLE 8. Variation in the number of gillrakers in Sebastes spp. of Oregon. Detail about rows in the text.

S p e c i e s	n	range	X	S.D	"v"
<u>aleutianus</u>	9	22-23	22.56	0.53	2.35
<u>alutus</u>	22	24-28	25.41	1.05	4.13
<u>babcocki</u>	21	20-23	21.50	0.68	3.16
<u>borealis</u>	25	19-22	20.42	0.71	3.48
<u>brevispinis</u>	23	22-25	23.90	0.85	3.56
<u>chlorostictus</u>	17	21-24	22.55	1.01	4.49
<u>ciliatus</u>	23	24-25	24.39	0.96	3.93
<u>crameri</u>	26	21-26	22.91	1.26	5.50
<u>diploproa</u>	24	22-26	24.23	0.82	3.39
<u>elongatus</u>	28	21-23	21.91	0.89	4.06
<u>entomelas</u>	21	24-27	25.86	0.89	3.45
<u>flavidus</u>	21	25-28	26.01	0.84	3.23
<u>goodei</u>	17	25-27	26.06	0.56	2.15
<u>helvomaculatus</u>	29	20-22	21.02	0.66	3.14
<u>jordani</u>	30	31-34	31.76	0.88	2.78
<u>maliger</u>	7	22-23	22.86	0.38	1.66
<u>melanops</u>	24	23-27	25.15	1.16	4.62
<u>mystinus</u>	16	23-26	24.87	0.96	3.94
<u>paucispinis</u>	22	20-22	20.78	0.65	3.14
<u>pinniger</u>	21	28-31	29.05	0.86	2.97
<u>polyspinis</u>	21	25-27	26.24	0.63	2.40
<u>proriger</u>	23	26-28	27.11	0.52	1.92
<u>rastrelliger</u>	8	14-17	15.38	1.19	7.73
<u>reedi</u>	23	23-26	24.11	0.97	4.02
<u>ruberrimus</u>	16	18-21	19.88	0.81	4.05
<u>saxicola</u>	22	22-26	23.41	1.26	5.38
<u>variegatus</u>	14	24-28	26.62	1.16	4.36
<u>wilsoni</u>	20	27-31	28.71	1.09	3.80
<u>zacentrus</u>	25	23-29	25.08	1.26	5.02

represented between 22 and 26 gillrakers. The sample range is known between 13 and 34 gillrakers. A normal distribution is displayed by all the ensemble.

If we recall the form of the gill arch, we will agree that the gillraker at the angle has to be acceptably long to cover the space corresponding to their filtering function. Logically it has to be the longest, but this is not always so, and many times other gillrakers exceed them in length, most of the times the angular gillraker is the longest of the series and/or the difference with other similar gillrakers is very small.

In considering the relationship of angular gillraker length to standard length, expressed as a percentage (FIG. 31) I found that, with the exception of six species with short gillrakers, the percentages fall between 4 and 6, with the means of the adjacent species close together. Correspondence with the "stout-intermediate-slender" groups is reasonably good for the "stout" and "intermediate-short" groups, as members of the stout group show 8 of the 9 lowest percentages and the intermediate-short group are together with means between 4.2 and 4.5. With one exception, all the members of the "intermediate-long" and "slender" groups fall between 4.5 and 6. The exception is S. entomelas,

which has gillrakers that are slender in comparison to their width, but that are short in relation to standard length (mean 4%).

A regression analysis of angular gillrakers length on standard length is shown in FIG. 32. Correlation coefficients "r" for this regression (TABLE 9) range from 0.257 to 0.944, with 8 of the 27 values below 0.600. A straight regression line is not adequate to describe the relationship of gillraker length to standard length in species such as S. borealis, in which angular gillrakers do not increase appreciably in length after the fish reaches about 300 mm. In this species the rakers are about 5.5% of standard length at a body length of 200 mm and 2% at 600 mm. Corresponding figures for S. ruberrimus are 3.5% and 1.7%.

There appears to be a tendency among species with short stout gillrakers to slow the growth of the rakers once a given body length is reached, as if an optimum raker length for handling the customary prey is attained. Species with long slender gillrakers generally maintain a constant relationship of gillraker length to standard length. S. pinniger, for instance, retains angular gillrakers of about 5.5 to 6 % of standard length over a length range of 200 to 500 mm.

Another way of regarding length of gillrakers is

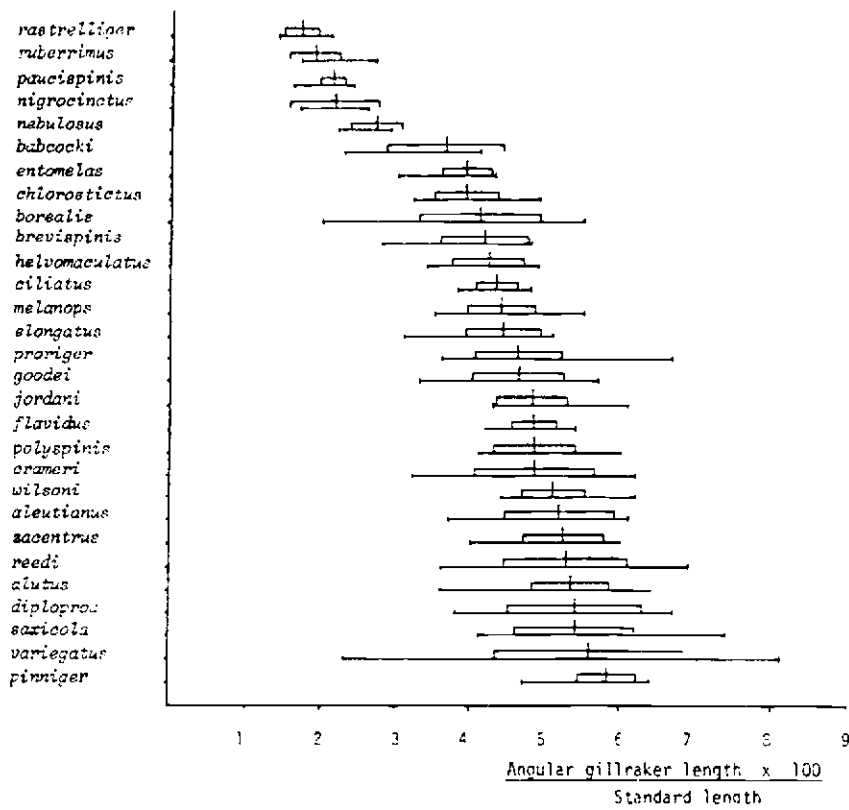


FIG. 31. Mean values, standard deviation and range for length of angular gillraker as percent of standard length, in *Sebastes* spp.

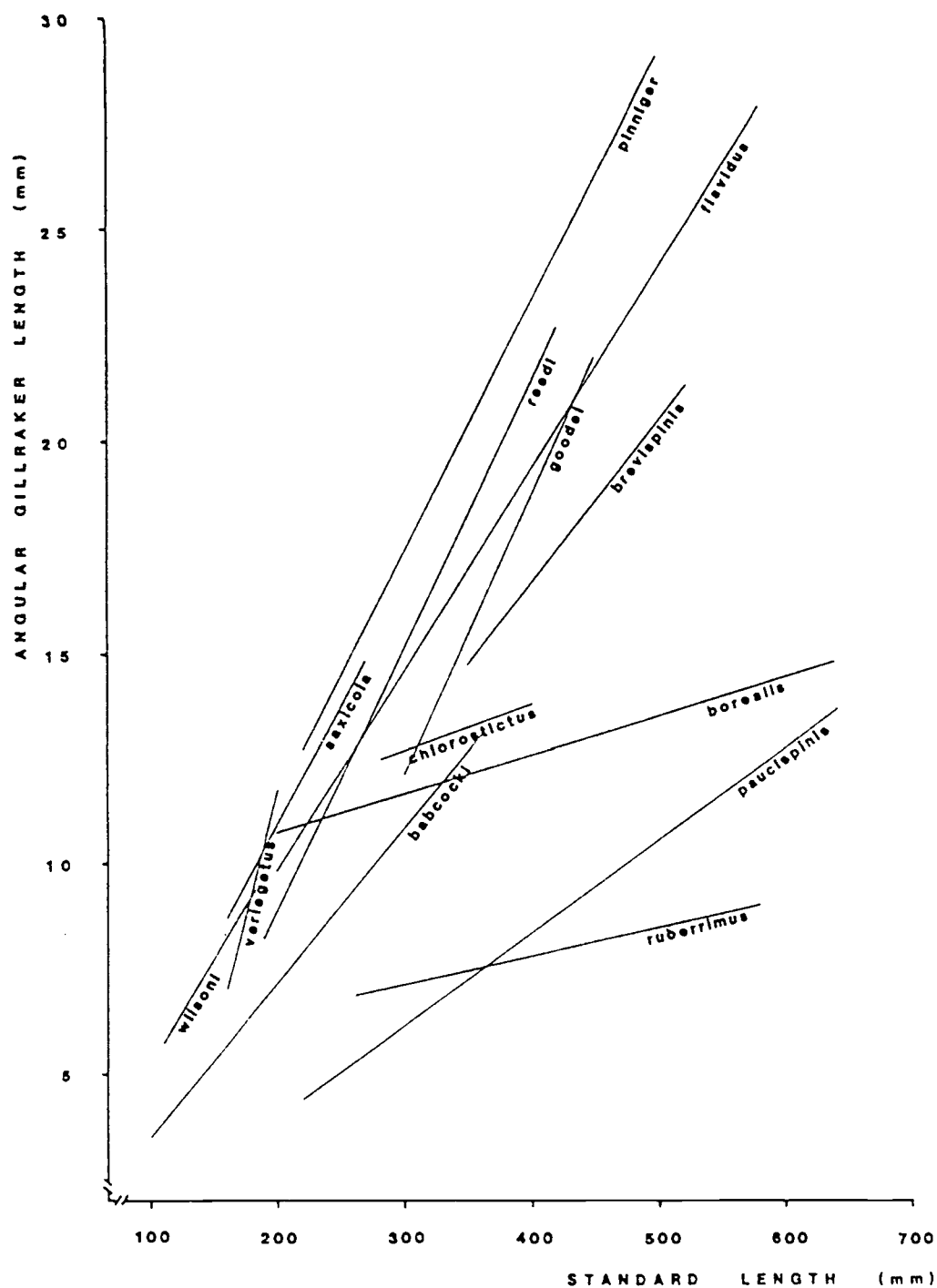


FIG. 32. Regression lines for angular gillraker length vs. standard length (mm), in selected *Sebastes* spp.

TABLE 9. Regression equations, correlation coefficients and number of specimens studied for length of angular gillraker vs. standard length, in Sebastes spp.

Species	Y = a + bx	"r"	n
<u>aleutianus</u>	Y = 3.7544 + 0.0358X	0.783	9
<u>alutus</u>	Y = 0.8457 + 0.0487X	0.910	22
<u>babcocki</u>	Y = -0.1782 + 0.0367X	0.683	21
<u>borealis</u>	Y = 8,8207 + 0.0093X	0.551	25
<u>brevispinis</u>	Y = 1.1257 + 0.0387X	0.549	22
<u>chlorostictus</u>	Y = 9.4206 + 0.0111X	0.257	17
<u>ciliatus</u>	Y = 1.2813 + 0.0385X	0.763	22
<u>crameri</u>	Y = 9.3143 + 0.0151X	0.547	24
<u>diploproa</u>	Y = 5.2432 + 0.033X	0.539	24
<u>elongatus</u>	Y = 3.624 + 0.0267X	0.834	28
<u>entomelas</u>	Y = -4.004 + 0.0503X	0.845	21
<u>flavidus</u>	Y = 0.335 + 0.0474X	0.939	21
<u>goodei</u>	Y = -7.5445 + 0.0654X	0.620	17
<u>helvomaculatus</u>	Y = 4.8942 + 0.0176X	0.517	29
<u>jordani</u>	Y = 3.6861 + 0.0279X	0.702	28
<u>melanops</u>	Y = 4.275 + 0.0311X	0.814	22
<u>mystinus</u>	Y = 2.6122 + 0.0308X	0.944	16
<u>paucispinis</u>	Y = -0.458 + 0.0221X	0.921	23
<u>pinniger</u>	Y = -0.8877 + 0.0598X	0.903	21
<u>polyspinis</u>	Y = 2.3714 + 0.0381X	0.611	20
<u>proriger</u>	Y = 1.4495 + 0.0396X	0.778	23
<u>reedi</u>	Y = -3.6797 + 0.0625X	0.845	23
<u>ruberrimus</u>	Y = 5.1538 + 0.0066X	0.600	15
<u>saxicola</u>	Y = -0.4954 + 0.0566X	0.713	22
<u>variegatus</u>	Y = -11.9047 + 0.1181X	0.536	14
<u>wilsoni</u>	Y = 0.2981 + 0.0492X	0.853	20
<u>zacentrus</u>	Y = 5.2634 + 0.0301X	0.648	25

=====

in relation to the length of the gill bars. Figure 33 shows the length of the angular gillrakers expressed as a fraction of the lower limb of the first branchial arch. Mean values range from less than 10% in S. rastrelliger to 35% in S. variegatus, and are generally low for species with low counts of gillrakers and high for those with high counts. Most of the means (20) are graduated by less than a percentage point difference between 22.5 and 30%. The seven lowest means are those of the groups judged to have relatively stout gillrakers. The three or four lowest of these appear to be specialists in capturing large prey. The eight highest means all belong to species from the group with slender gillrakers, but only the highest two, S. wilsoni and S. variegatus, seem to be much different from the others. Most of the species would seem to be equipped to capture prey of a given minimum dimension in relation to the fish. With some exceptions, such as S. entomelas, S. proriger and S. jordani, there is a general correspondence with the relationship between angular gillraker length and standard length. This is more evident in the lower means than in the higher. Non-correspondence between the two relationships as an expression of difference in the dimensions of the branchial apparatus itself, and whether the difference

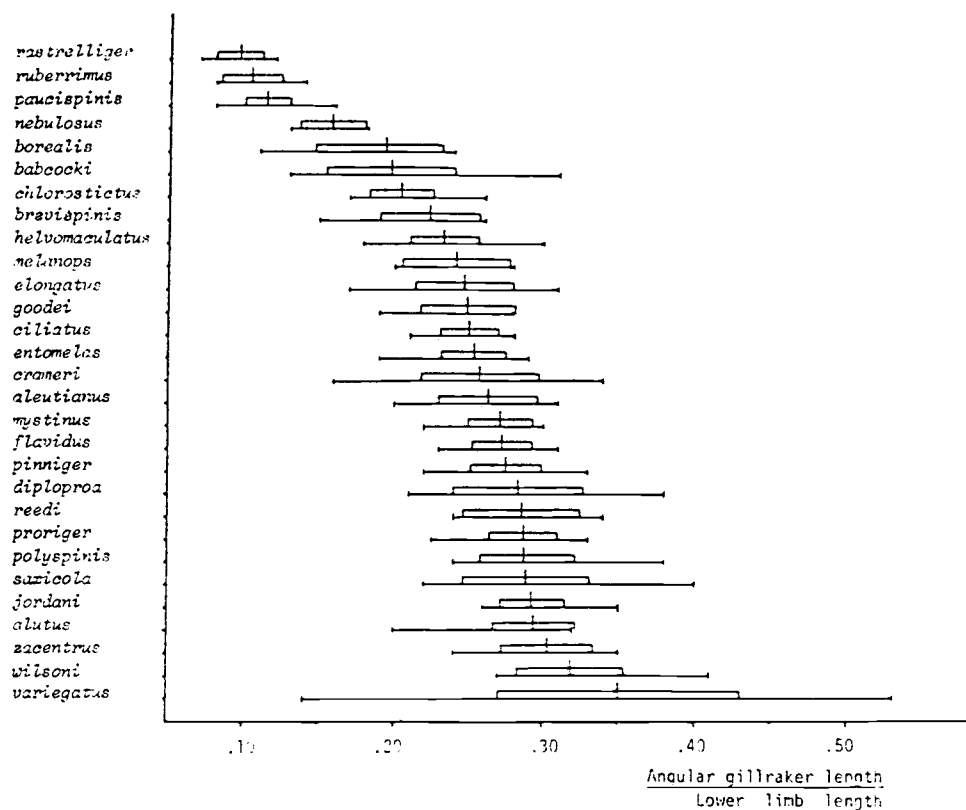


FIG. 33. Mean values, standard deviation and ranges for the ratio angular gillraker length/length of the lower limb of the first branchial arch, in Sebastes spp.

is due to demands of trophic or respiratory function cannot be answered here.

Scanning electron microscopy (SEM) analysis

In order to learn possible patterns in gillrakers and shape and disposition of small teeth or spinulae on them, I observed them through SEM. I studied only angular gillrakers, unless they were damaged, in which case I used the next lower gillraker. Sometimes, when evident abnormal angular gillrakers were observed by the light microscope, another angular gillraker from a different fish of the same species was prepared for SEM. For each gillraker mainly four positions were analyzed and pictures obtained: tip of the gillraker (magnification x 35), lateral view of the middle most spinulated borderside (x 130), upper view of the most spinulated inner edge area (x 35) and a general view of the inner or accessory gillraker (x 130). In exceptional cases, to show more details or different angle views, I have taken additional pictures. I analyzed the gillrakers in relation to the form and size of the spinulae, as well as coverage, and also in relation to the form and type of surface of the outer edge and, finally, size of the inner gillraker related to the outer. The results of this analysis are depicted in

Table 10. Results on SEM analysis. "X" denotes presence of a given characteristics.

Species	Spinulae							
	Shape				Size		Coverage	
	Tip Bladelike	Straight >50%	Curved >50%	Mixed	Small	Large	Sparse	Thick
<u>aleutianus</u>	-			x	x		x	
<u>alutus</u>	-			x	x		x	
<u>babcocki</u>	x			x	x		x	
<u>brevispinus</u>	-	x			x		x	
<u>caurinus</u>	x			x	x		x	
<u>cramerfi</u>	-	x			x		x	
<u>diploproa</u>	x		x		x			x
<u>elongatus</u>	x			x	x		x	
<u>entomelas</u>	-	x				x		x
<u>flavidus</u>	-		x			x		x
<u>helvomaenulatus</u>	x	x			x		x	
<u>jordanfi</u>	-		x		x		x	
<u>maliger</u>	-		x			x		x
<u>melanops</u>	-	x			x		x	
<u>minutus</u>	-	x		x	x		x	
<u>mystinus</u>	-	x			x		x	
<u>nebulosus</u>	x			x		x		x
<u>nigrocinctus</u>	x		x		x	x		x
<u>paucispinus</u>	-			x		x	x	
<u>piniger</u>	-		x			x		x
<u>polyspinis</u>	-	x			x		x	
<u>proiger</u>	-	x			x		x	
<u>rastralliger</u>	x		x			x	x	
<u>reedi</u>	x			x	x		x	
<u>rosenblattfi</u>	x		x			x		x
<u>ruberrimus</u>	x			x		x	x	
<u>saxicola</u>	-			x	x			x
<u>serranoides</u>	-			x		x	x	
<u>wilsonfi</u>	-	x			x		x	
<u>zacentrus</u>	-			x			x	

Table 10. Continued

Species	Gillraker								
	Edge Outer Gillraker			Surface Outer Gillraker			Size Inner Gillraker related to outer		
	Undulated	Curved	Straight	Grooves	Ridges	Smooth	Short	Int.	Long.
<u>aleutianus</u>			x		x			x	
<u>alutus</u>			x		x		x		
<u>babcocki</u>	x				x				x
<u>brevispinis</u>			x		x		x		
<u>caurinus</u>			x	x			x		
<u>crameri</u>			x		x		x		
<u>diploproa</u>			x		x			x	
<u>elongatus</u>			x		x		x		
<u>entomelas</u>	x				x		x		
<u>flavidus</u>	x				x				x
<u>helvumaculatus</u>	x				x			x	
<u>jordani</u>		x			x		x		
<u>maliger</u>	x					x		x	
<u>melanops</u>			x		x		x		
<u>mutatus</u>			x			x	x		
<u>mystinus</u>			x		x		x		
<u>nebulosus</u>		x			x				x
<u>oligrocinctus</u>		x			x			x	
<u>paucispinis</u>		x			x				x
<u>plantiger</u>	x				x		x		
<u>polyspinis</u>			x		x		x		
<u>proriger</u>	x				x			x	
<u>rastrelliger</u>			x		x		x		
<u>reedl</u>			x		x		x		
<u>rosenblatti</u>			x		x		x		
<u>ruberrius</u>			x		x			x	
<u>saxicola</u>	x	x				x		x	
<u>serripoides</u>	x				x		x		
<u>wilsoni</u>			x	x			x		
<u>zaccanthus</u>			x		x		x		



FIG. 34. Tip and part of the body of the angular gillraker of the first branchial arch of S. paucispinis, 243 mm SL (x 35), under SEM.

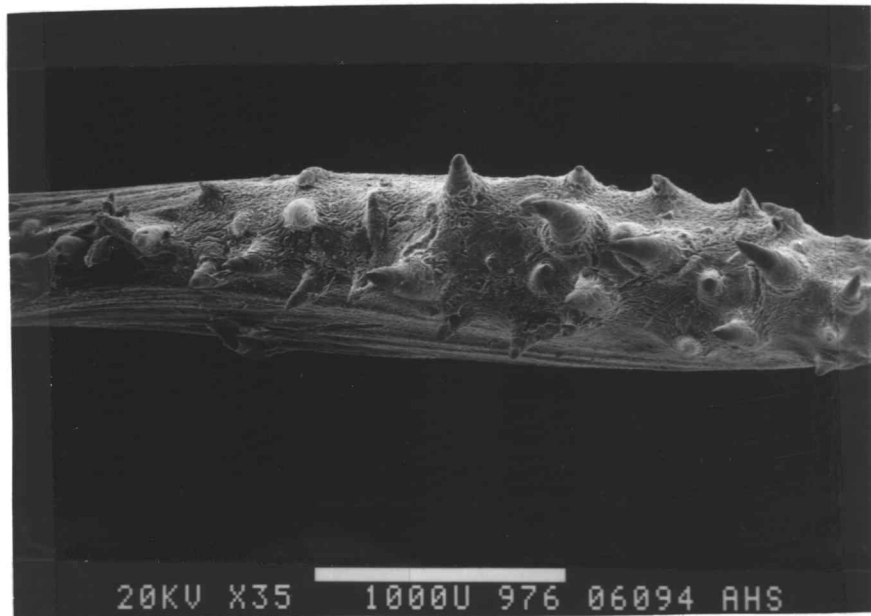


FIG. 35. Central-upper view of angular gillraker of S. paucispinis (x 30).

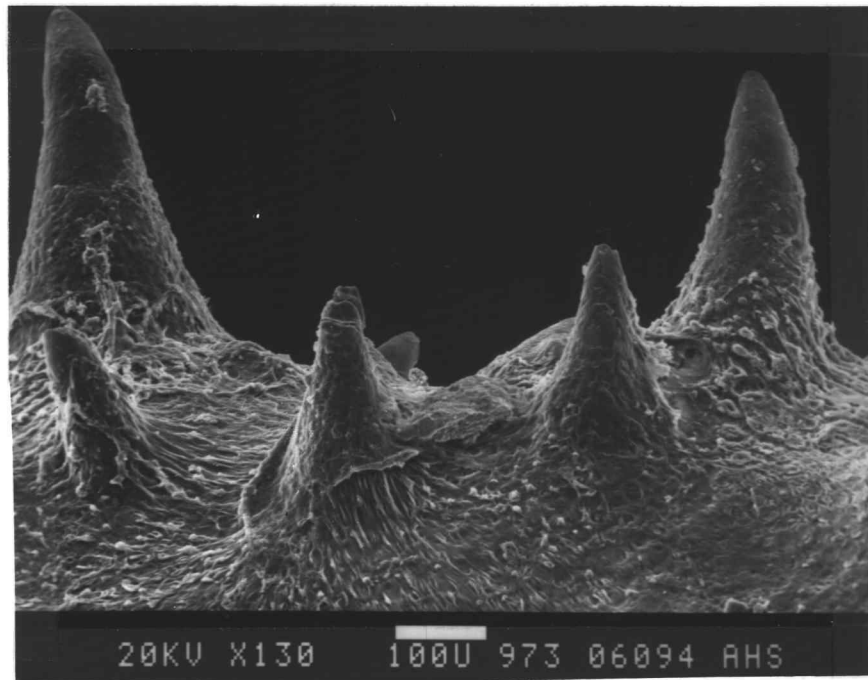


FIG. 36. Centro-lateral view of angular gillraker of *S. paucispinis* (x 130).



FIG. 37. Inner angular gillraker of *S. paucispinis* (x 30).

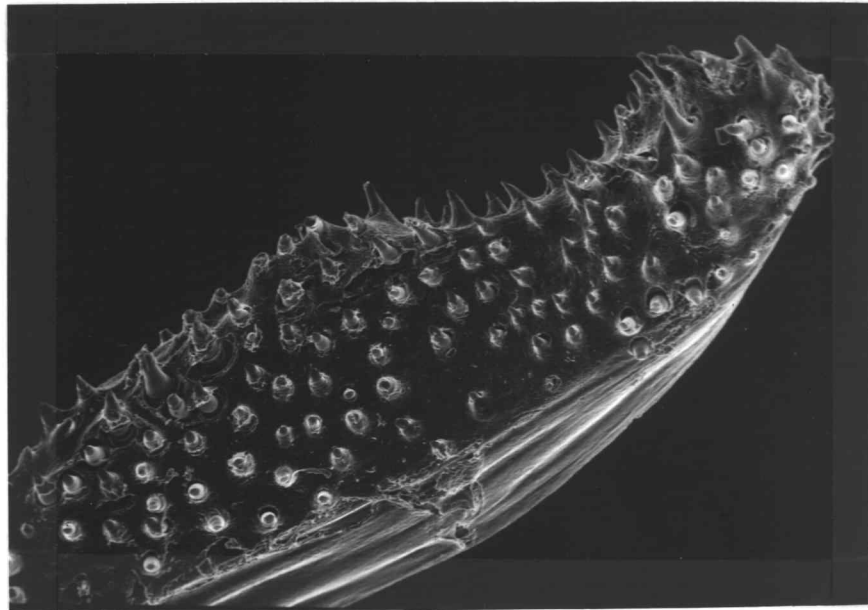


FIG. 38. Tip of angular gillraker of the first branchial arch of S. helvomaculatus, 257 mm SL (x 35).

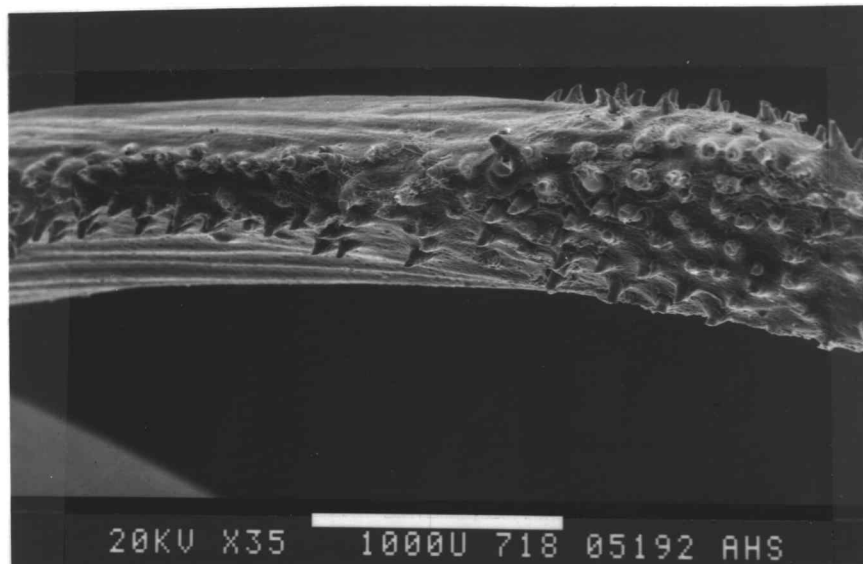


FIG. 39. Central-upper view of angular gillraker of S. helvomaculatus (x 35)

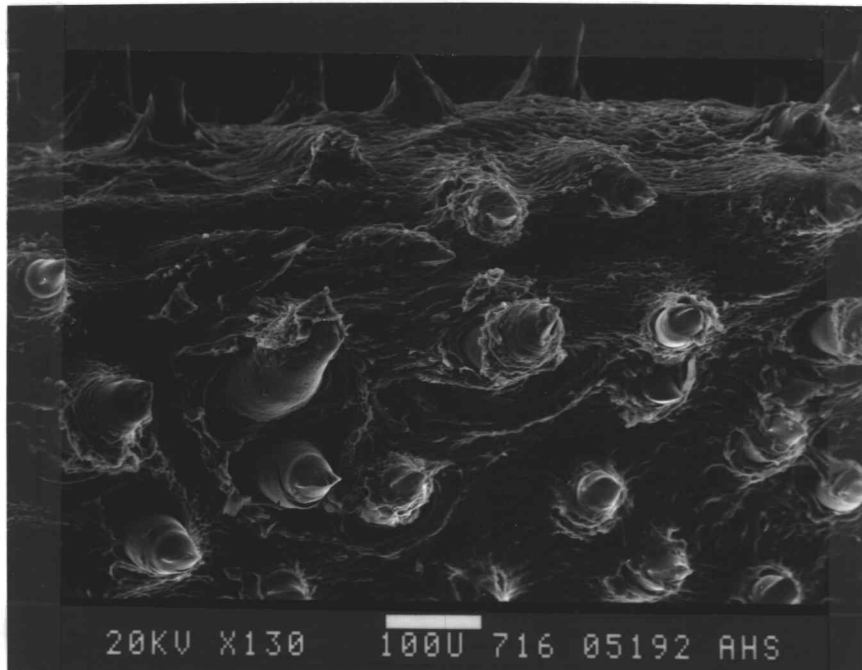


FIG. 40. Central-lateral view of angular gillraker of S. helvomaculatus (x 130).

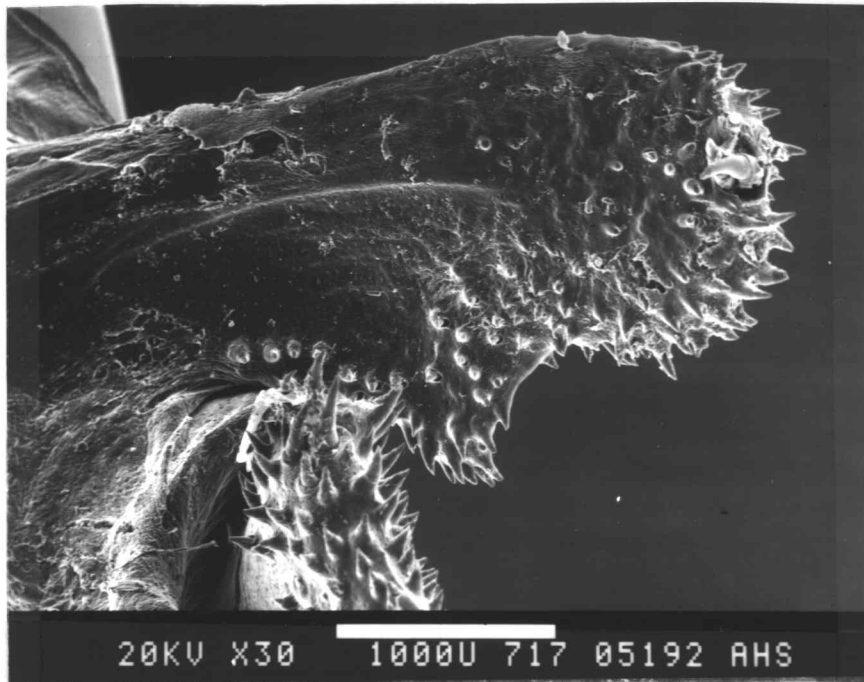


FIG. 41. Inner angular gillraker of S. helvomaculatus (x 30).

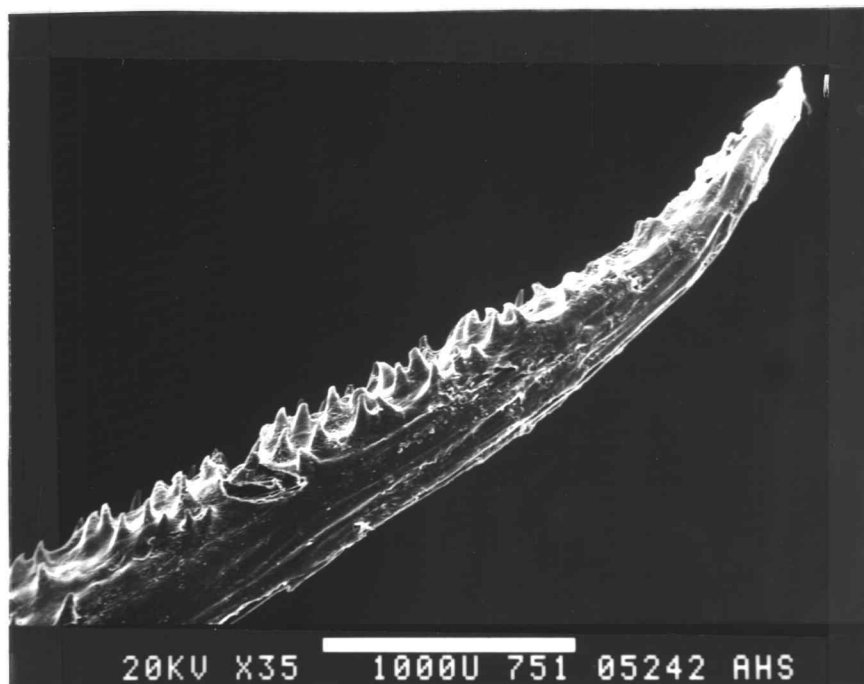


FIG. 42. Tip of the angular gillraker of the first branchial arch of *S. diploproa*, 205 mm SL (x 35).

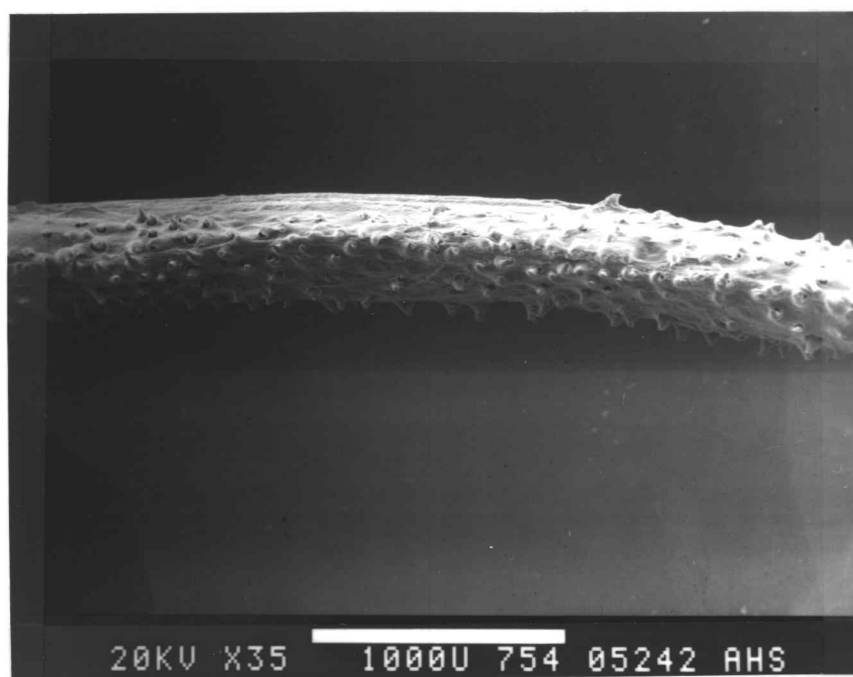


FIG. 43. Central upper view of angular gillraker of *S. diploproa* (x 35).

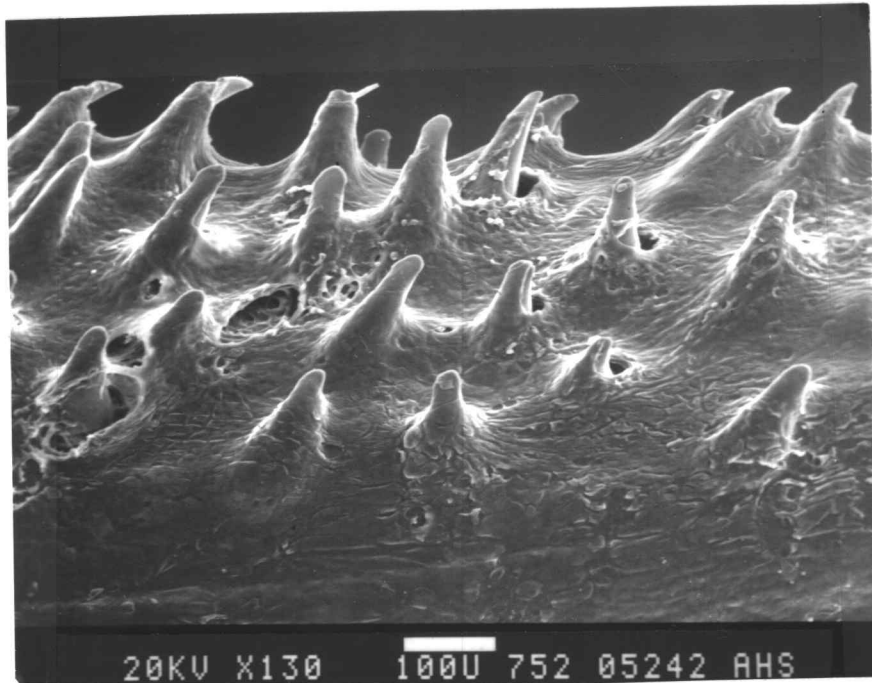


FIG. 44. Centro-lateral view of angular gillraker of *S. diploproa* (x 130).

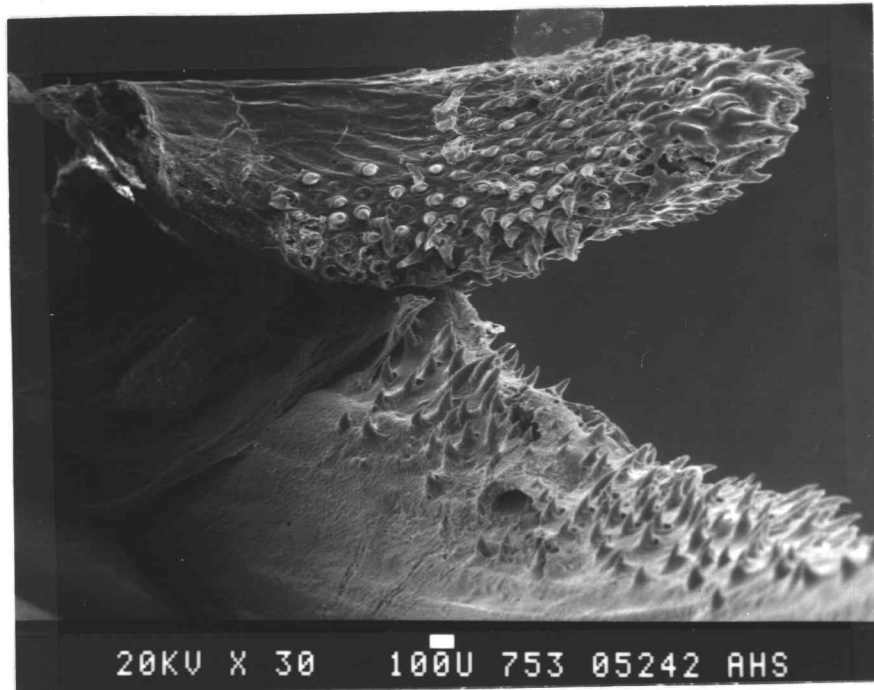


FIG. 45. Inner angular gillraker of *S. diploproa* (x 30).

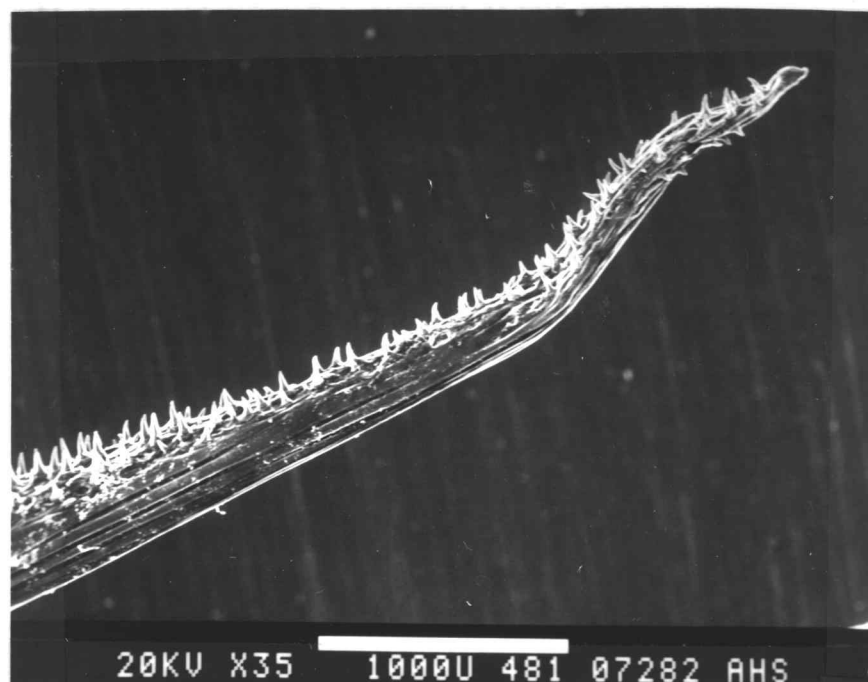


FIG. 46. Tip of the angular gillraker of the first branchial arch of *S. wilsoni*, 127 mm SL (x 35).

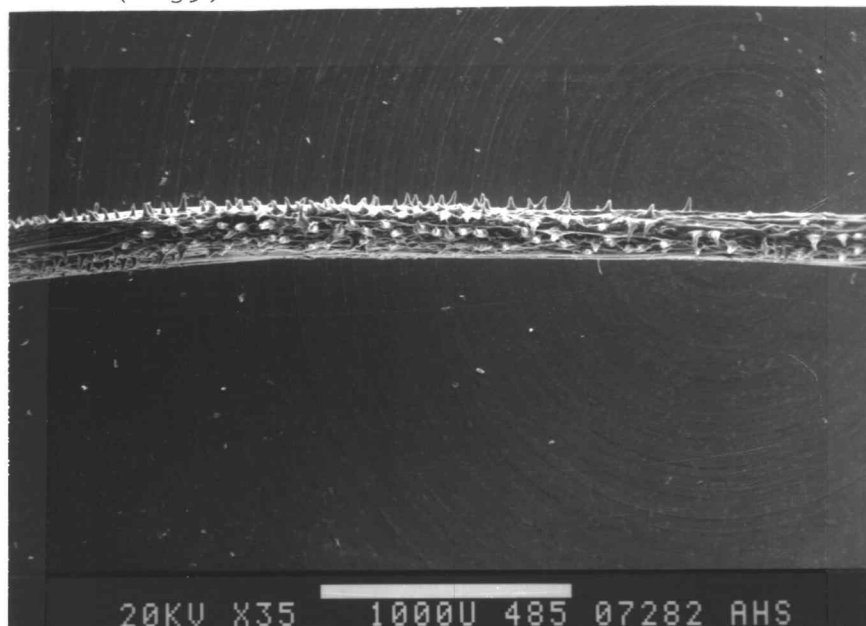


FIG. 47. Central-upper view, angular gillraker of *S. wilsoni* (x 35).

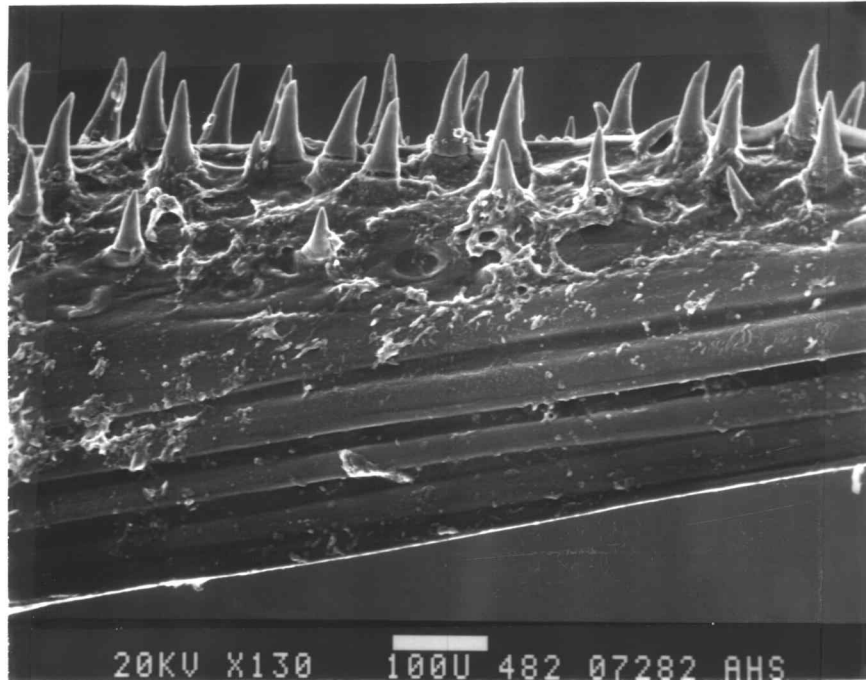


FIG. 48. Centro-lateral view of angular gillraker of S. wilsoni (x 130).

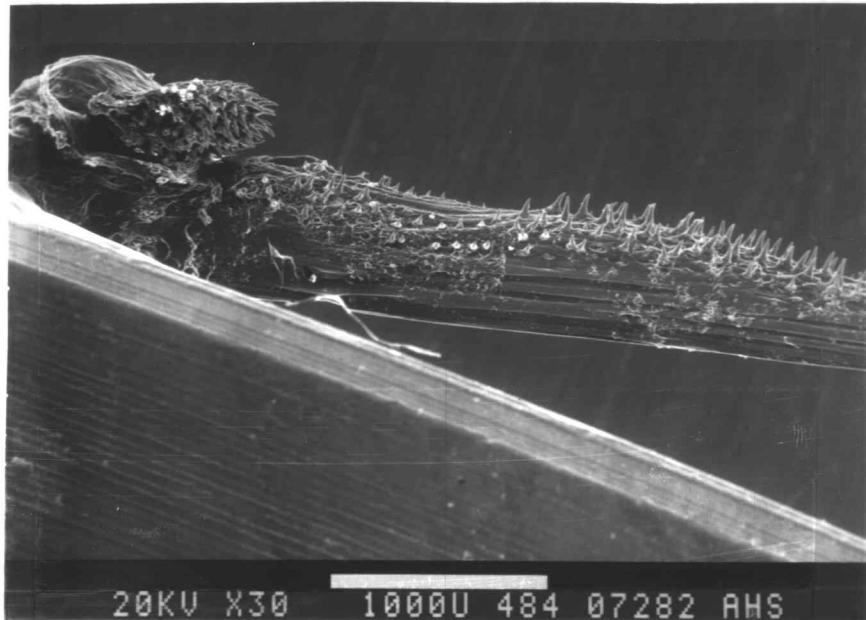


FIG. 49. Inner angular gillraker, near the root of the external gillraker of S. wilsoni (x 30).

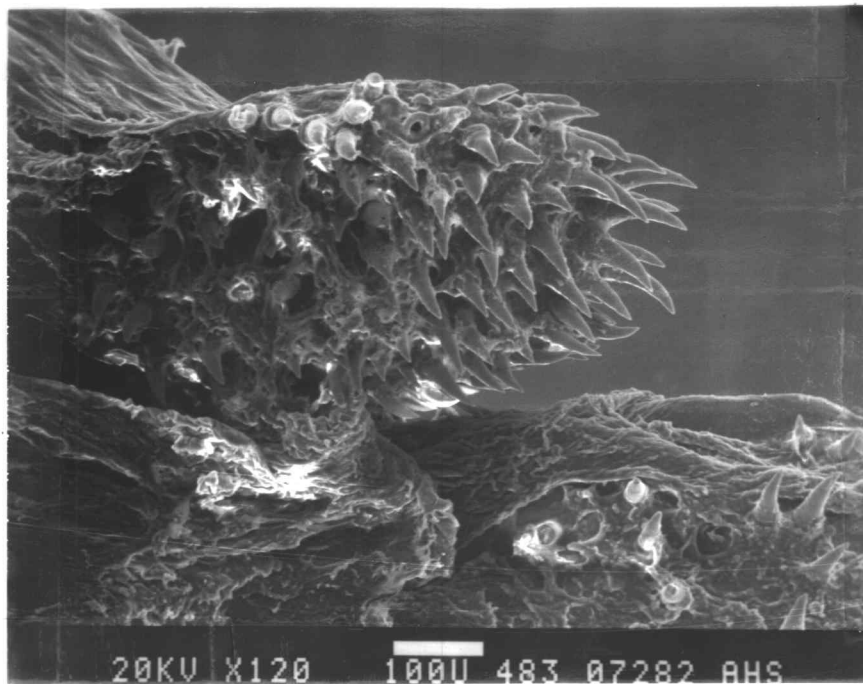


FIG. 50. Detail of the inner gillraker of S. wilsoni (x 120).

TABLE 10. Selected species belonging to the four types of gillraker form has been used to illustrate the four positions seen under SEM (FIGS. 34 to 50).

Study of selected features involved in food gathering and utilization.

Because of the importance of vision in prey capture, I examined the size of the eye, expressed in terms of the horizontal diameter of the orbit. Further, taking on account the possibility of soft organ differentiation according to a particular type of digestion, as mentioned by several authors (Al-Hussaini, 1947; Hatanaka et al., 1954; Barrington, 1957), I analyzed the small intestine length. Considering that the head is the hearer of most of the structures involved in food capture and initial processing, I measured the size of the head. A practical application of knowing the size of the head in relation to body length is that in studies of stomach contents, isolated heads can allow estimation of the size of the fishes consumed.

Orbital width

In the process of food gathering, many structures and in some moments the complete body seems to be

involved. The nervous system - mainly the sensory organs - are highly important in localization of food. The eye is generally the largest sensory organ in teleosts. The size of the eye is different according to life styles and habitats, as has been well shown with some oceanic groups of fishes (Marshall, 1971). Fishes living at or below the limit of light penetration, as many rockfishes do, tend to have larger eyes and have been assumed to have enhanced sensitivity (Nicol, 1978).

In many fishes, as they are caught, the eye ball suffers a deformation or destruction caused by pressure differences, in such a way that the measuring of the eye itself is generally prevented for our purposes. For this reason I measured the bony orbit. In our study, I analyzed three relationships: the orbital width as percent of standard length, the correlation between both characteristics and the ratio between orbital width and head length. Of the species measured, S. paucispinis is the species with the smallest relative eye size estimated the horizontal orbital width as percent of the standard length. It is followed by S. entomelas and S. mystinus. There is a welll gradient of increasing relative eye size that ends with S. helvomaculatus and S. diploproa. Indices of some

species, such as S. paucispinis, S. polyspinis and S. saxicola do not overlap (FIG. 51). The relationship between eye size and depth is not well marked. The species taken at the shallowest maximum depth (S. chlorostictus, 201 m.) and the species taken at the deepest (S. aleutianus, 732 m.), according to Eschmeyer et al.(1983), differ very little in eye size. The mean of the maximum recorded depths for those with an orbit with 9% or less of standard length is 353 m., and that for the species with orbit with greater than 9% is 442 m. The 9% proportion was selected because it is at a discontinuity of greater than one half a percentage point, and marks a 14-13 division of the 27 species studied.

I considered comparisons between horizontal diameter of the orbit and the head length. This relationship might be helpful if the bodies of the fishes are damaged and only heads are available for measurement. The orbital width as ratio of the head length (FIG. 52) shows the same species in the lowest and highest values as in FIG. 51. S. paucispinis has the lowest values and S. diploproa the highest. Between them, many species maintained similar positions within the gradient, principally in the higher values area, although S. entomelas and S. mystinus showed

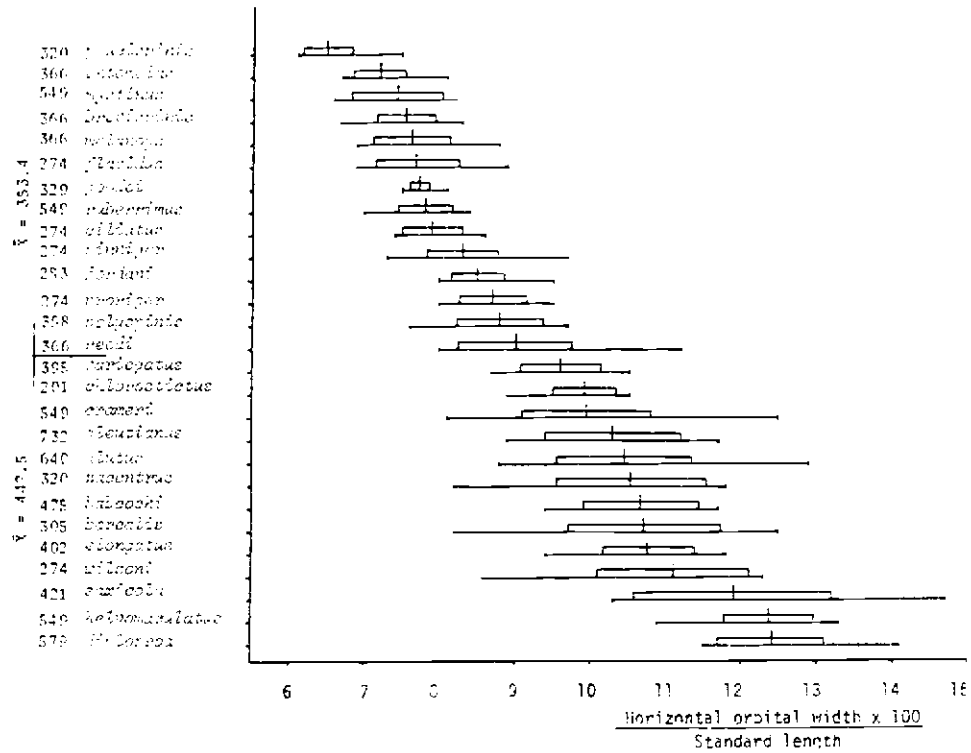


FIG. 51. Mean values, standard deviation and ranges of orbital width as percent of standard length in *Sebastes* spp. Numbers at left indicate maximum depth of captures.

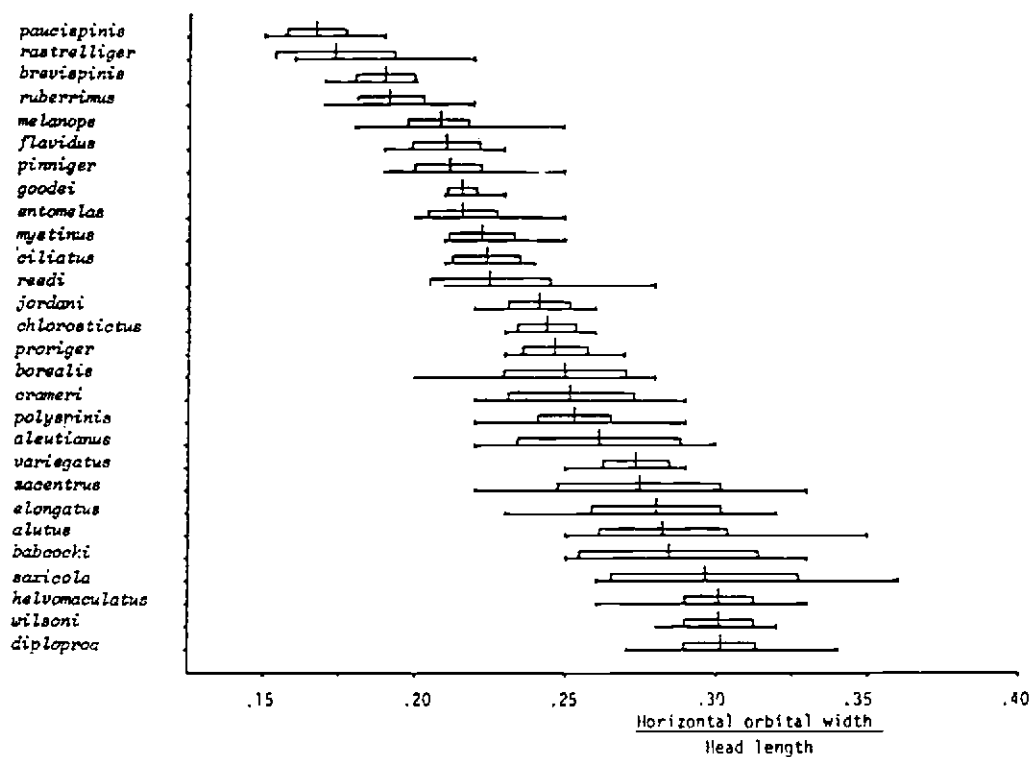


FIG. 52. Mean values, range and standard deviation of values of the ratio orbital width/head length, in Sebastes spp.

comparatively larger orbit in relation to head as the one seen related to standard length. Some species, S. borealis, for example, changed in the opposite way.

The regression analysis of the horizontal orbital width vs. standard length gives us the insight that S. paucispinis is clearly the lower boundary of the "fan" of species (FIG. 53). The correlation between the characteristics was generally very high, the poorest "r" value being the one of S. zacentrus ($r = 0.629$), the only one below 0.700. On 27 species analyzed, 18 have "r" over 0.900 (TABLE 11).

S. diploproa shows a slight relative increase of eye size with length, with the smaller S. helvomaculatus forming a similar slope. Species such as S. crameri, S. chlorostictus, S. babcocki and S. brevispinis, all maintain a constant relationship between growth of the eye and standard length. S. zacentrus and S. borealis have more reclined slopes than the rest. Their orbital diameter is more conservative in relation to increase in standard length. Most of the others show a slight decrease in relative eye size with increasing body length.

Intestine length

The intestine was measured from the pylorus to the

TABLE 11. Regression equations, correlation coefficients and number of specimens studied for orbital width vs. standard length in Sebastes spp. of Oregon.

S p e c i e s	Y = a + bx	"r"	n
<u>aleutianus</u>	Y = 9.5997 + 0.0626X	0.984	9
<u>alutus</u>	Y = 3.6064 + 0.0846X	0.939	22
<u>babcocki</u>	Y = 4.9129 + 0.0859X	0.963	21
<u>borealis</u>	Y = 13.0052 + 0.0626X	0.980	25
<u>brevispinis</u>	Y = 7.4426 + 0.0923X	0.911	22
<u>chlorostictus</u>	Y = -2.036 + 0.1054X	0.917	17
<u>ciliatus</u>	Y = 0.1843 + 0.0779X	0.868	23
<u>crameri</u>	Y = 2.6284 + 0.1086X	0.929	24
<u>diploproa</u>	Y = -0.6789 + 0.1265X	0.947	24
<u>elongatus</u>	Y = 4.1892 + 0.0877X	0.982	30
<u>entomelas</u>	Y = 5.8213 + 0.0563X	0.850	21
<u>flavidus</u>	Y = 8.3714 + 0.0548X	0.934	21
<u>goodei</u>	Y = 0.1837 + 0.0765X	0.970	17
<u>helvomaculatus</u>	Y = 2.3040 + 0.112X	0.913	29
<u>jordani</u>	Y = 3.5475 + 0.0651X	0.911	30
<u>melanops</u>	Y = 4.9342 + 0.0619X	0.932	23
<u>mystinus</u>	Y = 1.8440 + 0.0667X	0.967	16
<u>paucispinis</u>	Y = 2.6601 + 0.0591X	0.962	23
<u>pinniger</u>	Y = 5.7412 + 0.0688X	0.927	21
<u>polyspinis</u>	Y = 8.6106 + 0.0519X	0.716	20
<u>proriger</u>	Y = 6.8209 + 0.0602X	0.897	23
<u>reedi</u>	Y = 9.1092 + 0.0631X	0.950	23
<u>ruberrimus</u>	Y = 1.5514 + 0.074X	0.976	15
<u>saxicola</u>	Y = 8.7575 + 0.0751X	0.972	22
<u>variegatus</u>	Y = 0.7689 + 0.0923X	0.727	14
<u>wilsoni</u>	Y = 6.0542 + 0.12X	0.629	20
<u>zacentrus</u>	Y = 14.4403 + 0.0430X	0.629	25

anal sphincter. The difficulty in determining the separation between midgut and hindgut prevented measurement of them. Depending on the length of the intestine, it has one or more loops (Suyehiro, 1942, vide Harder, 1975). I looked for possible specific differences in the average length according to standard length (FIG. 54). The food habits of an animal, as well functional morphology, can change according to age, so I have used adults, as large as possible. Hence, limited shifts were expected in intestine length due to size of individuals and assumed differences in food habits. Within 27 species measured, S. helvomaculatus showed the shortest intestine, followed by S. variegatus. A sharp gradient of mean values starts with S. helvomaculatus and continues through the next 20 species, with very little discontinuity, until a sudden break in continuity delineates S. goodei, S. crameri, S. reedi and S. melanops as a group somewhat separated from S. mystinus and S. entomelas, which have the highest values.

In general those with short intestine showed less variability, but only S. helvomaculatus, S. variegatus, S. jordani, S. polyspinis, S. saxicola, S. paucispinis and S. brevispinis had narrow ranges. In many of the ranges, the upper values are twice the lowest, and many

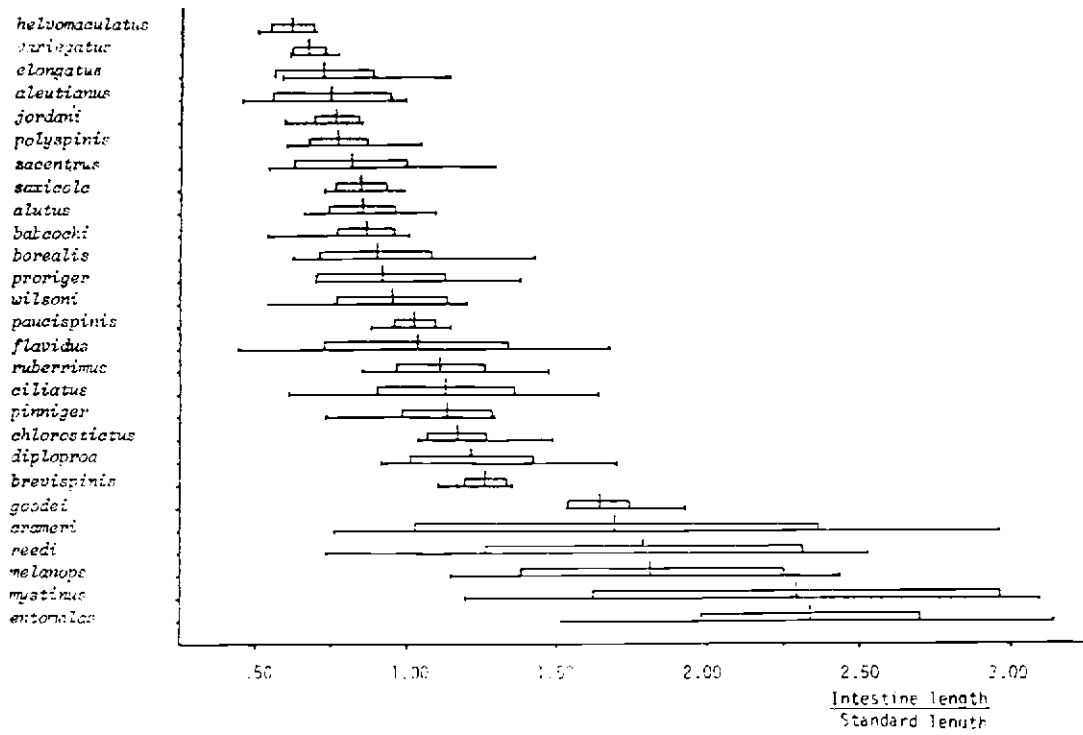


FIG. 54. Ratio intestine length/standard length in Sebastes spp.

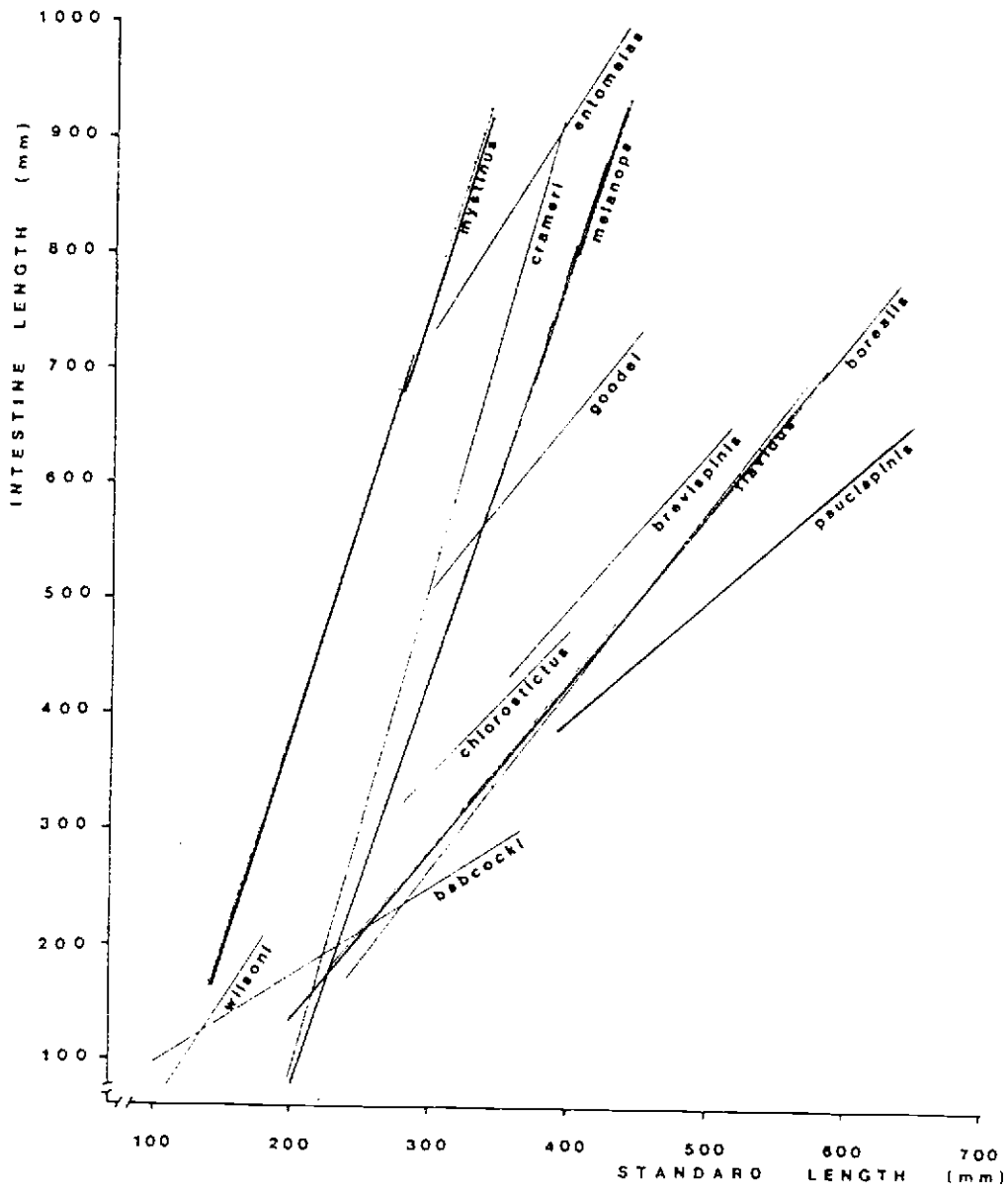


FIG. 55. Regression lines for intestine length, vs. standard length in selected *Sebastes* spp.

are greater than the lowest by factors of three and four. S. crameri was most variable, and the regression line (FIG. 55) shows that the species has the greatest increase in intestine length with increase in standard length. Allometry of a similar magnitude is evident in S. mystinus and S. melanops. S. babcocki shows a decrease in relative intestine length with increasing body size, as did S. helvomaculatus, S. proriger and S. variegatus, not shown in FIG. 55. The expectation that selection of adult fish would preclude diet shifts and changes in relative gut lengths was not realized. Variation in the gut length to standard length ratio can be appreciated by inspection of the ranges in FIG. 54 and "r" values in TABLE 12. There are 13 of the 27 "r" values greater than 0.800 and four lower than 0.600. The low extreme (0.221) is represented by S. proriger.

Pyloric caeca

These formations of the midgut are wart-to-tube-shaped evaginations of the wall of the intestine and are located directly beyond the point where the stomach terminates. Their length among teleosts varies greatly, as does their number (between 1 and more than 1,000). Within certain limits, the number of these structures

TABLE 12. Regression equations, correlation coefficients and number of specimens studied for intestine length vs. standard length in Sebastes spp. of Oregon.

S p e c i e s	Y = a + bx	"r"	n
<u>aleutianus</u>	Y = -132.71 + 1.3186X	0.932	9
<u>alutus</u>	Y = -28.35 + 1.007X	0.890	22
<u>babcocki</u>	Y = 24.04 + 0.75X	0.806	19
<u>borealis</u>	Y = -171.50 + 1.493X	0.885	24
<u>brevispinis</u>	Y = -62.13 + 1.389X	0.848	22
<u>chlorostictus</u>	Y = -32.03 + 1.2613X	0.662	17
<u>ciliatus</u>	Y = -188.90 + 1.809X	0.588	14
<u>crameri</u>	Y = -789.06 + 4.3584X	0.890	18
<u>diploproa</u>	Y = -165.11 + 1.872X	0.864	24
<u>elongatus</u>	Y = -125.1 + 1.356X	0.947	23
<u>entomelas</u>	Y = 172.4 + 1.8691X	0.441	21
<u>flavidus</u>	Y = -205.45 + 1.5659X	0.671	20
<u>goodei</u>	Y = 52.33 + 1.5156X	0.718	17
<u>helvomaculatus</u>	Y = 15.18 + 0.5470X	0.706	28
<u>jordani</u>	Y = -52.18 + 1.05X	0.872	28
<u>melanops</u>	Y = -655.39 + 3.6178X	0.638	20
<u>mystinus</u>	Y = -370.25 + 3.1848X	0.894	16
<u>paucispinis</u>	Y = -29.85 + 1.062X	0.891	21
<u>pinniger</u>	Y = -144.68 + 1.503X	0.949	9
<u>polyspinis</u>	Y = -159.20 + 1.426X	0.863	20
<u>proriger</u>	Y = 120.52 + 0.4397X	0.221	22
<u>reedi</u>	Y = -561.30 + 3.3738X	0.908	19
<u>ruberrimus</u>	Y = -117.26 + 1.4056X	0.867	15
<u>saxicola</u>	Y = 19.46 + 0.74X	0.866	17
<u>variegatus</u>	Y = 21.60 + 0.5601X	0.530	14
<u>wilsoni</u>	Y = -121.98 + 1.8216X	0.916	20
<u>zacentrus</u>	Y = -266.92 + 1.974X	0.889	24

can be characteristic for a species or genus. It is generally assumed that the appendices merely serve to enlarge the surface of the intestinal wall (Harder, 1975).

In our sample, the range in number was from 7 - S. wilsoni, S. paucispinis, S. variegatus and S. zacentrus - to 14 in S. melanops. One specimen of S. babcocki presented 6 pyloric caeca, 2 fewer than the usual range, but it was the smallest of the species sample and was not considered in the calculations. Although that specimen gave S. babcocki the lowest value in the ranges, S. wilsoni was the species with the lowest mean (FIG. 56), followed by S. rastrelliger, S. paucispinis and S. variegatus. A long series of species, starting with S. zacentrus showed a sharp slope towards high mean values, with no doubt about the extreme position of S. melanops. The three species with highest ratios for intestine length/standard length - S. melanops, S. mystinus, S. entomelas - have higher numbers of caeca, along with S. flavidus, which has an intestine of average length for the genus. S. elongatus, S. variegatus and S. zacentrus have short intestine and a low number of caeca.

If we compare the species with the five lowest means for number of pyloric caeca, three of them bear

typical long and slender gillrakers - S. wilsoni, S. variegatus, S. zacentrus - meanwhile the others - S. rastrelliger and S. paucispinis - are typical short and stout gillrakers bearers. At the other extreme, S. flavidus and S. entomelas, with rather long and slender gillrakers, are close to the species with the highest mean value, which is S. melanops. a rockfish considered to have intermediate-short type of gillrakers. I had only a few specimens of some species with short and stout gillrakers, i.e., S. nebulosus and S. nigrocinctus. Some had the intestine and pyloric caeca destroyed. Four specimens of S. rastrelliger were in condition to count, showing a mean value of 8.25.

Head length

Head length was studied not only to show its general relationship to body length (FIG. 57) and to establish any significant differences that might be used in recognition of species, but also to ascertain any relationships to selected trophic adaptations. S. entomelas and S. mystinus have the relatively shortest heads of those studied, but as in other features also studied, there is a gradual gradient of mean values between the lowest and highest percentages with much overlap of ranges and standard deviations. The greatest

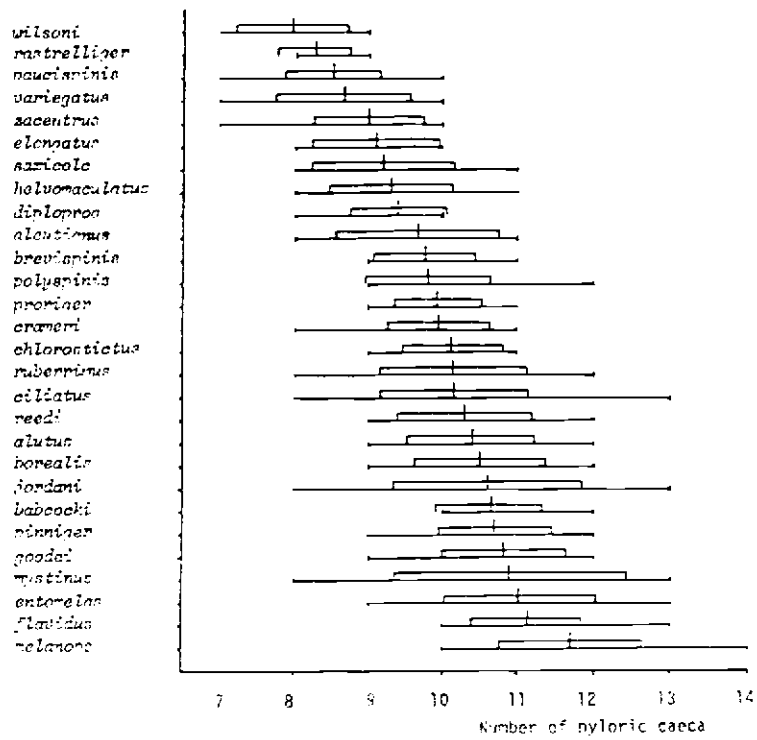


FIG. 56. Variation in the number of pyloric caeca in *Sebastes* spp.

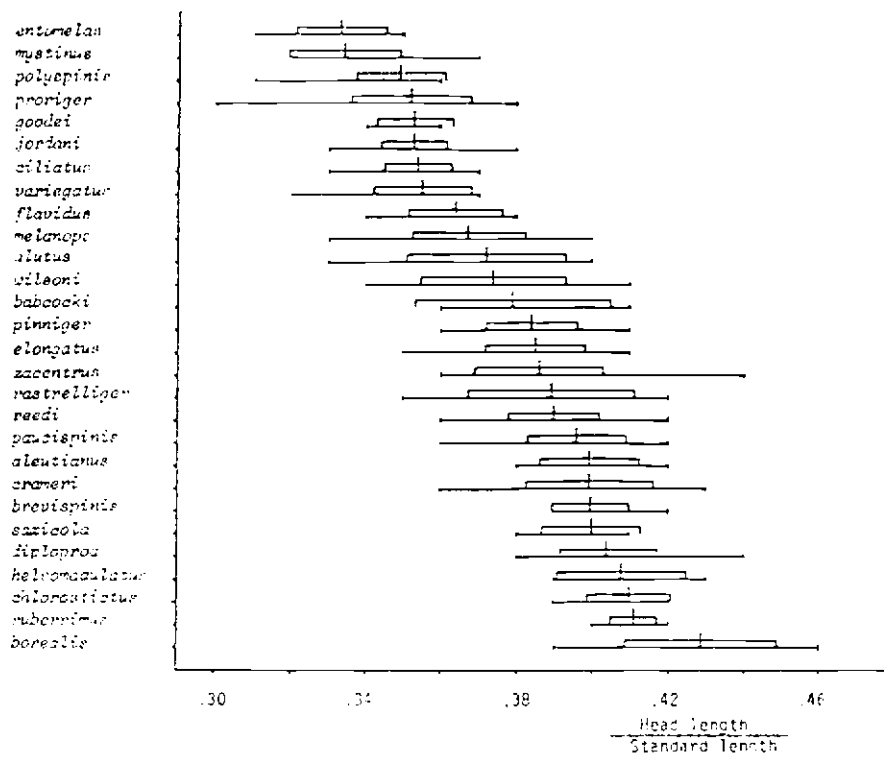


FIG. 57. Ratio between head length and standard length in *Sebastes* spp.

discontinuities are between S. mystinus and S. polyspinis (about 0.14) and between S. ruberrimus and S. borealis at the upper end of the distribution (about 0.18).

Relationships with other trophic features are tenuous. S. entomelas and S. mystinus, with the shortest heads have relatively long and slender gillrakers and have the greatest relative length of intestine, but other than those two, the relationship is erratic. The mean value for the means of head length as percentage of standard length is about 38%. All the species with short, stout gillrakers have heads longer than that.

If we consider 0.380 as the approximate mean values of the two extreme ranges, we will see that all the species we classified as bearers of short and stout gillrakers are over that arbitrary generalized mean, in the area near to the larger head sizes. S. entomelas and S. mystinus, species with rather long gillrakers and longer intestines are in the extreme of the short-headed fishes.

The study of the correlation between head and standard length showed very high "r" values, being only one species - S. variegatus - under 0.900 ($r = 0.802$), and some displayed almost perfect correlation as S.

TABLE 13. Regression equations, correlation coefficients and number of specimens studied for head length vs. standard length in Sebastes spp. of Oregon.

S p e c i e s	Y = a + bx	"r"	n
<u>aleutianus</u>	Y = -7.9852 + 0.4281X	0.992	7
<u>alutus</u>	Y = -1.1573 + 0.3782X	0.974	22
<u>babcocki</u>	Y = 5.9175 + 0.3581X	0.986	21
<u>borealis</u>	Y = 13.6892 + 0.3825X	0.992	25
<u>brevispinis</u>	Y = -11.003 + 0.4228X	0.965	22
<u>chlorostictus</u>	Y = 0.7044 + 0.4069X	0.962	17
<u>ciliatus</u>	Y = -9.4708 + 0.3881X	0.976	23
<u>crameri</u>	Y = -9.0878 + 0.4295X	0.985	24
<u>diploproa</u>	Y = 10.21 + 0.3642X	0.971	24
<u>elongatus</u>	Y = -7.0469 + 0.4188X	0.996	28
<u>entomelas</u>	Y = -25.59 + 0.403X	0.982	21
<u>flavidus</u>	Y = 9.8191 + 0.337X	0.986	21
<u>goodei</u>	Y = -28.75 + 0.4287X	0.918	17
<u>helvomaculatus</u>	Y = -4.9030 + 0.4329X	0.982	29
<u>jordani</u>	Y = 2.425 + 0.3403X	0.984	30
<u>melanops</u>	Y = 4.9197 + 0.3515X	0.958	23
<u>mystinus</u>	Y = 0.1081 + 0.3321X	0.987	16
<u>paucispinis</u>	Y = 9.3604 + 0.3773X	0.980	23
<u>pinniger</u>	Y = 2.7337 + 0.3774X	0.975	21
<u>polyspinis</u>	Y = 16.5067 + 0.2796X	0.918	20
<u>proriger</u>	Y = 9.1534 + 0.3162X	0.918	23
<u>reedi</u>	Y = 2.7262 + 0.3825X	0.982	23
<u>ruberrimus</u>	Y = -2.9091 + 0.4178X	0.977	15
<u>saxicola</u>	Y = 1.1490 + 0.3941X	0.983	22
<u>variegatus</u>	Y = 9.2415 + 0.3049X	0.802	14
<u>wilsoni</u>	Y = 8.8650 + 0.3103X	0.921	20
<u>zacentrus</u>	Y = 6.5314 + 0.3575X	0.953	25

elongatus ($r = 0.996$) and S. ruberrimus ($r = 0.997$) (TABLE 13).

Regression lines were plotted but are not shown here. There was very little allometry shown and most of the lines were parallel or coincident. S. helvomaculatus appears to have the greatest change of head length with increase of standard length, but as mentioned, the allometry is not great.

Use of triangular co-ordinate charts

Some species showed very similar or equal mean values in several characteristics studied. In order to learn how they can be distinguished by relating them to other structures linked to the food gathering process, I analyzed three characteristics for each case, using triangular co-ordinate charts (Burma, 1948; Mayr, 1969). This method is based on the Euclidean theorem on the equilateral triangle, which states that the addition of three lines drawn from a common point inside an equilateral triangle, perpendicularly towards the sides, are equal to the height of that triangle. Systematists consider height equal to 100% so each characteristic has values proportional to the other two used, while standardized in percentages among them, allowing differentiation after plotting and drawing

contour lines on the graphs.

I decided to use these charts in cases in which the overlap shown by other means give a rather difficult differentiation and some examples may be analyzed here. In S. reedi and S. pinniger the range and standard deviation were in overlap when I studied the ascendent premaxillary process length as percent of the standard length. I analyzed the horizontal orbital width, the preangular distance and the length of the lower limb of the first branchial arch of these species. The chart (FIG. 58) shows that the proportional values of the third character allows a displacement of both species toward different surfaces, with little overlap. S. reedi shows both higher proportional percentages of preangular distance and orbital width. In this case S. pinniger has outstanding higher values for the length of the lower limb of the first branchial arch, being only one extreme individual case the one producing surface overlap evident through contour drawing.

These interpretations for species with similar means in the ascendent premaxillary process length as percent of standard length, differentiated through triangular co-ordinates, gives us the possibility for analogous explanations in as many cases as necessary.

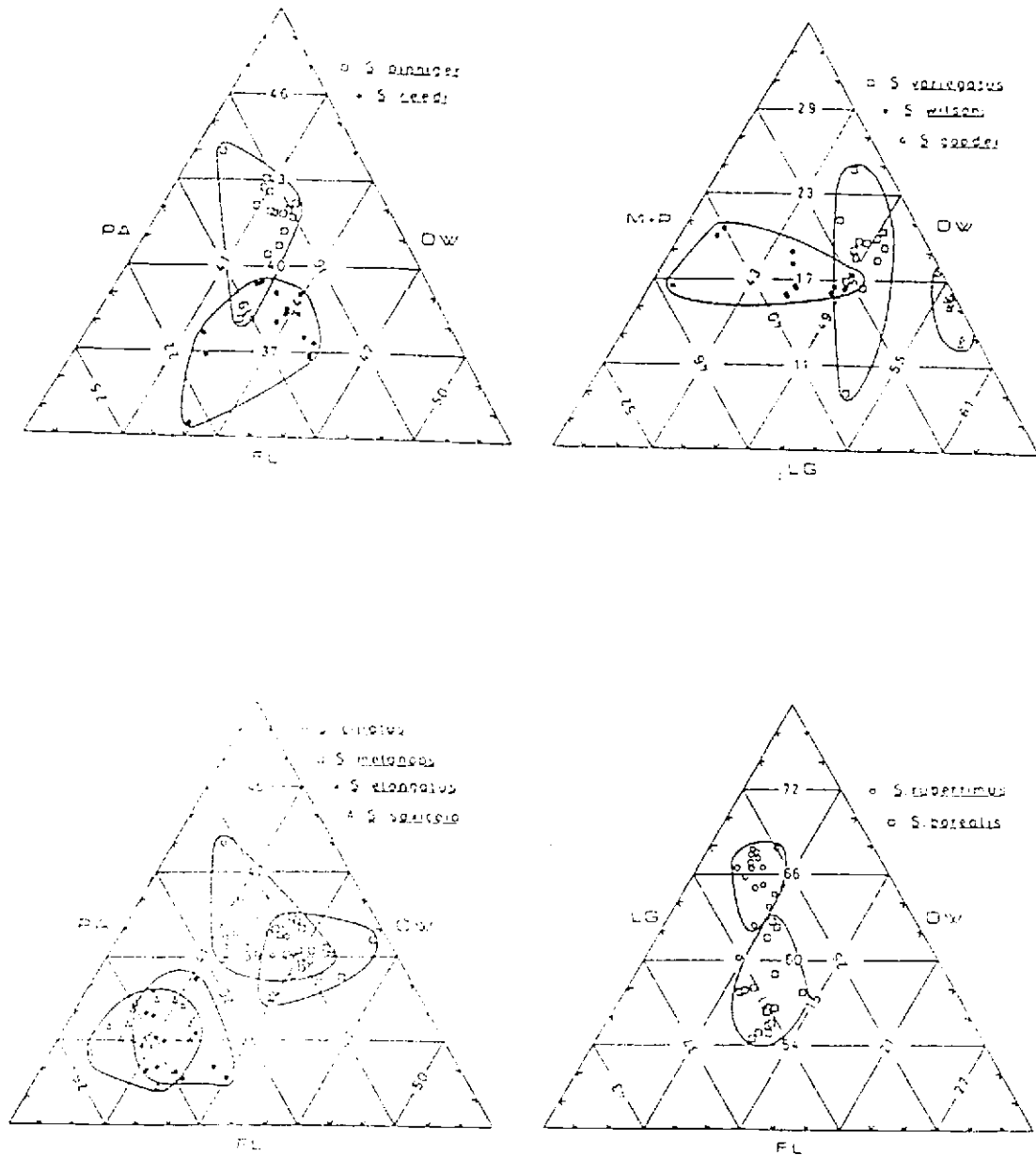


FIG. 58. Triangular co-ordinate analysis in several species of *Sebastes* from Oregon, using structures linked to food-gathering process. Symbols in TABLE 3.

To allow differentiation in other cases, we have made several analysis using different structures, all of them under our frame of reference. The reader will see how other species with similar close means for the same characteristic already showed, are displayed in different surfaces on the triangle : S. wilsoni- S. variegatus (FIG. 58), S. ciliatus- S. melanops (FIG. 58) and S. borealis- S. ruberrimus (FIG. 58).

Species with close mean for maximum maxillary width as percent of standard length, like S. wilsoni- S. goodei, S. melanops- S. elongatus- S. ciliatus - S. saxicola were also analyzed.

The study of other characters produced new cases, which were well displayed by these graphs in most cases. In particular cases, i.e., pinniger-reedi, ruberrimus- borealis and variegatus- wilsoni- goodei, the study of ratios and percentage indices showed little or no overlap in standard deviation, for the characters used in triangular co-ordinate analysis, however the ranges were overlaped and then, the triangular graph showed us another way of differentiate them.

Cluster analysis by multivariate statistics

In general, the cluster analysis corroborated the

very similar structure of rockfishes for the characteristics studied. Considered together (FIGS. 59, 60 AND 61), the flatness of the clusters indicate low dissimilarity (or high similarity), as expected from other analyses of the data. All three dendrograms separated S. ruberrimus and S. paucispinis from the others and the Bray-Curtis analysis placed them together with S. brevispinis and S. chlorostictus. The separation of S. paucispinis and S. ruberrimus is not thought to indicate that they are outliers, but that they are more similar to each other than to the remainder of the group, because of their large mouths and short ,stout gillrakers. Those characters, to a lesser degree, are shown by S. chlorostictus and S. brevispinis.

Although borealis and babcocki have short, stout gillrakers and large mouths, they are separated from the others mentioned in all three clusters, probably because of their relatively long premaxillary processes.

There is a tendency for those species with long, slender gillrakers, to cluster together at different points in the separate dendrograms, but that clustering is far from being consistent. The same can be said for clustering by length of intestine.

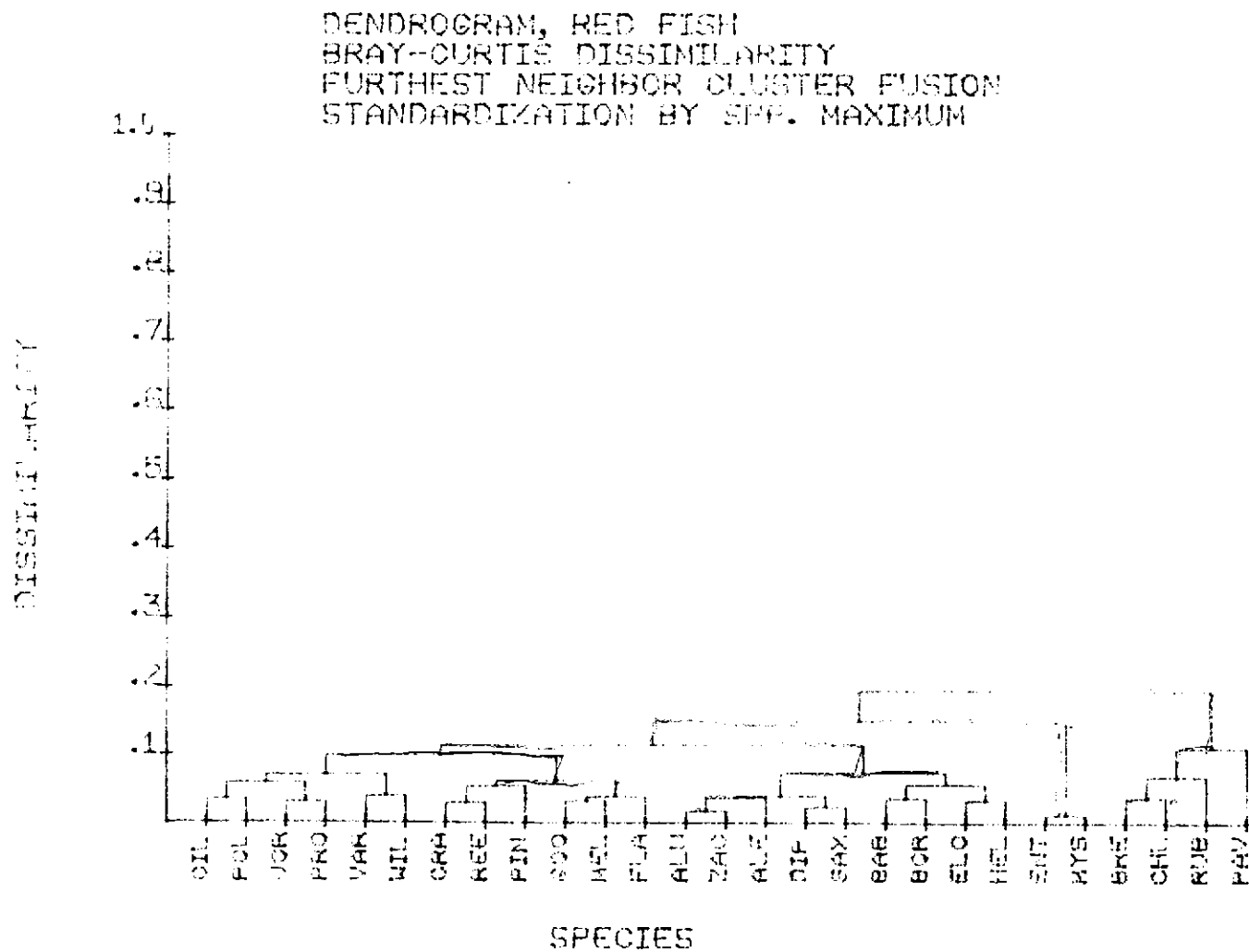


FIG. 59. Dendrogram from cluster analysis.

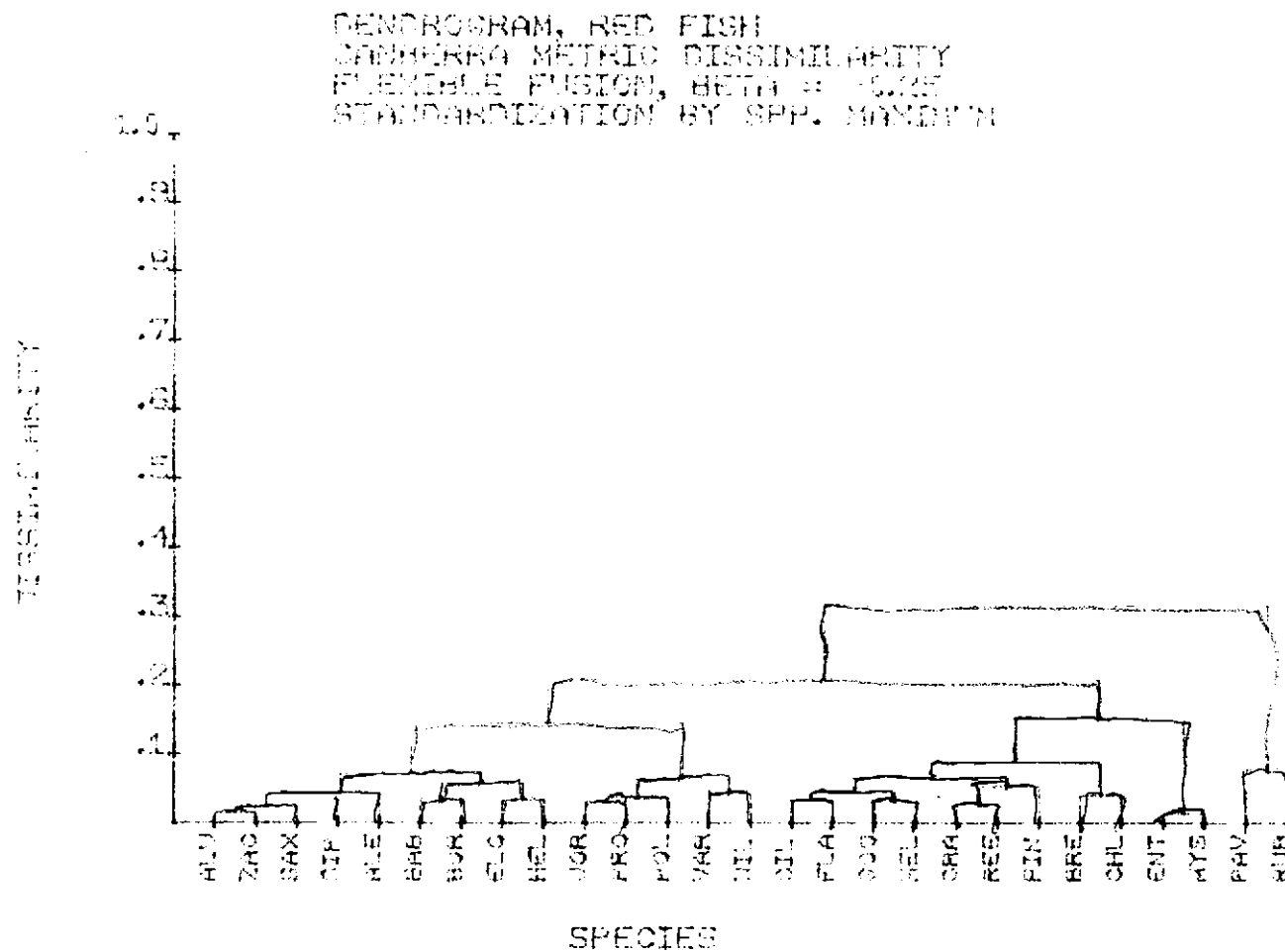


FIG. 60. Dendrogram from cluster analysis.

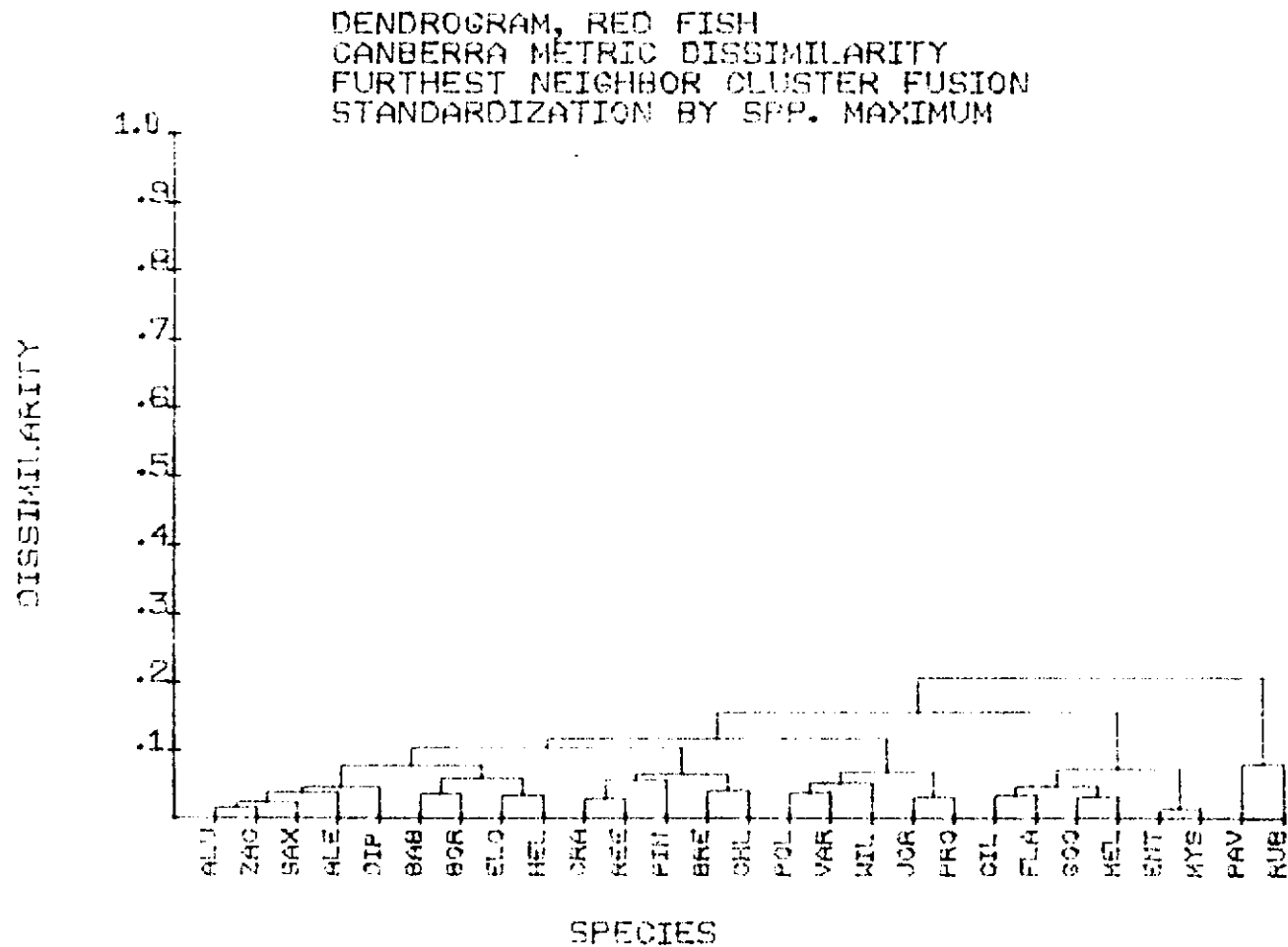


FIG. 61. Dendrogram from cluster analysis.

Overall the clusters indicate that there are pairs or trios of species that are quite similar to each other and that these smaller groups fit into larger clusters in which the relationships are complex. The clusters show no relationship to intrageneric classification.

DISCUSSION

An analysis of most of the common rockfish species of Oregon has shown a close relationship among structural features of their mouths. But it has also shown outstanding differences, which will be discussed below.

Previous studies of rockfishes tend to emphasize rather restricted features: osteology of cranium (Cramer, 1895), external morphology (Hitz, 1981), biochemical aspects (Tsuyuki et al., 1968), external morphology and color (Barss, 1980; Eschmeyer et al., 1983), combined general morphology and distribution (Phillips, 1957). Few ecological, behavioral, functional or environmental features were considered or discussed. Food habit studies, age and growth investigations and studies on early life histories have been developed mainly in the last 15 to 25 years (Wales, 1952; Morris, 1956; Phillips, 1964; Gotshall, et al, 1965, among others).

Data on food habits of several species inhabiting waters of Oregon, and also aspects dealing with habitats and aggregationsof species allow an attempt to relate morphological and

functional adaptation to ecological considerations, specifically as concerns feeding.

Rockfishes of the genus Sebastes constitute a remarkable evolutionary problem, with several species found along the coast in geographical and, in part, in environmental sympatry. Many species overlap in bathymetric and latitudinal distribution, although their centers of distribution and activity might be different. The fact that anglers catch several species from the same reef at the same depth argues for sympatric occurrence of some species. Their general morphology, from species to species, is similar, but although many appear to typify the generalized predator, natural selection has endowed them with differing adaptations for feeding. Differences may be subtle, but recognizable through proper study. The considerable variability within each species, shown in the Results section, points out the plasticity within the genus. The variability could be of importance in two ways: (1) it could allow a variable species to exploit a wider selection of prey than a species with low variability and (2) from the evolutionary standpoint, some phenotypes of the variable species might be favored under conditions of changing habitat.

If we recognize the role of the premaxillary in protrusion, we will agree that longer the premaxillary process, the higher the possibility of protrusion. If this is the case, S. ruberrimus, S. borealis and S. helvomaculatus may have possibilities of greater protrusion than other species. If we correlate the length of the upper jaw - which gives us the idea of large or small mouth opening - that combination gives to these species the characteristic of high protrusibility together with wide mouth opening. Paying attention to a third characteristic - form of gillraker - we will see that the first two mentioned were classified as bearers of short and stout gillrakers, and the third intermediate short. Although the food habits of S. borealis are practically unknown, S. ruberrimus is present in the literature as a predator on fishes (TABLE 14), with a tendency to consume crustaceans also. The intestine of S. ruberrimus - as well as in S. borealis - is moderately long, called intermediate in our sample, but S. helvomaculatus has a short intestine.

Species with relatively high potential for protrusibility also may have small mouth opening, as in S. zacentrus and S. alutus, which also share a

relatively large eye size and short intestine, both being bearers of long and slender gillrakers and very similarly equipped for feeding. The food habits of S. alutus are relatively well known; it chiefly eats euphausiids, with a tendency to consume generalized zooplankton and some cephalopods (TABLE 14). Although some distributional proximity may be deduced from current information (Gunderson and Sample, 1980), the two species are not reported in the same catches, so may not share the same habitat. Although they show great similarity, S. alutus seems to grow larger than S. zacentrus and joint occurrence of different size groups may be studied.

A low degree of protrusibility, based on short ascendent processes, also from some species with large mouth openings, as S. paucispinis, S. chlorostictus and S. brevispinis, bearers of rather short gillrakers and with intermediate-length intestines, if we look at the sample gradient. S. paucispinis is well known as predator of fishes, being secondarily a crustacean eater.

Low protrusibility may be attained in some species with small mouth opening, as happens in S. proriger and S. flavidus. Both of these bear long and

slender gillrakers and also small orbital width and intermediate intestine length.

These last four paragraphs gave us insight related to premaxillary process length and protrusibility in - at least - four groups of species selected from the complete sample. These species represent polarizations or kinds of patterns of structures, combinations of characteristics relating the food gathering process. According to Harder (1975), teleost fishes can lengthen the head by premaxillary protrusion from 5 to 25 %. Rockfishes, from the data presented here, are within this range. Even though the species of Sebastes seem very similar, the different lengths of premaxillary processes in the species give a range of protrusion estimated at from about 9 to over 20 %. This can be kept in mind and correlated to other structures related to food gathering and utilization (TABLES 14 and 15).

The variation of the mouth opening showed us how a gradient can provide information enough to appreciate the importance of the differences. If we look at this characteristic in relation to length of the angular gillraker, we will see a clear tendency of species with large mouths

TABLE 14. Principal food items described in the diet of rockfishes, Sebastes spp., after several authors.
Underlined figures represent the main item recorded in each case.

Species	Algae	GZF	Polychaeta	Crustacea				
				Copepoda	Isopoda	Amphipoda	Euphausiacea	Decapoda
<u>alutus</u>		(7)				(19)	(3)(7)(12)(19)(20)	
<u>caurinus</u>						(11)(15)		(11)(15)
<u>crameri</u>		(2)				(2)	(2)(12)	
<u>diploproa</u>		(2)					(2)(12)	
<u>entomelas</u>		(2)				(2)	(4)	
<u>flavides</u>				(12)		(12)	(2)(6)(12)(18)	(12)
<u>goodei</u>							(2)(9)	
<u>Jordanii</u>		(2)					(2)	
<u>melanops</u>								(8) ^a
<u>mystinus</u>	(5)	(8)(14)	(1)	(1)	(1) ^b	(1) ^b (5)		
<u>nebulosus</u>								(8)
<u>paucispinis</u>						(16)		(16)
<u>pinniger</u>		(2)					(2)(12)(13)	
<u>polyspinis</u>				(7)			(7)	
<u>rastrelliger</u>						(1)		(1)(16)
<u>ruherrius</u>						(10)		(8)
<u>saxicula</u>		(2)					(2)	

Note: Explanation of numbers on the following page.

TABLE 14. Continued.

Species	Mollusca		Chaetognatha	Chordata		
	Cephalopoda	Gastropoda		Salps	Clupeiforms	Perciforms, other
<u>alutus</u>	(7)					
<u>caurinus</u>					(11)	(15)
<u>crameri</u>	(2)			(2)	(2)	
<u>diploproa</u>				(2)	(2)(4)	
<u>entomelas</u>	(2)			(2)(4)	(2)(<u>6</u>)(12)(18)(<u>4</u>)	(<u>2</u>)(12)(17)(18)
<u>flavidus</u>	(2)(12)				(2)	(2)
<u>goudei</u>	(2)					
<u>jordani</u>						
<u>melanops</u>	(12)				(8)(9)	(12)(<u>8</u>)(<u>13</u>)(<u>17</u>)
<u>mystinus</u>	(1) ^b (9)			(<u>2</u>)	(1) ^b (5)	(1) ^b
<u>nebulosus</u>						
<u>paucispinis</u>	(2)(16)				(2)	(<u>2</u>)(16)
<u>pinolger</u>					(2)	(2)
<u>polyspinis</u>	(7)		(7)			
<u>rastrelliger</u>		(1)			(<u>1</u>)	(1)(9)(16)
<u>ruberrimus</u>						(<u>8</u>)(9)(10)
<u>saxicola</u>						

Note: Explanation of numbers on the following page.

Table 14. Continued.

- (1) Quast, 1968.
- (2) Phillips, 1964
- (3) Major and Shippen, 1970
- (4) Adams, 1980 and 1982
- (5) Gotshall, Smith and Holbert, 1964
- (6) Pereyra, Percy, and Carvey, 1969
- (7) Skalkin, 1968
- (8) Steiner, 1979
- (9) Author's personal observations
- (10) Hart, 1943 (In: Brodeur, 1983)
- (11) Prince, 1976
- (12) Brodeur, 1983
- (13) Leaman, 1972 (In: Steiner, 1983)
- (14) Love and Ebeling, 1973
- (15) Patten, 1973
- (16) Feder, Turner, and Limbaugh, 1974
- (17) Gunderson et al., 1986 (In: Brodeur, 1983)
- (18) Lorz, Percy, and Freidenburg, 1983
- (19) Isakson et al., 1971
- (20) Somerton, 1973

a = megalops

b = in juvenile fishes

GZF = Generalized zooplankton

TABLE 15. Mouth characteristics in selected species of Sebastes , with indication of orbital width, gillrakers and intestine types.

Small mouth and low protrusibility

<u>S. entomelas</u>	*	III	L
<u>S. goodei</u>	*	III	L
<u>S. mystinus</u>	*	III	L
<u>S. proriger</u>	*	IV	i
<u>S. flavidus</u>	*	IV	i

Small mouth and high protrusibility

<u>S. zacentrus</u>	o	IV	S
<u>S. alutus</u>	o	IV	S

Large mouth and low protrusibility

<u>S. paucispinis</u>	*	I	i
<u>S. chlorostictus</u>	o	I	i
<u>S. brevispinis</u>	*	II	i

Large mouth and high protrusibility

<u>S. ruberrimus</u>	*	I	i
<u>S. borealis</u>	o	I	i
<u>S. helvomaculatus</u>	o	II	S

Intermediate mouth and intermediate protrusibility

<u>S. melanops</u>	*	II	L
<u>S. ciliatus</u>	*	II	i

* = smaller eye; L = long intestine; o = larger eye;

S = short intestine; I, II, III and IV are gillraker types of increasing length and slenderness (see text).

to have proportionally short gillrakers, while those with small mouth openings showed proportionally longer gillrakers (FIG. 62). We can say that the species within our third group of gillraker types - intermediate long - fit very well in this figure and coincide with their ranking within long intestine species (FIG. 54). Only S. melanops is from the second group, but its location in the graphic is quite near the third, but ratifies it, when we recall that is mainly a fish eater, but is somewhat euryphagous preying also on many different invertebrates. Species such as S. entomelas, S. goodei, S. crameri and S. mystinus all consume macrozooplankton, but of different kinds. S. entomelas showed the longest intestine, together with S. mystinus and both eat many invertebrates rich in chitin, as polychaetes and amphipods. S. mystinus is known to eat gelatinous zooplankton that is low in calories and high in water (Hobson and Chess, 1976). Braking up and digestion of such animals will require more time or retention (Tyler, 1973). I would say that fish cannot slow the rate of passage without jeopardizing the minimum rate of calories they need by unit of time for their vital processes. Enlargement of the intestine probably

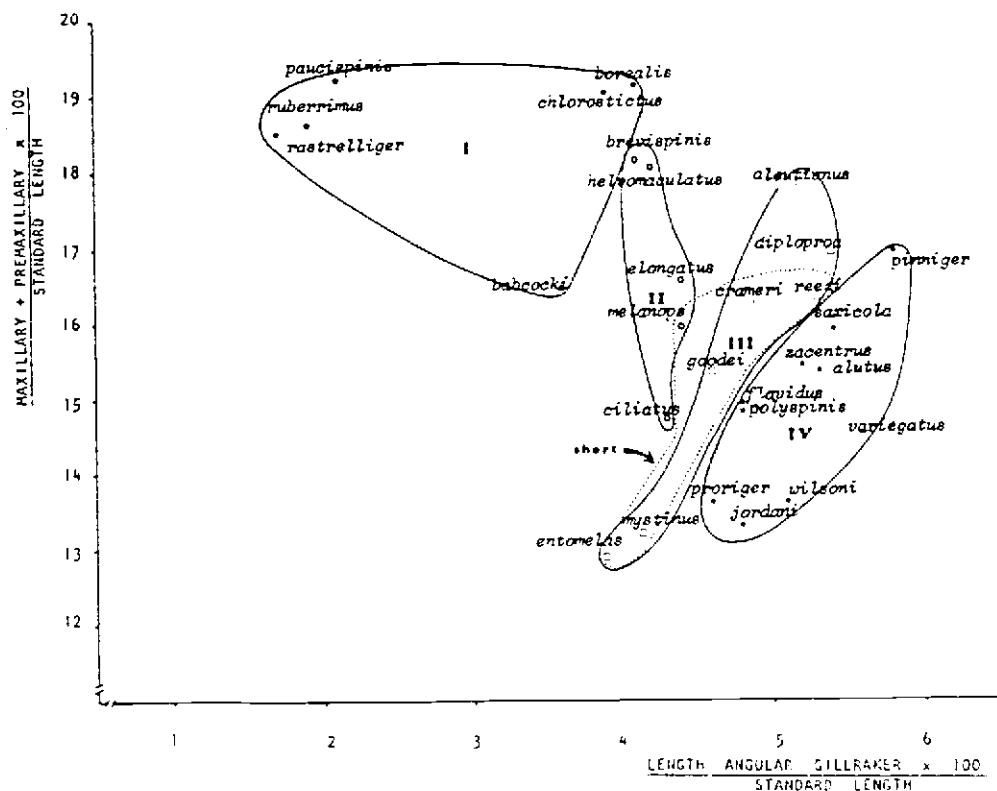


FIG. 62. Mean values for maxillary plus premaxillary as percent of standard length in *Sebastes* spp. of Oregon, according to their angular gillraker length as percent of standard length. Dotted area enclose surface in which species with proportionally short intestine concentrate.

allows for greater frequency of feeding along with greater retention time, and greater opportunity for absorption of water.

With exceptional findings of algae in food contents of S. mystinus, all the species studied are carnivorous, although there are possibilities of finding some omnivores among the ones living in kelp beds, that are still poorly known. The range of intestine is in agreement with some data summarized in literature for other kind of species (Bond, 1979).

Our view on relative length of gillrakers and relative length of intestine may help to understand their forms and functions (FIG. 63).

Tooth bands are wider in species we classified under groups I and II type of gillrakers. Species like S. ruberrimus have a very wide band and is a major predator on fish and crabs. Very probably species such as S. chlorostictus and S. nebulosus are predators on rather mobile animals and they need both wide tooth bands and stout rakers to seize and immobilize relatively large and active prey. S. paucispinis does not have a typical wide tooth band, but has an anterior patch of powerful teeth or enlargement of the tooth band, which surely enables

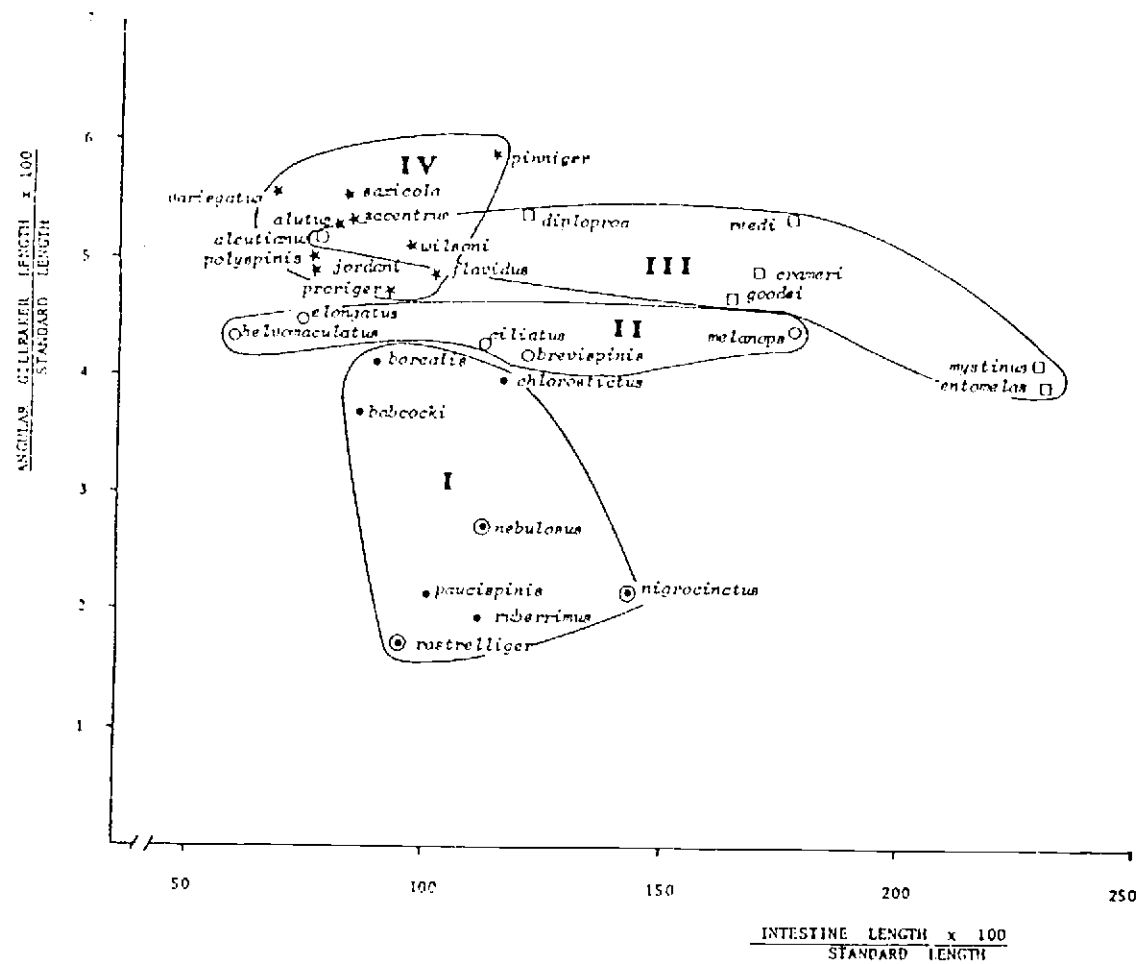


FIG. 63. Scatter diagram showing relationships between mean values of length of angular gillraker as percent of standard length and intestine length as percent of standard length. Roman numbers and contours indicate groups according to gillrakers forms.

the species to secure its prey, and helped by the large mouth opening, swallowing may be quite fast and the handling process shortened. This species does not need wide lateral tooth band using that feeding strategy.

Possibly the fact that S. mystinus, S. flavidus and S. melanops have rather cardiform teeth means the size and texture of their prey is similar even if that prey belongs to a variety of taxa. But as Liem (1980) pointed out - in cichlids - species with a dentition seemingly closely correlated with a special diet are by no means restricted to this diet. Looking at the maximum maxillary width, we will see that most species with powerful maxillae are the ones with large mouth and shorter gillrakers as S. paucispinis, S. ruberrimus, S. brevispinis, among others. This confirms the adaptation of such forms to prey on larger organisms, which requires stronger action to seize and swallow with a minimum of energy expenditure in processing. Species such as S. jordani, S. entomelas, S. proriger and S. mystinus, with narrower maxillae, are typical forms with comparatively longer gillrakers and are invertebrate eaters. They have smaller mouth with low protrusibility - excepting S. jordani, with intermediate pre-

maxillary process length - and seem to be adapted to ingest smaller, less active prey.

The preangular distance gives us a double kind of information: an approach about mouth opening size and a general idea about prognathism. S. paucispinis, which has the longest upper jaw length (FIG. 14) has also the longest preangular distance, which confirms that the species has a larger mouth than any other species in the sample, and has a major projection of the lower jaw.

S. brevispinis, in which the upper jaw is not very long - compared with S. paucispinis - is clearly prognathous. S. chlorostictus has almost no prognathism, nor does S. entomelas. The preangular distances of these two are conservative in respect to the maxilla plus premaxilla length. Those with the prognathous lower jaw, appear to be piscivorous.

Although the species differ in the ratio height/length of the articular bone, there is not a clear relationship with the length of the lower jaw or other characteristics, with exception of S. paucispinis, which is very prognathous and also has - an expected - longer articular.

Form and size of gillrakers have been formulated as related to feeding activity, the long

and slender being generally more numerous, typical for planktophagic organisms, and the short, stout and less numerous, of predatory fishes (Nikolski, 1963; Warren, 1971). Our classification in four groups according to the form of gillrakers, fits well with our knowledge on food habits for most of the species studied (TABLE 14).

Although no clear patterns of distribution of spinulae is seen under SEM, abundance or density of these structures may vary among species, but differences do not depend on size and shape of the gillraker only, except in some cases such as S. paucispinis, which has short gillrakers and very few spinulae. The differences are probably involved in some other aspects, such as specificity of prey and habitat of prey. The gillrakers may be involved also in protecting the gills from foreign material taken in with respiratory water or food, and the probability of introducing such material in a given species feeding may influence the type of spinulae.

The possibility of daily shifting from generalized zooplankton to nektonic preys may require presence of many longer spinulae in a species whose gillrakers are not the longest seen in our sample, S. entomelas, for instance. This species

has been found with a wide range of food content (TABLE 13). Although our analysis considered almost 450 SEM micrographs, I would recommend a higher number of samples, about 5 to 10 fishes by species to match qualitative and - if possible - quantitative characteristics with knowledge of food habits.

Species with high gillraker number tend to have comparatively shorter lower limb of the first gill arch, as in S. jordani, S. wilsoni, S. proriger and S. variegatus. S. pinniger is an exception probably because of a high specialization to prey on euphausiids, which are not the smallest of the crustacean prey. Many slender gillrakers fitting on a short arch constitutes an effective filter for small organisms, even though larger crustaceans and small fishes could be eaten. Meanwhile other species of our first group, such as S. borealis, S. ruberrimus, S. paucispinis and S. chlorostictus have rather long lower limbs, although they have few gillrakers. As we formerly said, they are stout and suitable for holding large prey, without filtering small organisms.

Four groups of Sebastes spp. based on gillraker shape seems justified, and more studies would confirm these groupings. But a view of

generalized mean averages of upper jaw as percent of standard length plotted against proportional length of the angular gillrakers helps to see clearly how the species groups are displayed in a gradient-like relationship, with cases typifying such a trend, and other being rather exceptional within their own groups (FIG. 64).

Also the mouth size seems to have some relationship to maximum size attained by each species, according to different authors (Miller and Lea, 1972; Hitz, 1931). Although there is a gradient we may understand well in our groups I and IV form of gillrakers, this is not so clear for intermediate groups which tend to melt between the extreme mentioned. However, large-mouthed fishes as S. paucispinis, S. borealis and S. ruberrimus, showed a large maximum length. S. aleutianus, poorly known as to food habits - thought to be shared between crustaceans, principally, and small fish - to correlate these factors with its maximum longevity, assumed about 100 years (Archibald et al., 1981), has a moderated sized mouth and a length of nearly a meter. Fishes with smaller mouths showed smaller maximum sizes, as in S. zacentrus, S. jordani and the well-named "pigmy rockfish", S. wilsoni (FIG. 64).

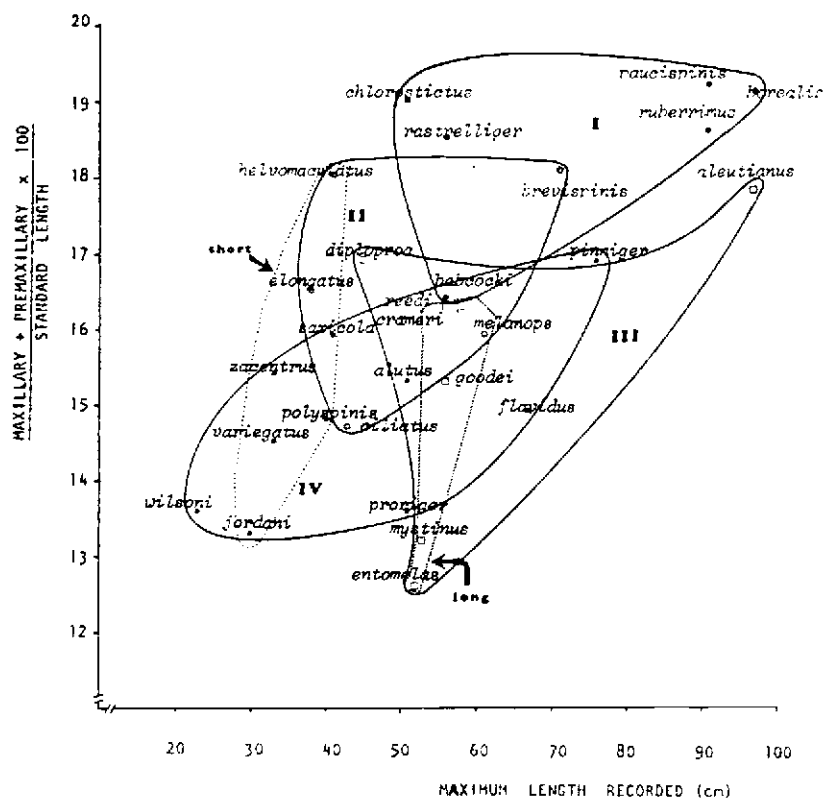


FIG. 64. Mean values for maxillary plus premaxillary as percent of standard length in different *Sebastes* spp. of Oregon, according to their maximum recorded length. Dotted line enclose area in which typically short intestine species concentrate, meanwhile dashed line enclose those with proportionally long intestines.

The vomer also looks complex in respect to specific level relationships, but S. pinniger, which has the widest vomer, also is owner of the widest palatine. In the predatory S. ruberrimus, the vomer and the palatines are wide with powerful tooth patches. S. proriger has a slender vomer and palatines. S. paucispinis, whose palatines are long, has an intermediate type of vomer. Thus, we can see all the series, but it is highly speculative to assume this or that function without accurate knowledge on food habits of all the ensemble. Unfortunately the food habits of some of our species have never been studied.

Although differences in the parasphenoid are evident at the species level, the relationships of some characteristics with feeding activities is not clear. In such a case are the wing processes, which are displaced forward or backward, and thus allow a slightly different articulation with the neurocranium elements. However, the lower surface of the bone showed that at least two species - S. nigrocinctus and S. nebulosus - have sharp edges on the ventral apophysis, with some fine serration-like structures. Most of the species suffer complete, and always partial absorption of these process, which is

in agreement with early studies (Cramer, 1895). Some authors emphasize that higher teleosts do not have teeth on the parasphenoid (Gosline, 1973), so we might be tempted to say that probably the two mentioned species may have a readaptation of the bone for retention and trituration of prey as some ancestral fishes did. However convergence cannot be proposed at all, because there is not a tooth patch as such and, anyway, the processes are covered by mouth mucosa, but the ridges may contribute to holding prey. This characteristic may unite two species whose habitats are - if not the same - very similar, on the shallow continental shelf. Barss (1980), indicated that distribution of S. nebulosus is from 6 to 70 fathoms, meanwhile S. nigrocinctus is from 33 to 150. Both have the same known latitudinal distribution, from California to South Eastern Alaska (Hitz, 1981), and share several characteristics as lower number of gillrakers, short gillrakers, wide tooth bands on the gape and rather high bodies. If S. nebulosus preys mainly on decapod crustaceans, maybe S. nigrocinctus does the same at greater depths. They seem to be a case similar to S. carnatus and S. chrysomelas, a pair of species studied in California, in

in which bathymetric segregation by inter-specific territoriality and resources partitioning was described (Larson, 1980).

Pharyngeal bones may be related more easily to some other structures and functions. Some species with wide tooth bands on the premaxilla have rather short and wide lower pharyngeal bones, as seen in S. ruberrimus, S. nigrocinctus and S. chlorostictus, which also have short gillrakers. Because S. ruberrimus is a known predator on fishes and decapod crustaceans, probably these other species are also predators on mobile animals and the need for securing the prey is still necessary at the pharyngeal level. At this point also a high pressure against the prey is expected from upper and lower pharyngeals, since it is the last possibility of trituration before swallowing.

The glossohyal looks like a spatula in some species - S. flavidus, S. entomelas, S. melanops and S. ruberrimus - which probably needs to handle preys in the mouth for a longer time than predators as S. brevispinis or S. paucispinis, which seem to swallow their prey without any important oropharyngeal processing and whose glossohyal is a mere stick-like bone.

In referring to the orbital width and head length, it is the opportunity to review some concepts dealing with our results and opinions. Some authors have thought about the size of the eyes. Young (1962), stated that the eyes may be small or absent in fishes living in caves, muddy waters or the deep sea. In this last habitat, below the limit of solar light, however, many have exceptionally large eyes, with apparently high sensitivity. This is in agreement with the observation that teleosts show a very wide range of adaptive radiation in their eyes, according to their habitats.

In many deep sea forms the eyes are very large, presumably to pick-up the faint light of luminiscent organisms (Yapp, 1965). Both opinions can be fitted with a third, considering that the eyes of teleosts vary greatly in size, being large in carnivorous fishes and certain deep-sea forms dwelling in regions of dim light, but small in bottom feeders (Walter, 1940).

Looking at the relationship between horizontal orbital width as ratio of the head length (FIG. 52), could give us a better insight about the small size of the eye, coincident in species with shorter gillrakers, such as S. paucispinis, S. rastrelliger

and S. ruberrimus, while - in general - those with large orbital width as S. wilsoni, S. diploproa and S. saxicola have also longer and slender gillrakers. A planktivorous diurnal fish, with long intestine and third gillrakers type, as S. entomelas (Adams, 1982) which does not need large eyes, has his position near S. paucispinis (FIG. 51). This is in agreement with the idea that nocturnal, planktivorous fishes, have larger eyes than diurnal feeders (Ebeling and Bray, 1977).

The length of the intestine in Sebastes seems to have a general relationship with the type of food. The outliers in our graphics are due to small samples of certain sizes, inherent variability and the effect of individual diet (FIGS. 55 and 63). We suggest that species preying on hard-shelled animals need a larger type of intestine to achieve full utilization of them, in agreement with Tyler (1973). Shorter intestine is found in rather small size species, carnivorous but probably not ichthyophagous, as S. jordani and S. saxicola seem to be (TABLE 14), but for which food habits are unknown.

Some authors (Barrington, 1957; Barnard, 1973) said that in some teleosts, pyloric caeca are

folded, narrow extensions of the intestine, increasing the surface area for digestion and absorption. The relationship of the number and volume of pyloric caeca to diet differs among families of fishes; some predators, such as pikes, have none, but other predators such as salmon, may have over 200. Some omnivores such as carps and certain catfishes have none, and some planktophagous fishes have many. In Sebastes, fishes with a long intestine - S. entomelas, S. mystinus, S. melanops and S. goodei - have a higher number of pyloric caeca compared to the ones with short intestine as S. variegatus, S. helvomaculatus, S. elongatus, S. zacentrus and S. saxicola (FIG. 56). It is not clear whether they are carnivorous or omnivorous, because the complexity of the omnivorous diet is little known. S. melanops, being a good ichthyophage has a long intestine and relatively high average number of pyloric caeca. S. flavidus, another mainly ichthyophagous fish, has only an intermediate length intestine, but S. mystinus, a zooplanktophagous also has a long intestine and a high number of pyloric caeca.

We do not confirm findings of Svetovidov (1934, vide : De Groot, 1969) findings, neither those of

Martin and Sandercock (1967), because in our results we find that species with more pyloric caeca may have either a high or a low number of gillrakers

Those with more pyloric caeca have an intermediate number of gillrakers, which is in agreement with the idea that those appendices are more related to a kind of extension of the intestine in fishes eating some invertebrates, like polychaetes. Those fish do not need high or low number of gillrakers, neither too long or too short. For De Groot (1969) pointed out "polychaete feeders do not need large gillrakers, for once the prey has been sucked in, easily passes through to the stomach". Our findings showed that fishes with more pyloric caeca are rather intermediate type in gillrakers and also have longer intestine, which means a third, different theorization if compared to the propositions of Svetovidov (Op. Cit.) and Martin and Sandercock (1967).

Our insight on ecological relationships may be improved if a review of summarized information on joint captures of different species is made (TABLE 16). Also our current knowledge on Sebastes allows us to essay possible mechanisms working to allow

TABLE 16. Examples of possible associations in Sebastes spp., after field observations by several authors.

Species and locality	Author
Cape Flattery to Cape Blanco 91-181 m. <u>entomelas-priger-paucispinis</u> 91-181 m <u>pinniger-flavidus-brevispinis</u> 183-364 m <u>alutus</u> 183-366 m <u>crameri-zacentrus</u> 366-475 m <u>alutus-aleutianus</u>	Gunderson and Sample (1980).
Cape Blanco to Cape Mendocino 91-181 m <u>flavidus-saxicola</u> 100- m <u>crameri-diploproa</u>	
Cape Mendocino to Pt. Hueneme 91-181 m <u>paucispinis-saxicola</u> 183-364 m <u>diploproa</u> 366-475 m <u>diploproa</u>	
Vancouver-Columbia Midwater- <u>entomelas</u>	
Kodiak- Unalaska 95-190 m <u>polyspinis-alutus</u> (juv.)	Westrheim and Tsuyuki (1971)
Bering Sea, Pribilof Is. <u>polyspinis-alutus</u>	Andriashev 1937 (In: Westrheim and Tsuyuki 1971).
Off Newport, Oregon <u>crameri-alutus-diploproa</u>	Alverson and Welander (1952)
Reefs of Sta. Barbara, California <u>paucispinis-miniatus-entomelas</u>	Love (1981)
Off Newport, Oregon <u>diploproa</u> <u>babcocki-crameri-helvomaculatus-</u> <u>jordani</u> and <u>zacentrus</u> ; <u>diploproa-saxicola-elongatus-zacentrus</u> ; <u>babcocki-diploproa-elongatus-jordani-</u> <u>saxicola</u> and <u>helvomaculatus</u> ; <u>jordani-proriger</u>	Long (Pers.Comm.)

the sympatry but explaining the allotopy of these selected species. Several mechanisms could be working - resource partitioning in space, diurnal/nocturnal habits, different age/size groups associations, migration and homing, wide spectrum of foods - after reviewing of literature and origin of our samples (TABLE 1 and TABLE 17). The idea that heterogeneity in the environment allows specialization (Ricklefs, 1973) fits well in Sebastes' case. These polarized type of data facilitate our understanding on rockfishes and their behavior in nature. Species with different characteristics and feeding habits and behavior may live together because they are not competing at all, not for space, neither for food. In other cases - i.e. S. alutus and S. zacentrus - we may understand that they generally do not appear together because are very similar and - to the best of our knowledge - one of them, S. zacentrus, is following a strategy of attaining a smaller comparative size, but might feed partially on the same prey species.

In general, Sebastes spp. have developed broad ability to exploit available food. Each has particular characteristics that should enable it to hold a

TABLE 17. Mechanisms allowing sympatry in selected species of Sebastes spp. according to different authors.

Mechanisms	<u>Sebastes</u> spp. involved	Authors
Territory-resource partitioning	<u>nebulosus</u> (shallow)- <u>ulgrocinctus</u> (deep) <u>plumiger</u> (shallow)- <u>diploproa</u> (deep) <u>chrysomelas</u> (shallow)- <u>carnatus</u> (deep) <u>rubrivinctus</u> (rocky substrate)- <u>hobcocki</u> (smooth)	Barss (1980) Boehlert (1980) Larson (1980) Rosenblatt and Chen (1972)
Diurnal-nocturnal habits	<u>plumiger</u> - <u>flavidus</u> (items exchange) <u>alutus</u> , juvenile (nocturnal) <u>entomelas</u> (diurnal) <u>flavidus</u> (diurnal) <u>atrovirens</u> (nocturnal) <u>serranoides</u> , large juvenile (nocturnal)	Brodeur (1983) Somerton (1978) Adams (1982) Lorz, Percy and Freilenburg (1983) Hobson and Chess (1976) Hobson and chess (1976)
Different age-size group associations	<u>polyspinis</u> (adult)- <u>alutus</u> (young) <u>entomelas</u> and <u>proriger</u> (smaller)- <u>paucispinis</u> (larger)	Welstrheim and Tsuyuki (1971) Gunderson and Sample (1980)
Movements and homing	<u>alutus</u> <u>flavidus</u> <u>paucispinis</u> , <u>entomelas</u> , <u>minutatus</u>	Lyubimova (1964) Carlson and Haigh (1972) Love (1981)
Wide feeding spectrum	<u>mystinus</u> <u>flavidus</u>	Love and Ebeling (1978) Brodeur (1983)

particular niche if competition were to become a factor.

Systematically speaking our study does not reject the current - and old - view of subgeneric groups started by Jordan and Evermann (1898). Although these authors and other modified the criteria of subgenera creating several genera (Jordan, Evermann and Clark, 1830), we agree with newer opinions which consider all these fishes as belonging to one single genus (Phillips, 1957). We support the idea of considering the subgeneric range for some groups within the genus, because as former authors pointed out - with not much discussion - some characteristics are firm enough to think that way (Jordan and Evermann, 1898). We recall that the cranial characteristics studied by these late authors, based on older divisions of Sebastes (Eigenmenn and Beeson, 1893), like shape of skull's base and separation of the parietals by the supraoccipital - among other - are not adaptations to short time environmental changes. These have been long term acquisitions and probably have originated two large rockfish groups, theme to be developed in future studies. At any case, radiation of the rockfishes in the North Pacific - and other oceans -

does not seem alike in terms of monolinear speciation. Probably it has been a process of division of subdivisions, etc. and so on and so forth. From that kind of multiple invasion of different environments, we have possibilities to see speciation of forms with convergent patterns within the frame of divergent evolution. This can be seen as originated from a common ancestor, if we agree with some principles of phylogenetic systematics (Hennig, 1966). If speciation started with a pair of incipient species going toward two different habitats or geographical areas, each of them should speciate in turn and according to available habitats and foods they could evolve in such a way that derivative species could start spreading into new habitats. In that process they could find related species already using resources in that habitat. If the new species become "sympatric" (*sensu lato*), with the resident species they could do so by avoiding competition. That is the way I propose they evolved (FIG. 65). If A and B separated their stocks geographically but contiguously, we have the possibility that derivative species living in similar environments become convergent in many morphological features, but they differenti-

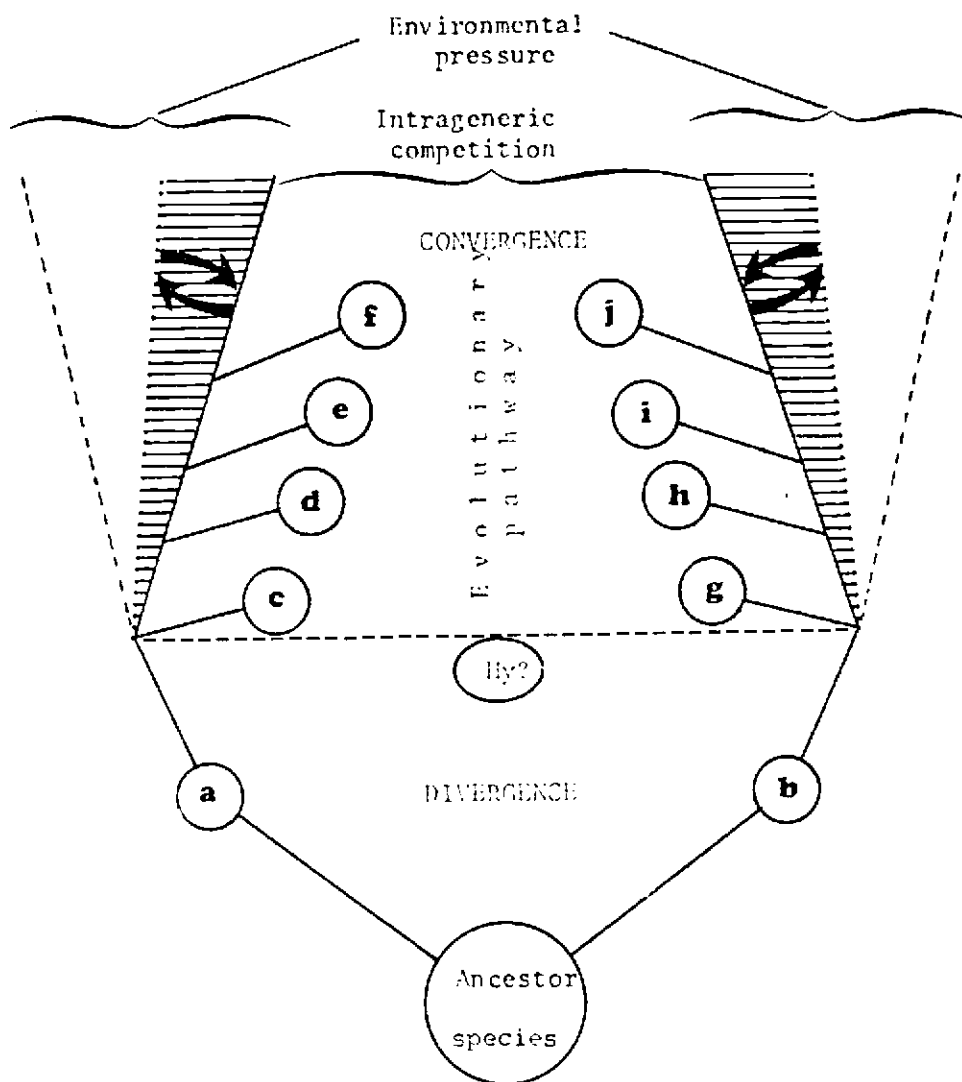


FIG. 65. Diagrammatic description on the possible
evolutionary development of some rockfish,
Sebastes spp., of the North Eastern Pacific.
More explanations in the text.

ate, more or less, avoiding direct competition. This is why they are so similar, but they use different mechanisms to be sympatric but not syntopic, with possible exceptional cryptic species, and they live within a similar latitudinal range, but not in the same habitat. There are several studies providing evidence of various mechanisms acting in environmental separation of *Sebastes* species, as shown in TABLE 16. Isolation of "candidates" for speciation have started on the basis of differential and gradual change in feeding behavior of two groups of fishes within a single species, with some groups of individuals becoming more allotopic.

Genetic separation could have been produced by this means, which has support in former studies in which sympatric speciation has been analyzed upon presence of stable polymorphic populations (Maynard Smith, 1966), and also in other examples (Hubbs, 1961).

Although the basis of the feeding apparatus is on bones, there is no clear evidence that these structures may provide a first level taxonomic tool, in consideration of the plasticity that can allow them to change according to environmental conditions and food habits shifts according to age or

competition, probably producing character displacement in its classical concept (Brown and Wilson, 1965).

The adaptive value of specialized food gathering structures played a main role in differentiation of Sebastes spp., and our interpretation of these adaptations seem to fulfill reasonable doubts of classical thought (Huxley, 1964). If we agree that differentiation of Sebastes involve response to the stimulus of the presence of particular prey, which rewards the fish if capture is good, we could recognize the need to develop behavioral studies on it. Aspects of competition and coexistence may be analyzed from modern standpoints (Pontin, 1982).

However, the studied structures have proved to be useful in distinction of older specimens, which could characterize each species because simply they survived using such structures, among others. Our grouping of rockfishes according to differences in mouth and other food gathering structures may definitely help in recognition of species, but it is doubtful that are a primary base to build a key to determination of species. If such attempt is made, the limitations of geographical differentiations and other short term changes may jeopardize any

specific identification.

The use of triangular co-ordinate graphics proved to be an interesting tool for differentiation of species in many cases and its practice is encouraged. There are possibilities to have only one specimen with doubtful determination at specific level and then, the checking of some measurements within a known triangular chart may help if the fish fits within the contour of other typifying plots. That might be useful in identifying remains in food habit studies, in which many specimens appear semi-digested, or in cases in which a particular fish has been partially destroyed by the gear, for instance.

BIBLIOGRAPHY

- Adams, P.B. 1980. Morphology and distribution patterns of several important species of rockfishes (Genus Sebastes). Mar. Fish. Rev., 42(3-4): 80-82.
- Adams, P.B. 1982. Feeding behavior of the widow rockfish (Sebastes entomelas): a diurnal feeding rockfish, pp. 198-204, IN: C.M. Cailliet and Simenstad (Eds.), Gutshop '81, Fish Food Habits Studies, Wash. Sea Grant Progr., Univ. Wash. Seattle, 312 p.
- Alexander, R. McN. 1967. The functions and mechanisms of the protrusible upper jaws of some Acanthopterygian fish. J. Zool. (Lond), 151:43-64.
- Al-Hussaini, A.H. 1947. The anatomy and histology of the alimentary tract of the plankton-feeder Atherina forskali Rupp. J. Morph. 80: 251-286.
- Alverson, D.L., A.T. Prutter and L.I. Ronholt. 1964. A study of demersal fishes and fisheries of the Northeastern Pacific Ocean. H.R. McMillan Lectures in Fisheries, Univ. Br. Col., Vancouver, 190 p.
- Archibald, C.P., W. Shaw and B.M. Leaman. 1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters. 1977-1979. Can. Tech. Rept. Fish. Aqu. Sci., 1048: IV + 57 p.
- Ayres, W.O. 1854. Descriptions of new fishes from California. Proc. Calif. Acad. Sci. 1:3 - 32.
- Bailey, R.M., J.E. Fitch, E.S. Herald, E.A. Lachner, C.C. Lindsey, C.R. Robins and W.B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada. 3rd. Ed., Am. Fish. Soc. Spec. Publ. 6.
- Barnard, E.A. 1973. Digestion, pp. 133-139, IN: C.L. Prosser (ed.), Comparative Animal Physiology,

- W.B. Saunders Co., Philadelphia, 966 p.
- Barrington, E.J.W. 1957. Digestion in fishes, IN: M. E. Brown (Ed.), The Physiology of Fishes, Vol. 1, Academic Press, New York, 447 p.
- Barss, W.H. 1980. Identification of Oregon rockfish. Oregon Dept. Fish and Wildl., Portland, 29 p.
- Boehlert, G.W. 1977. Timing of the surface-to-benthic migration in juvenile rockfish, Sebastes diploproa, off Southern California. Fish. Bull. 75:887-890.
- Boehlert, G.W. and R.F. Kappenman. 1980. Variation in growth with latitude in two species of rockfish (Sebastes pinniger and S. diploproa) from the Northeast Pacific Ocean. Mar. Ecol. Progr. Ser. 3:1-10.
- Bond, C.E. 1979. Biology of fishes. W.B. Saunders Co., Philadelphia, 514 p.
- Boesch, D.F. 1977. Application of numerical classification in ecological investigations of water pollution. E.P.A.-600/3-77-033 Spec. Scientific Rept.(77): 1-115.
- Briggs, J.C. 1955. A monograph on the cling fishes (Order Xenopterygii). Stanford Ichthyol. Bull. 6: 1-224.
- Brodeur. 1983. Foods habits, dietary overlap and gastric evacuation rates of rockfishes (Genus Sebastes). M. Sc. Thesis, Oregon State Univ., Corvallis, 102 p.
- Brown, W.L. and E.O. Wilson. 1965. Character displacement. Syst. Zool. 5: 49-64.
- Burma, B. 1948. Studies in quantitative paleontology: I. Some aspects of the theory and practice of quantitative invertebrate paleontology. J. of Paleont., 22 (6): 725-761.
- Carlson, H.R. and R.E. Haight. 1972. Evidence for a homesite and homing of adult yellowtail rockfish, Sebastes flavidus. J. Fish. Res. Bd. Can. 29: 1011-1014.

- Chen, L-C. 1971. Systematics, variation, distribution and biology of rockfishes of the subgenus Sebastomus (Pisces, Scorpaenidae, Sebastes). Bull. Scripps. Inst. Oceanogr., Univ. Calif. 18, 115 p.
- Chen, L-C. 1975. The rockfishes (Genus Sebastes), of the Gulf of California, including three new species, with a discussion of their origin. Proc. Calif. Acad. Sci. 40: 109-141.
- Cramer, F. 1895. On the cranial characters of the genus Sebastodes (rockfish). Proc. Calif. Acad. Sci., Ser. 2, 5(1): 573-610.
- De Groot, S.J. 1969. Digestive system and sensorial factors in relation to the feeding behavior of flatfish (Pleuronectiformes). J. du Conseil, 32(3):385-395.
- De Martini, E.E. 1969. A correlative study of the ecology and comparative feeding mechanism morphology of the Embiotocidae (surf-fishes) as evidence of the family's adaptive radiation into available ecological niches. Wasmann J. Biol. 27:177-247.
- Dunn, F.R. and C.R. Hitz. 1969. Oceanic occurrence of black rockfish (Sebastes melanops) in the Central North Pacific. J. Fish. Res. Bd. Can. 26:3094-3097.
- Ebeling, A. and R.N. Bray. 1977. Day vs night activity of reef fishes in a kelp forest off Santa Barbara, California. Fish. Bull. 74:703-718.
- Eigenmann, C.H. and C.H. Beeson. 1893. Preliminary note on the species usually united under the generic name Sebastodes. Am. Nat. 27:668-671.
- Eschmeyer, W.N., E.S. Herald and H. Hamann. 1983. A field guide to Pacific coast fishes of North America. Houghton Mifflin Co., Boston, 336 p.
- Feder, H.M., C.H. Turner and C. Limbaugh. 1974. Observations on fishes associated with kelp beds in Southern California. Calif. Fish and Game, Fish. Bull. 160: 1-138.

- Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge, 298 p.
- Gill, T. 1864. Critical remarks on the genera Sebastes and Sebastodes of Ayres. Proc. Acad. Nat. Sci. Philad. 16:145-147.
- Goodrich, E.S. 1930. Studies on the structure and development of vertebrates. Vol. 1 (Repr.1958), Dover Publs.,Inc., New York, 485 p.
- Gosline, W.A. 1973. Functional morphology and classification of teleostean fishes. The Univ. Press of Hawaii, Honolulu, 208 p.
- Gotshall, D. 1964. Increasing tagged rockfish (Genus Sebastodes) survival by deflating the swimbladder. Calif. Fish and Game 50(4):253-260.
- Gotshall, D., J.G. Smith and H. Holbert. 1965. Food of the blue rockfish Sebastodes mystinus. Calif. Fish and Game 51(3):147-162.
- Gregory, W.K. 1933. Fish skulls. A study of the evolution of natural mechanisms. Trans. Am. Phil. Soc. 23:75-481.
- Gunderson, D.R. and T.M. Sample. 1980. Distribution and abundance of rockfish off Washington, Oregon and California during 1977. Mar. Fish. Rev. 42(3-4):2-16.
- Hallacher, L.E. 1974. The comparative morphology of extrinsic gasbladder musculature in the scorpionfishgenus Sebastes (Pisces, Scorpaenidae). Proc. Calif. Acad. Sci.(4th Ser.),40(3):59-86.
- Harder, W. 1975. Anatomy of fishes. Part I, Text, 612 p.; Part II, Figs. and Plates, 132 p. + 13 plates. E. Schweitzerbat'sche Verlasgb., Stuttgart.
- Hatanaka, M., M. Mosaka, Y. Sato, K. Yamaki and K. Fukui. 1954. Interspecific relations concerning the predacious habits among the benthic fish. Tohoku J. Agr. Res. 5(3):177-189.

- Hennig, W. 1966. Phylogenetic systematics. Univ. of Illinois Press, Urbana, 263 p.
- Hitz, C.R. 1961. Occurrence of two species of juvenile rockfish in Queen Charlotte Sound. J. Fish Res. Bd. Can. 18:279-281.
- Hitz, C.R. 1981. Field identification of the Northeastern Pacific rockfish (Sebastodes). US Dept. Interior, Fish. Wildl. Serv., Circular 203: 1-62.
- Hobson, E.S. and J.R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina island, California. Fish. Bull. 74(3):567-598.
- Hubbs, C.L. 1951. Allosebastes, new subgenus for Sebastodes sinensis, scorpaenid fish of the Gulf of California. Proc. Biol. Soc. Washington 64:129-130.
- Hubbs, C.L. 1961. Isolating mechanisms in the speciation of fishes, pp.5-23, IN: W.F. Blair (Ed.), Vertebrate speciation, A Univ. of Texas Symposium, The Univ. of Texas Press, Austin, 642 p.
- Huxley, J. 1964. Evolution, the modern synthesis. John Wiley and Sons, New York, 653 p.
- Isakson, J.S., C. A. Simenstad and R.L. Burgner. 1971. Fish communities and food chains in the Amchitka area. BioScience 21(12):666-670.
- Jordan, D.S. and B.W. Evermann. 1898. The fishes of North and Middle America. Bull. US Nat. Mus. 47(2):1758-1835.
- Jordan, D.S., B.W. Evermann and H.W. Clark. 1930. Checklist of the fishes and fish-like vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rept. US Comm. Fish. 1928, Part 2, 670 p.
- Jordan D.S. and C.H. Gilbert. 1882. Synopsis of the fishes of North America. Bull. US Nat. Mus. 16: 1-1018.

- Keniston, W. C. 1978. Program CLUSTER
Oregon State Univ., Marine Science Ctr.,
(mimeogr.), 23 p.
- Lance, G.N. and W.T. Williams. 1966. A generalized
sorting strategy for computer classifications.
Nature, 212: 218.
- . 1967. A general theory of classificatory
sorting strategies. I, Hierarchical systems.
Computer Jour., 9: 373-380.
- Larson, R.J. 1980. Competition, habitat selection,
and bathymetric segregation of two rockfish
(Sebastes) species. Ecol. Monogr. 50:221-239.
- Lenarz, W.H. 1980. Shortbelly rockfish, Sebastes
jordani: a large unfished resource in waters
off California. Mar. Fish. Rev. 42(3-4):34-40.
- Liem, K. 1980. Adaptive significance of intra- and
interspecific differences in the feeding
repertoires of cichlid fishes. Am. Zool. 20:
295-314.
- Lorz, H.W., W.G. Pearcy and M. Freidenburg. 1983.
Notes on the feeding habits of the yellowtail
rockfish, Sebastes flavidus, off Washington
and in Queen Charlotte Sound. Calif. Fish and
Game 69(1):33-38.
- Love, M.S. 1980. Isolation of olive rockfish,
Sebastes serranoides, populations off
Southern California. Fish. Bull. 77(4):975-983.
- Love, M.S. 1981. Evidence of movements of some
deepwater rockfishes (Scorpaenidae: Genus
Sebastes) of Southern California. Calif. Fish.
and Game, 67(4):246-249.
- Love, M.S. and A. W. Ebeling. 1978. Food and habitat
of three switch-feeding fishes in the kelp
forests off Santa Barbara, California. Fish.
Bull. 76(1):257-271.
- Lyubimova, T.G. 1964. Biological characteristics of
the school of Pacific rockfish (Sebastes
alutus G.), in the Gulf of Alaska. Trudy,
53 (3): 208-216, Soviet Fisheries
Investigations in the North East Pacific, Part
III.

- Major, R.L. and H.H. Shippen. 1970. Synopsis of biological data on Pacific Ocean perch, Sebastes alutus. F.A.O. Sp. Synop. 79 :1-38.
- Marshall, N.B. 1971. Explorations in the life of fishes. Harvard Univ. Press, Cambridge, 204 p.
- Martin, N.V. and F.K. Sandercock. 1967. Pyloric caeca and gillraker development in lake trout, Salvelinus namaycush, in Algonquin Park, Ontario. J. Fish. Res. Bd. Can. 24:965-974.
- Maynard Smith, J. 1966. Sympatric speciation. Am. Nat. 100(916):637-650.
- Mayr, E. 1950. Principles of systematic zoology. McGraw Hill Book Co., New York, 428 p.
- Miller, D. J. and R.N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Fish. and Game, Fish. Bull. 157 :1-249.
- Morris, R. W. 1956. Early larvae of four species of rockfish, Sebastes. Calif. Fish and Game 42(2):149-153.
- Moser, H.G. 1967. Reproduction and development of Sebastes paucispinis and comparison with other rockfishes off Southern California. Copeia 1967(4):773-797.
- Moser, H.G. 1972. Development and geographic distribution of the rockfish Sebastes macdonaldi (Eigenmann and Beeson, 1893), family Scorpaenidae, off Southern California and Baja California. Fish. Bull. 70(3):941-958.
- Moser, H.G., E.H. Ahlstrom and E.M. Sandknop. 1977. Guide to the identification of scorpionfish larvae (Family Scorpaenidae) in the Eastern Pacific, with comparative notes on species of Sebastes and Helicolenus from other oceans. NOAA Tech. Rep. NMFS Circular 402, 71 p.
- Nicol, J.A.C. 1978 . Bioluminescence and vision, pp. 367-398, IN: P.J. Herring (Ed.), Bioluminescence in action. Academic Press, London, 570 p.

- Nikolski, G.W. 1963. The ecology of fishes. Academic Press, New York, 352 p.
- Norman, J.R. and P.H. Greenwood. 1975. A history of fishes. John Wiley and Sons, New York, 467 p.
- Patten B.C. 1973. Biological information on copper rockfish in Puget Sound, Washington. Trans. Am. Fish. Soc. 102(2):412-416.
- Pereyra, W.T., W.G. Pearcy and F.E. Cavey, Jr. 1969. Sebastes flavidus, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Bd. Can. 26(8):2211-2215.
- Phillips, J. 1957. A review of the rockfishes of California. Calif. Fish and Game, Fish Bull. 104:1-158.
- Phillips, J. 1964. Life history studies on ten species of rockfishes (Genus Sebastes). Calif. Fish and Game, Fish Bull. 126: 1-70.
- Pianka, E. 1970. On r and k selection. Am. Nat. 104: 592-597.
- Pimentel, R. 1979. Morphometrics. Kendall/Hunt Publ. Co., Dubuque, 276 p.
- Pontin, A. J. 1982. Competition and coexistence of species. Pitman Books Lts., London, 102 p.
- Prince, E.D. and D.W. Gotshall. 1976. Food of the copper rockfish, Sebastes caurinus, associated with an artificial reef in South Humboldt Bay, California. Calif. Fish and Game 62(4): 274-285.
- Quast, J.C. 1968. Observations on the food of the kelp bed fishes, pp. 109-142, IN: W.J. North and C.L. Hubbs (Eds.), Utilization of kelp bed resources in Southern California. Calif. Fish and Game, Fish Bull. 139.
- Richardson, S.L. and W.A. Laroche. 1979. Development and occurrence of larvae and juveniles of the rockfishes Sebastes crameri, Sebastes pinniger and Sebastes helvomaculatus (Family Scorpaenidae) off Oregon. Fish. Bull.

77(1):1-46.

- Ricklefs, R. 1973. Ecology. Chiron Press, Newton, Massachusetts, 861 p.
- Romer, A.S. 1955. The vertebrate body. 2nd Ed., W.B. Saunders Co., Philadelphia, 644 p.
- Rosenblatt, R.H. and L-C. Chen. 1972. The identity of Sebastes babcocki and Sebastes rubrivinctus. Calif. Fish and Game. 58(1):32-36.
- Schultz, L.P. and A. C. DeLacy. 1936. Fishes of the American Northwest. A catalogue of the fishes of Washington and Oregon, with distributional records and a bibliography (second installment). Mid. Pac. Mag., J. Pan.- Pac. Res. Inst. 11 (1): 63-78.
- Six, L.D. and H.F. Horton. 1977. Analysis of age determination methods for yellowtail rockfish, canary rockfish and black rockfish, off Oregon. Fish. Bull. 75:405-414.
- Simpson, G.G. and A. Roe. 1939. Quantitative zoology. McGraw Hill Co., Inc., New York, 414 p.
- Skalkin, V.A. 1968. Diet of rockfish in the Bearing Sea. , IN: P.A. Moiseev (Ed.), Soviet Fisheries Investigations in the Northeast Pacific, Part III, p. 159-174 (Trans. Isr.Progr.Sci.Transl.).
- Snytko, V.A. and V.V. Fedorov. 1974. New data on the distribution of scorpaenid fishes of the subfamily Sebastinae and notes on their biology. J. of Ichthyol. 14(6):811-818.
- Somerton, D. 1978. Competitive interaction of walleye, pollock and Pacific Ocean perch in the Northern Gulf of Alaska (Abstract), IN: S.J. Lipovski and C.A. Simenstad (Eds.), Gutshop '78, Fish Food Habit Studies, Wash. Sea Grant Publ., Univ. of Washington, Seattle, 222 p.
- Steiner, R.G. 1978. Food habits and species composition of neritic reef fishes off Depoe Bay, Oregon. M.Sc. Thesis, Oregon State Univ., Corvallis, 59 p.

- Tsuyuki, H., E. Roberts , R.H. Lowe and W. Hadaway.
1968. Contribution of protein electrophoresis to
rockfish (SCorpaenidae) systematics. J. Fish.
Res.Bd. Can. 25:2477-2501.
- Tyler, A.V. 1973. Alimentary tract morphology of
selected North Atlantic fishes in relation to
food habits (Manuscript). Fish. Res. Bd. Can.,
Tech. Rept.,361: 1-23.
- Wales, J.H. 1952. Life history of the blue rockfish
Sebastes mystinus. Calif. Fish and Game.
38(4):485-498.
- Walter, H.E. 1940. Biology of the vertebrates. The
McMillan Co., New York, 882 p.
- Warren, C.E. 1971. Biology and water pollution
control. W.B. Saunders Co.,Philadelphia, 434 p.
- Weistrheim, S.J. and H. Tsuyuki. 1971. Taxonomy,
distribution and biology of the northern
rockfish ,Sebastes polyspinis. J. Fish.
Res. Bd. Can. 28:1621-1627.
- Yapp, W.B. 1965. Vertebrates, their structure and
life. Oxford Univ. Press, New York, 525 p.
- Young, J.Z. 1962. The life of vertebrates. Oxford
Univ. Press, New York, 820 p.

APPENDIX

APPENDIX 1. The classification of the Sebastes,
as seen by Jordan and Evermann (1898).

Subgenera	Species
<u>Emmelas</u>	<u>S. glaucus</u>
<u>Sebastodes</u>	<u>S. jordani</u> <u>S. goodei</u> <u>S. paucispinis</u>
<u>Sebastosomus</u>	<u>S. flavidus</u> <u>S. serranoides</u> <u>S. melanops</u>
<u>Primospina</u>	<u>S. ciliatus</u> <u>S. mystinus</u>
<u>Acutomentum</u>	<u>S. entomelas</u> <u>S. rufus</u> <u>S. macdonaldi</u> <u>S. brevispinis</u> <u>S. ovalis</u> <u>S. eigenmanni</u> <u>S. hopkinsi</u> <u>S. alutus</u> <u>S. proriger</u>
<u>Rosicola</u>	<u>S. pinniger</u> <u>S. miniatus</u>
<u>Zalopyr</u>	<u>S. aleutianus</u> <u>S. atrorubens</u> <u>S. atrovirens</u>
<u>Eosebastes</u>	<u>S. saxicola</u> <u>S. crameri</u> <u>S. semicinctus</u> <u>S. diploproa</u> <u>S. aurora</u> <u>S. melanostomus</u> <u>S. introniger</u>

APPENDIX 1. (CONT.).

<u>Sebastomus</u>	<u>S. ruberrimus</u> <u>S. constellatus</u> <u>S. umbrosus</u> <u>S. rosaceus</u> <u>S. ayresi</u> <u>S. rhodochloris</u> <u>S. eos</u> <u>S. gilli</u> <u>S. chlorostictus</u> <u>S. rupestris</u>
<u>Hispanicus</u>	<u>S. sinensis</u> <u>S. zacentrus</u> <u>S. elongatus</u> <u>S. levis</u> <u>S. rubrivinctus</u>
<u>Auctospina</u>	<u>S. auriculatus</u> <u>S. auriculatus dallii</u>
<u>Pteropodus</u>	<u>S. rastrelliger</u> <u>S. caurinus</u> <u>S. vexillaris</u> <u>S. maliger</u> <u>S. gilberti</u> <u>S. carnatus</u> <u>S. chrysomelas</u> <u>S. nebulosus</u>
<u>Sebastichthys</u>	<u>S. serriceps</u> <u>S. nigrocinctus</u>
