

# MORPHOMETRIC VARIATION OF PACIFIC OCEAN PERCH, *SEBASTES ALUTUS*, OFF WESTERN NORTH AMERICA

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## ABSTRACT

Pacific ocean perch, *Sebastes alutus*, vary in body form over the eastern Pacific Ocean and southeastern Bering Sea. When related to a 260 mm standard length, a small adult size, most of 18 body measurements change from east to west as V-shaped clines. Belly size, however, lengthens as a single cline from the Vancouver vicinity westward, and the lengthening is coupled with shortening of measurements complementary to the belly measurement, from head to belly and belly to tail. Most adult body dimensions are sexually dimorphic, but the dimorphism is slight. Growth inflections may occur but, if so, are hidden in the data. Body form does not change markedly with growth except for the symphyseal knob, which becomes relatively larger, and the 3d anal-fin spine, which becomes relatively shorter. Putative subspecies of *S. alutus* probably are premature because supportive morphometric comparisons and criteria on the subspecies seem based on too few data, and do not adequately consider complex clinal variation and growth allometry evidenced in the eastern part of the species range. Also, significant morphometric variation may be phenotypic.

Pacific ocean perch, *Sebastes alutus*, a commercially important rockfish (Scorpaenidae) in the North Pacific Ocean, range from northern Honshu, Japan, to California. To date, the species' taxonomy has been based on relatively limited local representation, on preserved material, and on analyses without probabilistic interpretation or attention to allometric growth. Matsubara (1943) identified a Honshu representative as a new species (*Sebastes paucispinosus*), but Barsukov (1964), after examining specimens taken across the North Pacific Ocean, suggested that the variation he found indicated, at most, possible eastern and western Pacific subspecies, with both possibly occurring off the Aleutian Arc. Chen (1971) demonstrated that growth rate, can influence body proportions in a *Sebastes* species, and Westheim (1973) found a cline of increasing growth rate in *S. alutus* from the northern Gulf of Alaska to Washington (Quast<sup>2</sup> found that the cline may be more related to latitude than temperature).

Because of the commercial importance of Pacific ocean perch and the lack of definitive information on possible subspecies or genetic stocks at the onset of the study, the National Marine

Fisheries Service gathered morphometric data on representatives from the Gulf of Alaska and eastern Bering Sea from 1968 to the mid-1970's. We sought evidence of disjunct geographic variation that might indicate genetic stocks, and analyzed for characteristics of growth and sexual variation of possible taxonomic significance. Sampling was in the shallow range of the species distribution, at <200 fathoms (366 m).

## METHODS

The prohibitively large volume needed for specimen storage for an extensive statistical study and the shrinkage, bending, and other distortions caused by preservation were avoided by photographing freshly trawled Pacific ocean perch. A portable stand supported a 35 mm camera and flash unit 145 cm above a V-shaped easel, which helped restrain the fish from vessel motion. The long focal distance minimized foreshortening in the photographs, and a 100 mm telephoto lens reduced field size to include only the specimen, a centimeter scale, a numbered theater ticket, and a plastic card with pencil-inscribed catch information. Specimens were flattened, straightened, and centered on the easel; fins were placed as erect as possible; and the lower jaw was propped closed with handheld forceps. Later, in the laboratory, body measurements were taken from images projected from the color transparencies onto the back of a ground-glass screen. The images

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<sup>2</sup>Jay C. Quast. Annual growth in Pacific ocean perch, *Sebastes alutus*: variation, stanzas, compensation, and simulation. Manusc. in prep.

were brought to natural size by reference to the centimeter scale in each photograph. Accuracy was ensured for body-depth measurements by using a right-angle scale on the body axis.

The study used 18 linear measurements<sup>3</sup> (nearest millimeter) in addition to standard length (SL) of approximately 1,500 specimens sampled from the Bering Sea and Gulf of Alaska during summers of 1968-70 (Fig. 1, Table 1). The measurements gave major dimensions of the body and accessory structures, similar to those standard in taxonomic studies (Hubbs and Lagler 1949):

*Standard length.*—From tip of the premaxillary to the skin deflection (evidenced by a change in shading) at end of the hypural plate.

*Nape.*—From tip of premaxillary to the anterior insertion (junction of anterior outline with body profile) of the first spinous ray in the dorsal fin.

*Spinous dorsal-fin length.*—From anterior insertion of the spinous dorsal fin to the posterior

insertion (junction of posterior outline of spine with body profile) of the 13th spinous fin ray.

*Hind-trunk dorsal.*—From posterior insertion of the 13th spinous fin ray to end of the hypural plate.

*Hind-trunk ventral.*—From posterior insertion of the second anal-fin spine to end of the hypural plate.

*Belly.*—From posterior insertion of the pelvic fin to posterior insertion of second anal-fin spine.

*Pelvic insertion.*—From tip of the premaxillary to posterior insertion of the pelvic fin.

*Head.*—From tip of the premaxillary to posterior edge of the opercular flap.

*Body-depth pelvic.*—Dorsoventral distance, taken perpendicular to the longitudinal axis of the fish, from the posterior insertion of pelvic fin to dorsal body outline.

*Body-depth anal.*—Dorsoventral distance, taken perpendicular to the longitudinal axis of the fish, from the anterior insertion of first anal spine to dorsal body outline.

*Caudal peduncle.*—Shortest distance across caudal peduncle, taken perpendicular to its longitudinal axis.

*Orbit.*—Greatest diameter between opposite sides of the orbit, taken parallel to longitudinal axis

<sup>3</sup>Data for the measurements, including additional measurements not given in this paper, are available on tape as JQUAST/MORF1 on file at the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, 2725 Montlake Blvd. East, Seattle, WA 98112.

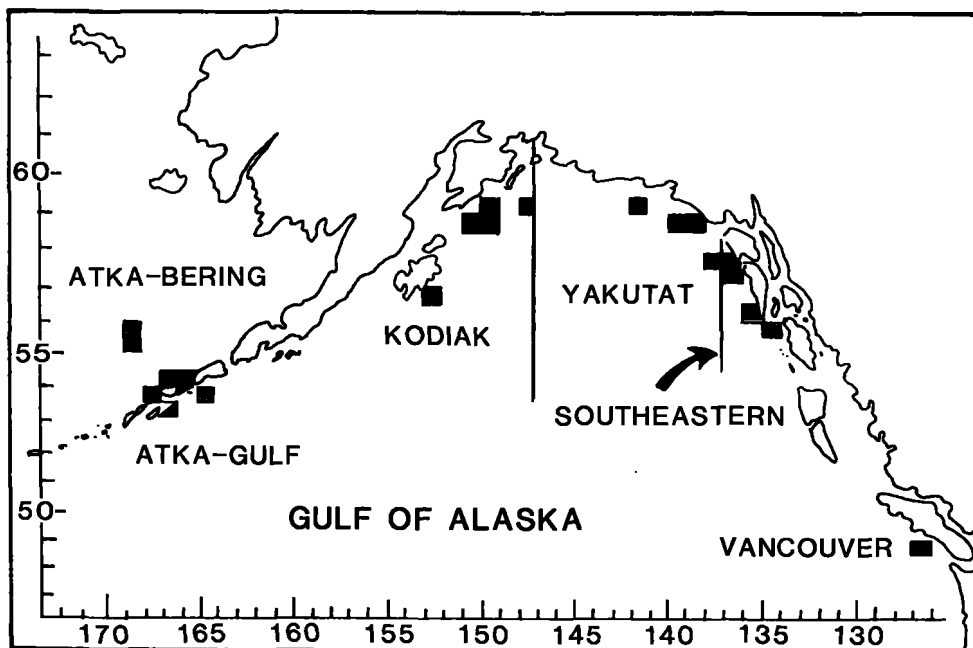


FIGURE 1.—Geographic regions and statistical areas (dark rectangles) where Pacific ocean perch were obtained for this study.

TABLE 1.—Standard-length (SL) frequencies of Pacific ocean perch used in this study. Geographic zones are shown in Figure 1. M = male; F = female.

Standard length (mm)		Atka-Bering		Atka-Gulf		Kodiak		Yakutat		South-eastern		Vancouver	
Class	Midpoint	M	F	M	F	M	F	M	F	M	F	M	F
115-134	125.5	5	5	—	—	—	—	—	—	—	1	—	—
135-154	145.5	3	4	—	1	—	—	—	—	—	1	—	—
155-174	165.5	4	5	1	—	4	4	—	—	1	2	—	—
175-194	185.5	16	14	2	4	14	15	2	5	4	5	—	—
195-214	205.5	20	15	13	9	6	7	4	11	15	7	—	—
215-234	225.5	13	26	51	55	10	6	16	24	13	8	—	—
235-254	245.5	36	22	49	52	6	7	14	19	7	5	5	—
255-274	265.5	22	19	25	12	7	8	9	10	12	17	4	2
275-294	285.5	16	22	15	13	19	9	4	10	16	9	10	4
295-314	305.5	10	13	26	21	65	33	6	7	23	5	13	3
315-334	325.5	17	25	13	22	16	35	4	8	11	5	9	4
335-354	345.5	3	26	1	7	4	18	4	4	—	—	2	8
355-374	365.5	3	17	—	1	—	2	1	5	—	1	2	1
375-394	385.5	—	2	—	—	—	—	2	—	1	—	—	1
395-414	405.5	—	—	—	—	—	—	—	—	1	—	—	1
Total by sex:		168	215	196	197	151	144	66	103	104	66	45	24
Region totals:		383		393		295		169		170		69	
Average SL, by region:		260.5		257.9		281.4		261.5		261.2		308.4	
Average SL, all data <sup>1</sup> :		266.41 (N = 1,479)											

<sup>1</sup>Class midpoints weighted by frequency.

of the fish.

*Longest pectoral-fin ray.*—From tip of the longest ray to its origin.

*Upper-jaw length.*—Greatest distance from tip of the premaxillary to posterior edge of the maxillary.

*Upper-jaw width.*—Greatest width of this part taken perpendicular to axis of the mouth line in a closed mouth.

*Symphyseal knob.*—From tip of symphyseal knob to its posterior insertion.

*6th dorsal spinous fin ray.*—From tip of this fin ray to its posterior insertion.

*13th spinous ray in dorsal fin.*—From tip of this ray to its posterior insertion.

*3d anal-fin spine.*—From tip of this spine to its posterior insertion.

The data were divided into six geographic regions (Atka-Bering, Atka-Gulf, Kodiak, Yakutat, Southeastern, and Vancouver (Fig. 1)), and measurements regressed on SL by sex after all variates were log<sub>10</sub> transformed. (Transformation allowed measurements to be expressed as linear functions of SL and stabilized the variance.) Geographic and sexual variation were tested by analysis of covariance (ANCOVA), with statistical tests “significant” when  $P \leq 0.05$ .

In “allometric” growth in fishes, the size of one variate bears a power relationship to an index of

body length. The power exponent can be expressed as the slope of a simple linear regression fit to log-transformed variates, the “allometric equation”, as used in this study. A slope greater than unity, “positive allometry” (Simpson et al. 1960), indicates that growth in a body dimension relative to growth in fish length (SL in the present paper) increases as fish length increases; a slope less than unity, “negative allometry”, indicates that growth in a body dimension decreases; and a slope of unity, “isometry”, indicates that it stays the same.

A preliminary survey of the measurement data disclosed that most body dimensions probably grow allometrically, although not strongly so because slopes are near unity (Table 2). Because body proportions that relate size of a character to SL are specific to body length when growth is allometric, both proportions and dimensions must be referred to a size standard if either are to be objectively compared. For this reason, measurements and proportions used here are usually referred to a hypothetical fish of 260 mm SL, a size near the average for all specimens in the study (Table 1), and likely a common collection size. In most instances, body proportions represented by estimated dimensions at the standard size need not be limited to exactly that size for purposes of general comparison because of the proximity of allometric slopes to unity (Table 2). The data

TABLE 2.—Parameters for linear regressions (data  $\log_{10}$  transformed) of measurements on standard length (mm) for Pacific ocean perch sampled from the Bering Sea (Atka-Bering region) to Vancouver Island, British Columbia. Slopes in italics are significantly different from one ( $P \leq 0.05$ ). ANCOVA indicates significance of tests for geographic variation over the six zones by analysis of covariance (if slopes tested significantly different, intercepts were not tested).

Region	Males				Females			
	N	Intercept	Slope	R <sup>2</sup>	N	Intercept	Slope	R <sup>2</sup>
NAPE								
Atka-Bering	168	-0.57942	<i>1.04767</i>	0.986	215	-0.54925	<i>1.03434</i>	0.988
Atka-Gulf	196	-0.49916	<i>1.01264</i>	0.946	197	-0.59329	<i>1.05137</i>	0.964
Kodiak	150	-0.52788	<i>1.02511</i>	0.984	144	-0.50253	<i>1.01401</i>	0.989
Yakutat	66	-0.52515	<i>1.02721</i>	0.965	102	-0.37849	<i>0.96596</i>	0.960
Southeastern	103	-0.52149	<i>1.02716</i>	0.984	65	-0.31086	<i>0.92727</i>	0.983
Vancouver	45	-0.60283	<i>1.06479</i>	0.957	24	-0.55937	<i>1.04431</i>	0.947
ANCOVA		—	***			—	***	
SPINOUS DORSAL-FIN LENGTH								
Atka-Bering	168	-0.46575	<i>1.00808</i>	0.970	215	-0.51738	<i>1.03007</i>	0.984
Atka-Gulf	196	-0.48033	<i>1.01155</i>	0.938	197	-0.53388	<i>1.03434</i>	0.950
Kodiak	151	-0.40715	<i>0.98179</i>	0.968	144	-0.47812	<i>1.01100</i>	0.937
Yakutat	65	-0.41767	<i>0.98430</i>	0.945	103	-0.60298	<i>1.06233</i>	0.939
Southeastern	104	-0.65332	<i>1.07876</i>	0.965	66	-0.66303	<i>1.08146</i>	0.975
Vancouver	45	-0.18623	<i>0.88693</i>	0.887	24	-0.46602	<i>1.00011</i>	0.895
ANCOVA		—	***			***	NS	
HIND-TRUNK DORSAL								
Atka-Bering	168	-0.34928	<i>0.96296</i>	0.977	213	-0.31407	<i>0.94808</i>	0.981
Atka-Gulf	196	-0.43921	<i>1.00161</i>	0.932	197	-0.34985	<i>0.96475</i>	0.958
Kodiak	151	-0.52480	<i>1.03743</i>	0.977	144	-0.49997	<i>1.02683</i>	0.973
Yakutat	65	-0.48155	<i>1.01525</i>	0.965	103	-0.48653	<i>1.01744</i>	0.955
Southeastern	104	-0.31689	<i>0.94900</i>	0.976	66	-0.55759	<i>1.05007</i>	0.978
Vancouver	45	-0.43589	<i>0.99412</i>	0.900	24	-0.52323	<i>1.02901</i>	0.930
ANCOVA		—	***			—	***	
HIND-TRUNK VENTRAL								
Atka-Bering	168	-0.36545	<i>0.95394</i>	0.976	215	-0.17229	<i>0.86822</i>	0.970
Atka-Gulf	196	-0.36803	<i>0.95720</i>	0.908	197	-0.15326	<i>0.86477</i>	0.908
Kodiak	151	-0.30535	<i>0.93808</i>	0.928	144	-0.14297	<i>0.86656</i>	0.942
Yakutat	65	-0.21169	<i>0.89828</i>	0.900	103	-0.10019	<i>0.84914</i>	0.872
Southeastern	104	-0.36519	<i>0.96875</i>	0.978	66	-0.30279	<i>0.94197</i>	0.980
Vancouver	45	-0.15815	<i>0.88163</i>	0.942	24	-0.06116	<i>0.79192</i>	0.804
ANCOVA		***	NS			***	NS	
BELLY								
Atka-Bering	168	-0.37364	<i>0.94635</i>	0.956	215	-0.70418	<i>1.09162</i>	0.965
Atka-Gulf	196	-0.33800	<i>0.92788</i>	0.808	197	-0.62569	<i>1.05150</i>	0.906
Kodiak	151	-0.60457	<i>1.02908</i>	0.832	144	-0.85483	<i>1.14125</i>	0.909
Yakutat	63	-0.97655	<i>1.17854</i>	0.880	97	-1.03204	<i>1.20777</i>	0.872
Southeastern	102	-0.61599	<i>1.01693</i>	0.903	66	-0.83303	<i>1.11490</i>	0.919
Vancouver	45	-0.81199	<i>1.10045</i>	0.802	24	-1.13734	<i>1.24044</i>	0.862
ANCOVA		—	***			—	*	
PELVIC INSERTION								
Atka-Bering	168	-0.55435	<i>1.06386</i>	0.988	215	-0.46702	<i>1.02686</i>	0.988
Atka-Gulf	196	-0.51060	<i>1.04589</i>	0.958	197	-0.55050	<i>1.06143</i>	0.976
Kodiak	151	-0.43680	<i>1.01440</i>	0.973	144	-0.44339	<i>1.01430</i>	0.982
Yakutat	61	-0.40669	<i>1.00918</i>	0.961	97	-0.29310	<i>0.95993</i>	0.959
Southeastern	104	-0.40062	<i>1.00887</i>	0.970	66	-0.24953	<i>0.94551</i>	0.968
Vancouver	45	-0.53731	<i>1.06759</i>	0.944	24	-0.54122	<i>1.06600</i>	0.926
ANCOVA		—	*			—	***	
HEAD								
Atka-Bering	167	-0.66929	<i>1.08599</i>	0.985	211	-0.54938	<i>1.03404</i>	0.986
Atka-Gulf	193	-0.62867	<i>1.06805</i>	0.956	95	-0.66243	<i>1.08088</i>	0.974
Kodiak	149	-0.58928	<i>1.04964</i>	0.974	141	-0.46700	<i>0.99665</i>	0.987
Yakutat	65	-0.56204	<i>1.04073</i>	0.961	103	-0.38096	<i>0.96489</i>	0.962
Southeastern	104	-0.52223	<i>1.02793</i>	0.979	65	-0.25528	<i>0.91393</i>	0.979
Vancouver	45	-0.45179	<i>1.00443</i>	0.935	24	-0.41197	<i>0.98543</i>	0.935
ANCOVA		—	*			—	***	

NS =  $P > 0.05$ ; \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.005$ .

QUAST: MORPHOMETRIC VARIATION ON PACIFIC OCEAN PERCH

TABLE 2.—Continued.

Region	Males				Females			
	N	Intercept	Slope	R <sup>2</sup>	N	Intercept	Slope	R <sup>2</sup>
BODY-DEPTH PELVIC								
Atka-Bering	168	-0.51033	1.00257	0.976	215	-0.54783	1.01989	0.980
Atka-Gulf	196	-0.53594	1.00921	0.928	197	-0.69474	1.07506	0.951
Kodiak	151	-0.52962	1.00452	0.967	144	-0.62554	1.04313	0.982
Yakutat	65	-0.61821	1.04588	0.961	103	-0.55126	1.01765	0.946
Southeastern	104	-0.71748	1.08660	0.978	66	-0.64909	1.05958	0.982
Vancouver	45	-0.79012	1.12032	0.951	24	-1.02734	1.21485	0.973
ANCOVA		—	***			—	***	
BODY-DEPTH ANAL								
Atka-Bering	168	-0.31899	0.88824	0.970	215	-0.23926	0.85418	0.959
Atka-Gulf	196	-0.35517	0.89798	0.903	197	-0.31260	0.87925	0.930
Kodiak	150	-0.48843	0.94820	0.949	144	-0.48666	0.94522	0.972
Yakutat	66	-0.44835	0.93799	0.930	103	-0.46838	0.94474	0.933
Southeastern	104	-0.60709	1.00067	0.958	66	-0.69547	1.03764	0.960
Vancouver	45	-0.45563	0.94021	0.848	24	-0.47752	0.94904	0.769
ANCOVA		—	***			—	***	
CAUDAL PEDUNCLE								
Atka-Bering	168	-0.89038	0.92634	0.970	215	-0.75477	0.86857	0.964
Atka-Gulf	196	-0.96731	0.95528	0.932	197	-0.83252	0.89772	0.928
Kodiak	151	-1.03039	0.97784	0.954	144	-1.04643	0.98133	0.972
Yakutat	66	-0.90622	0.93157	0.947	103	-0.86913	0.91426	0.944
Southeastern	102	-0.98737	0.96392	0.958	66	-0.99718	0.97023	0.964
Vancouver	45	-0.86566	0.91611	0.818	24	-0.88816	0.92524	0.838
ANCOVA		—	***			—	***	
ORBIT								
Atka-Bering	168	-1.12729	1.03674	0.943	215	-0.97536	0.97242	0.949
Atka-Gulf	196	-1.02260	0.99192	0.793	197	-1.05490	1.00415	0.861
Kodiak	151	-1.07754	1.00791	0.802	144	-0.83433	0.90505	0.786
Yakutat	65	-0.89752	0.92381	0.866	102	-0.71441	0.84725	0.830
Southeastern	103	-1.16845	1.03324	0.899	66	-0.83621	0.89158	0.903
Vancouver	45	-0.14594	0.62383	0.862	24	-0.22779	0.65647	0.667
ANCOVA		—	***			—	**	
LONGEST PECTORAL-FIN RAY								
Atka-Bering	168	-0.64359	1.02265	0.970	215	-0.53922	0.97618	0.978
Atka-Gulf	196	-0.63481	1.01701	0.937	197	-0.51453	0.96360	0.948
Kodiak	151	-0.55655	0.98090	0.947	144	-0.44668	0.93236	0.961
Yakutat	66	-0.72067	1.04225	0.923	102	-0.61357	0.99762	0.942
Southeastern	101	-0.88825	1.12077	0.968	66	-0.78218	1.07402	0.956
Vancouver	45	-0.50319	0.96330	0.901	23	-0.73958	1.05622	0.934
ANCOVA		—	**			—	**	
UPPER-JAW LENGTH								
Atka-Bering	168	-1.07654	1.10238	0.947	215	-0.92793	1.03735	0.955
Atka-Gulf	196	-1.11966	1.12050	0.854	195	-1.04190	1.08558	0.910
Kodiak	151	-0.84319	1.00090	0.898	144	-0.65487	0.91998	0.932
Yakutat	64	-0.64407	0.91575	0.788	101	-0.57472	0.88516	0.770
Southeastern	104	-0.99592	1.06287	0.838	66	-0.81778	0.98171	0.819
Vancouver	45	-0.52744	0.86802	0.711	24	-0.16892	0.72101	0.651
ANCOVA		—	***			—	***	
UPPER-JAW WIDTH								
Atka-Bering	168	-1.37815	1.03050	0.891	215	-1.38585	1.02967	0.915
Atka-Gulf	196	-1.49225	1.07165	0.804	197	-1.41203	1.03808	0.838
Kodiak	151	-1.23784	0.96166	0.776	143	-1.20719	0.94924	0.880
Yakutat	66	-1.31512	1.00107	0.844	103	-1.20986	0.95659	0.839
Southeastern	104	-1.56596	1.11473	0.880	66	-1.00614	0.87986	0.881
Vancouver	45	-1.91421	1.25943	0.775	23	-1.81392	1.21350	0.748
ANCOVA		—	*			—	***	

NS = P > 0.05; \*P ≤ 0.05; \*\*P ≤ 0.01; \*\*\*P ≤ 0.005.

TABLE 2.—Continued.

Region	Males				Females			
	N	Intercept	Slope	R <sup>2</sup>	N	Intercept	Slope	R <sup>2</sup>
SYMPHYSEAL KNOB								
Atka-Bering	166	-3.09541	1.56992	0.769	215	-2.81549	1.44987	0.814
Atka-Gulf	196	-2.80011	1.43432	0.540	197	-2.87970	1.46848	0.576
Kodiak	151	-3.82404	1.87456	0.876	144	-3.23909	1.63193	0.857
Yakutat	66	-3.01114	1.52401	0.785	103	-2.54090	1.32784	0.714
Southeastern	104	-2.53152	1.32159	0.808	65	-3.23953	1.60663	0.817
Vancouver	45	-2.90945	1.47650	0.638	24	-2.42106	1.28184	0.570
ANCOVA		—	***			***	NS	
6TH SPINOUS RAY IN DORSAL FIN								
Atka-Bering	167	-0.94686	1.00886	0.882	209	-0.79653	0.94481	0.900
Atka-Gulf	194	-0.99815	1.03241	0.735	191	-1.07166	1.05966	0.783
Kodiak	148	-0.82023	0.95342	0.836	136	-0.62671	0.86992	0.845
Yakutat	64	-1.19498	1.10184	0.818	97	-0.91257	0.98441	0.800
Southeastern	90	-1.17989	1.10021	0.894	59	-1.00276	1.02520	0.877
Vancouver	44	-0.64705	0.88566	0.616	19	-0.81268	0.94818	0.649
ANCOVA		***	NS			—	**	
13TH SPINOUS RAY IN DORSAL FIN								
Atka-Bering	165	-0.87157	0.91366	0.804	208	-0.72181	0.85087	0.834
Atka-Gulf	192	-0.98173	0.96415	0.621	183	-1.02884	0.98308	0.730
Kodiak	141	-0.85834	0.91216	0.766	133	-0.90253	0.92803	0.780
Yakutat	63	-0.94187	0.94260	0.771	87	-0.85833	0.90897	0.744
Southeastern	95	-0.79462	0.88878	0.816	57	-0.95486	0.95753	0.783
Vancouver	42	-0.39052	0.73692	0.394	20	-1.10477	1.01967	0.638
ANCOVA		***	NS			***	NS	
3D ANAL-FIN SPINE								
Atka-Bering	147	-0.50863	0.81717	0.849	190	-0.39317	0.76948	0.865
Atka-Gulf	166	-0.24648	0.71104	0.682	172	-0.18951	0.68697	0.696
Kodiak	131	-0.36994	0.75870	0.785	126	-0.32305	0.73849	0.818
Yakutat	62	-0.14422	0.66714	0.690	93	-0.45754	0.79909	0.714
Southeastern	66	-0.15004	0.67029	0.061	44	-0.54744	0.82184	0.742
Vancouver	40	+0.33516	0.46515	0.374	19	+0.28173	0.48651	0.451
ANCOVA		—	***			***	NS	

NS =  $P > 0.05$ ; \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.005$ .

agree with visual impressions of negligible proportional changes with growth, gained from working with the species in the field.

To compare measurement variability for sexual and geographic factors in untransformed data, in the section on character discrimination, I obtained symmetrical estimates of variation about mean values by taking limits formed by one standard deviation (about each regression by sex within region) on each side of the transformed means. I then back-transformed the limits and halved the difference between them. This symmetrical substitute for the asymmetrical standard deviation about regression is called the "alternate standard deviation".

Westrheim (1975) studied sexual maturity in Pacific ocean perch from the Gulf of Alaska and concluded that onset occurred between 195 and 260 mm SL [fork length (FL) converted to SL by relationships established from the present morphometric data:  $SL = -3.272 + 0.879 FL$ , where  $N = 1,528$  and  $R^2 = 0.997$ ]. In the present study,

the boundary between juveniles and adults is taken as 230 mm SL.

### Body Form Varied Geographically and by Sex

Although later, more detailed, analyses disclosed that the constant slopes required by the ANCOVA program BMDP P2V (Dixon et al. 1977) for each character (transformed data) were technically unmet, a preliminary analysis with this program indicated likely significant geographic and sexual variation in all characters (subsequently confirmed in detailed analyses with a more general ANCOVA model, Table 2), and a general lack of interaction between these factors. Also, I determined that only negligible bias has been induced in the regressions by logarithmic transformation of data by computing mean response variables, at 260 mm SL, for untransformed measurements fit by nonlinear least squares (BMDP PAR, Dixon et al. 1977). For six

measurements, by sex and region, over which the two methods were compared, the prediction of character sizes in fish of 260 mm SL by nonlinear least squares was close to the mean and within the 95% confidence interval for prediction from transformed data (Fig. 2) and did not change the results.

Graphical comparison of character measurements, related to the standardized fish of 260 mm SL, also disclosed that geographic and sexual variation were frequent:

**Nape** (Fig. 2A).—Geographic variation in distance between tip of snout and the dorsal fin was significant. Napes averaged shortest in the Atka-Gulf and Kodiak regions and lengthened in a cline to the Vancouver region. Females averaged smaller napes than males in all regions.

**Spinous dorsal-fin length** (Fig. 2B).—Geographic variation in length of spinous dorsal fin was significant, and the fin shortened in a cline from the Bering Sea to the Southeastern and Vancouver regions. Because geographic variation in length of the spinous dorsal fin was nearly opposite to geographic variation in the nape, changes in position of the anterior fin insertion probably caused the reciprocal clines. Sexual dimorphism was not important.

**Hind-trunk dorsal** (Fig. 2C).—Distance between the spinous dorsal fin and the tail changed significantly between regions. It averaged largest in specimens from the middle regions (Atka-Gulf and Kodiak) and smallest in the Vancouver region. Sexual dimorphism was not important.

**Hind-trunk ventral** (Fig. 2D).—Distance between the second spine of the anal fin and the tail changed significantly between regions. It averaged largest in the Southeastern and Vancouver regions and shortest in the Atka-Bering region. The data formed a geographic cline opposite to that of the belly measurement. From the Yakutat region westward, females averaged significantly shorter in this measurement than males.

**Belly** (Fig. 2E).—Distance between the pelvic fins and anal-fin spines varied significantly geographically and decreased in a cline from northwest to southeast (Atka-Bering region to the Southeastern and Vancouver regions). Belly measurements averaged about 1.6 cm smaller in the southeastern extreme of the sampling range than in the northwestern. The

cline apparently is caused by opposing relational movements of pelvic girdle and anal-fin spines along the body axis because the pelvic insertion and hind-trunk ventral measurements decreased from southeast to northwest. Sexual dimorphism was significant, with bellies of males averaging about 4 mm smaller than those of females.

**Pelvic insertion** (Fig. 2F).—Geographic variation in distance between snout and pelvic fins was significant, and the distance increased from northwest to southeast, from the Atka-Bering region to the Vancouver region. The measurement averaged shorter in females than males in all regions, evidence for significant sexual dimorphism.

**Head** (Fig. 2G).—Geographic variation in head length was significant, and heads averaged shortest in the Kodiak region and longest in the Vancouver region. Sexual dimorphism was usually significant, and females averaged smaller heads than males. Trends in geographic and sexual variation between the head and pelvic insertion were similar, probably because both measurements include similar regions of the head.

**Body-depth pelvic** (Fig. 2H).—Geographic variation in body depth at the pelvic fins was significant and formed a broken cline. Deepest bodies occurred at the extremes of the sampling range (Atka-Bering and Vancouver regions), and were shallowest in the Kodiak region. Sexual dimorphism was inconsistent.

**Body-depth anal** (Fig. 2I).—Geographic variation in body depth at the anal spines was significant, and depth was shallowest in Kodiak specimens and deepest in Atka-Bering specimens. Body depths averaged smaller in females than in males from the Yakutat region to the Atka-Bering region, but the differences may not be significant.

**Caudal peduncle** (Fig. 2J).—Geographic variation in depth of caudal peduncle was significant, but important geographic differences were limited to regions west of Yakutat. Specimens from the Kodiak region averaged narrowest peduncles, and specimens from the Atka-Bering, Southeastern, and Vancouver regions averaged widest peduncles. Caudal peduncles averaged significantly narrower in females than in males except in the Southeastern and Vancouver regions.

**Orbit** (Fig. 2K).—Geographic variation in orbit diameter was significant. Diameters were

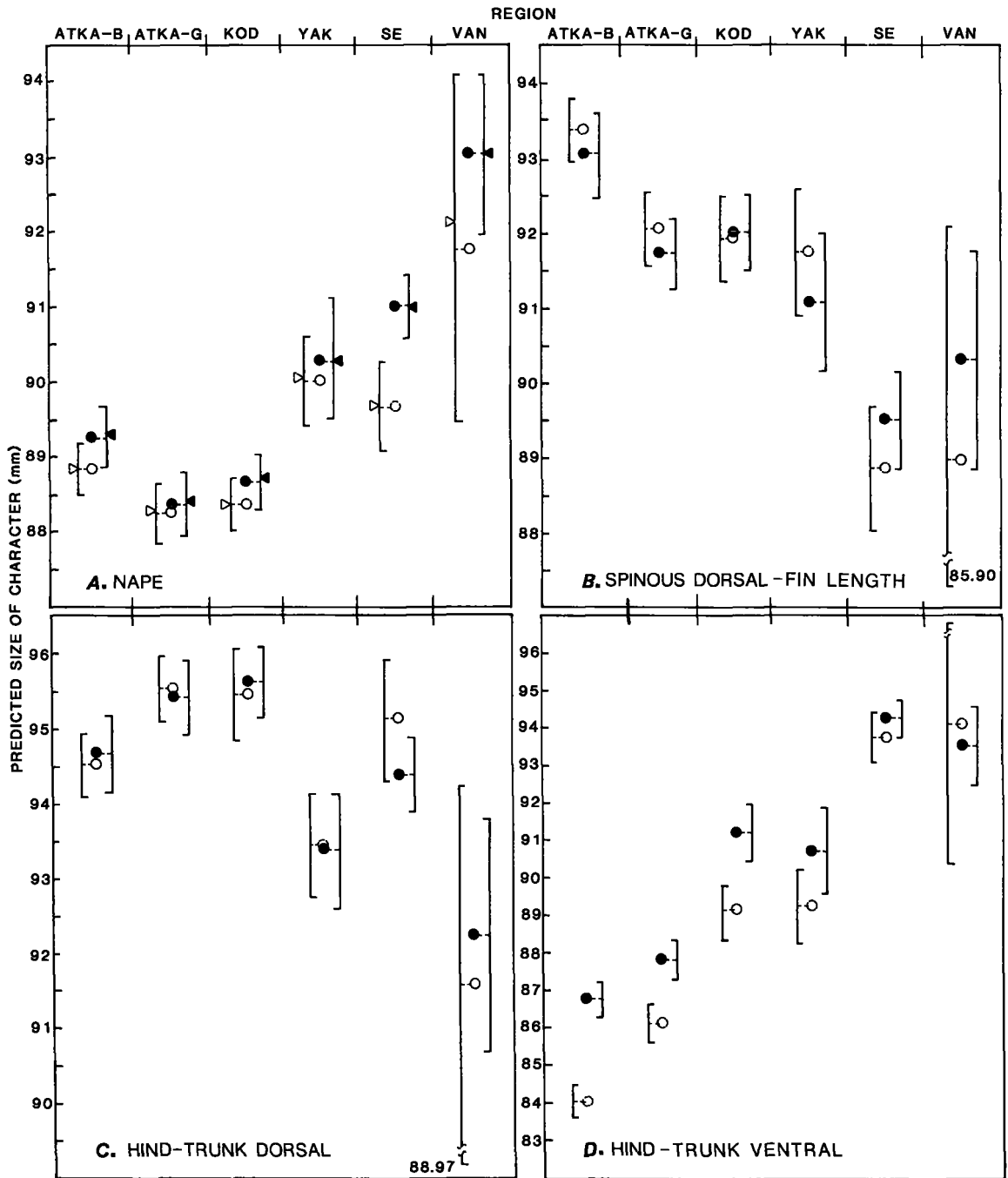


FIGURE 2.—Geographic and sexual variation in measurements of Pacific ocean perch in the northeastern Pacific Ocean and eastern Bering Sea as represented by mean responses to regression functions (Table 2) (circles) and 95% confidence intervals (brackets) for these responses as related to a standard-sized fish of 260 mm SL. Solid symbols represent males and open symbols females. Triangles represent mean responses by nonlinear least squares analysis (Dixon et al. 1977) for 260 mm SL fish.



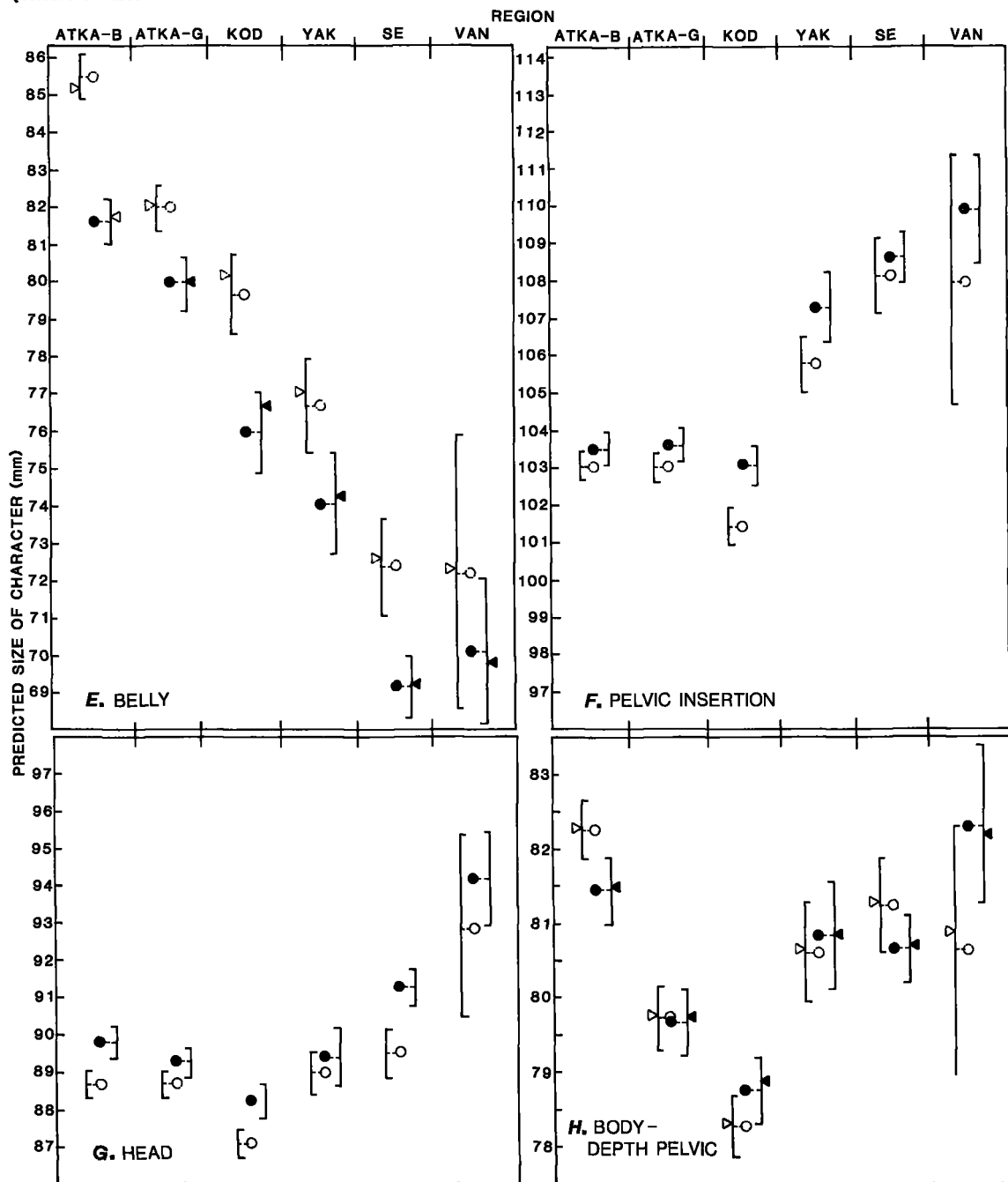


FIGURE 2.—Continued.

largest in the Atka-Bering and Atka-Gulf regions and smallest in the Southeastern region. Diameters decreased continuously from the Atka-Bering region to the Southeastern region, but the trend was broken by Vancouver samples. Although not significant within regions,

sexual differences in orbit diameter probably were significant overall because females averaged smaller orbits than males in all regions. *Longest pectoral-fin ray* (Fig. 2L).—Geographic variation in length of pectoral fins was significant. The fins averaged longest at the eastern

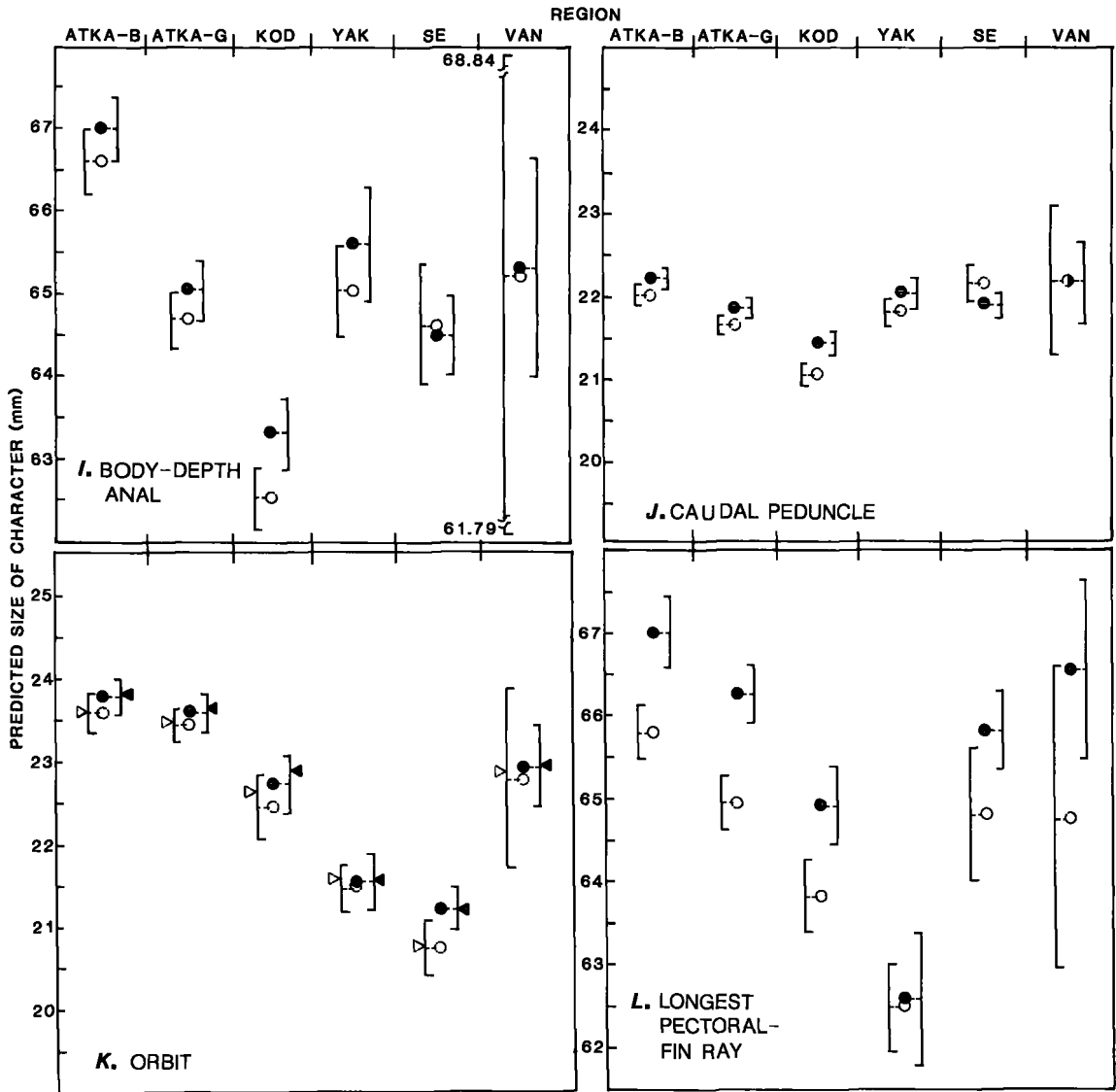


FIGURE 2.—Continued.

and western extremes of the sampling range and shortest in the Yakutat region. In all regions but Yakutat, sexual dimorphism was high and significant, and fins in females averaged  $>1$  mm shorter than in males.

**Upper-jaw length** (Fig. 2M).—Geographic variation was significant, and jaws averaged longest in eastern Aleutian samples (Atka-Bering and Atka-Gulf regions). Sexual dimorphism was significant in three regions (Atka-Bering, Atka-Gulf, and Southeastern), with females averaging shorter upper jaws than males in each.

**Upper-jaw width** (Fig. 2N).—Geographic variation was significant, with upper jaws averaging narrowest in the Kodiak region. Sexual dimorphism was important in only the Atka-Bering and Southeastern regions, where females averaged narrower upper jaws than males.

**Symphyseal knob** (Fig. 2O).—Geographic variation was significant but erratic. On average, specimens from the Atka-Gulf region probably have the largest symphyseal knobs. Sexual dimorphism seems unimportant.

**6th spinous ray in dorsal fin** (Fig. 2P).—Geo-

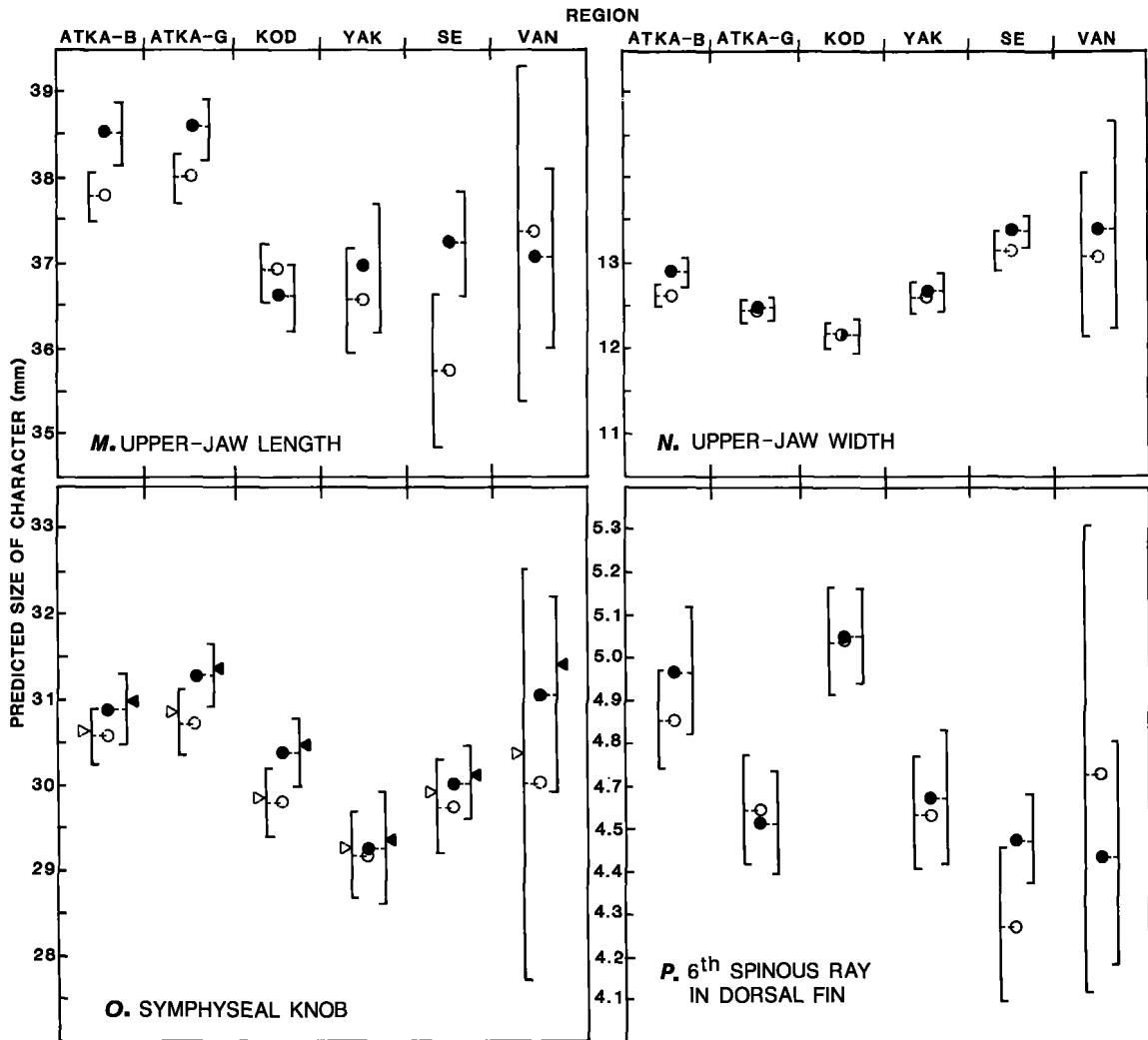


FIGURE 2.—Continued.

graphic variation was significant but erratic in this index to height of the spinous dorsal fin. Kodiak specimens had the highest spinous dorsal fins, on average. Sexual variation was inconsistent and is probably unimportant.

**13th spinous ray in dorsal fin (Fig. 2Q).**—Geographic variation was significant but erratic in this index to height of the notch between spinous and soft dorsal fins. Sexual dimorphism seems generally unimportant.

**3d anal-fin spine (Fig. 2R).**—Geographic and sexual variation in length of the spinous ray was minor, except that the fin spine was unusually short in females from the Southeastern region.

The measurements (as related to the standardized fish of 260 mm SL) usually varied geographically either in generally monotonic clines over the study area (Atka-Bering to Vancouver regions) or V-shaped clines that were broken in the Yakutat or Kodiak region. Only two sets of characters varied almost monotonically, and variation within each can be ascribed to a progressive shift in boundary features for body regions: Length of nape generally decreased and length of the spinous-dorsal fin increased from southeast to northwest (Fig. 2A, B), probably because of a relational shift in the dorsal-fin insertion. Belly size increased from southeast to northwest (Fig. 2E), probably because the pectoral girdle and associ-

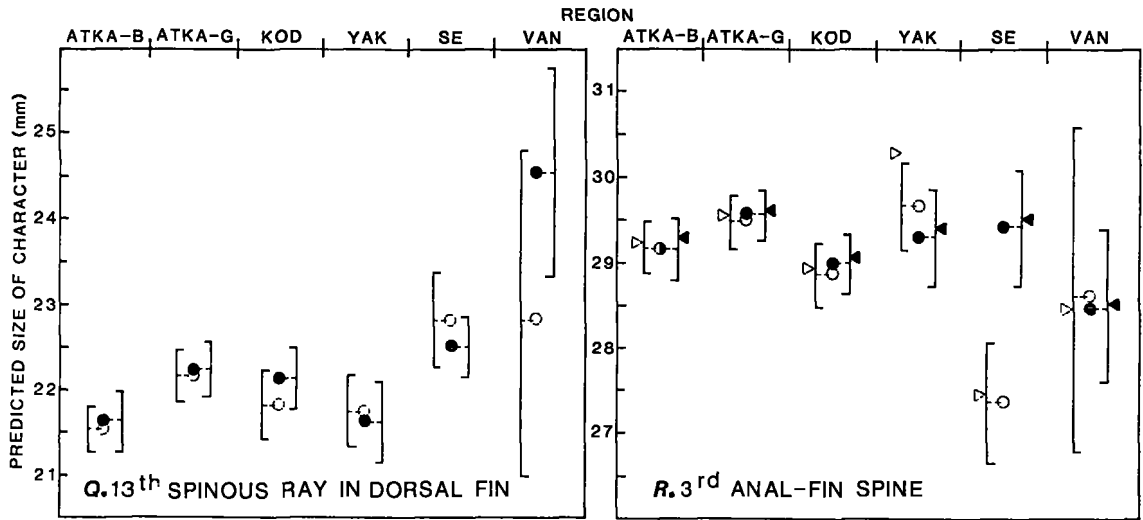


FIGURE 2.—Continued.

ated pelvic fins and the complex of anal-fin spines moved relationally apart (Fig. 2F, D). In contrast, depth of the entire body of Pacific ocean perch varied similarly geographically because the three measures of body depth—body-depth pelvic, body-depth anal, and caudal peduncle—varied concordantly (Fig. 3).

Sexual dimorphism was significant in most measurements, and except for belly size, measurements usually averaged larger in males than in females. The combined effects of geographic and sexual variation meant that belly measurements averaged about 16 mm larger in standardized females from the Atka-Bering region than in males from the Southeastern or Vancouver region (Fig. 2E).

Slopes in over one-half of the measurement regressions differed significantly from unity (Table 2), indicating growth allometry, particularly when differences from unity were consistent. The symphyseal knob was the only character with strong positive allometry (Table 2). Only two characters were strongly or consistently negatively allometric (Table 2): hind-trunk ventral, significant in 11 of 12 sex/region cells (slopes averaging 0.94 in males and 0.87 in females); and length of 3d anal-fin spine, significant in all 12 sex/region cells (slopes averaging 0.72 in males and 0.74 in females). With growth, the trunk posterior to the anal-fin spines becomes proportionally smaller relative to the rest of the body because of negative allometry in the body-depth

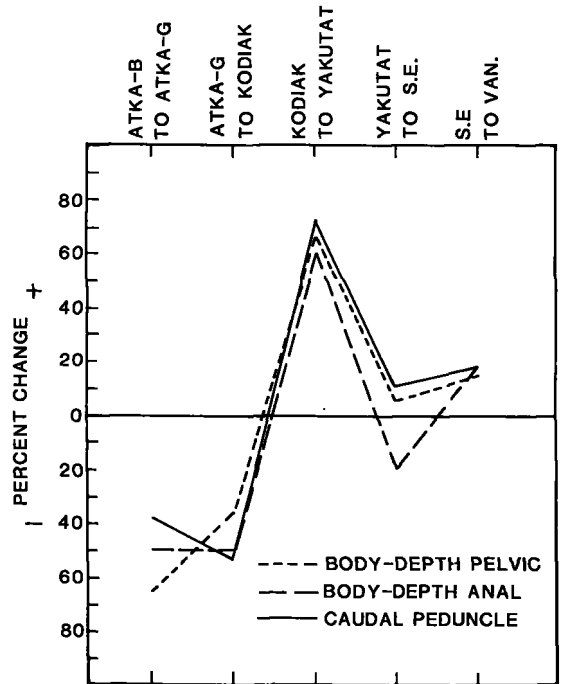


FIGURE 3.—Geographic variation in depth measurements of three body characters in Pacific ocean perch. Character measurements were related to a standard-sized fish of 260 mm SL from regressions in Table 2, then back transformed. Because measurements for males and females were usually different (Fig. 2), midvalues between sexes were used. Percentage change is the change in a measurement between neighboring regions as a percentage of the measurement's range over the geographic range.

anal, hind-trunk ventral, and caudal peduncle measurements.

## Inflections and Sexual Crossover in the Regressions

I examined 216 computer-drawn scattergrams for sexes within regions that represented the measurement regressions (Table 2), by transparent overlay with incised straight line. None shows obvious curvature, and only three show possible inflections: In females, the regression appears to bend upward about  $8.3^\circ$  at about 262 mm SL for belly measurements in the Atka-Bering region; downward about  $7.0^\circ$  at about 242 mm SL for hind-trunk ventral in the same region; and possibly upward about  $13.5^\circ$  at about 260 mm SL for the belly in the Southeastern region. Whether the apparent breaks in the three regressions are artifacts or real is moot. Evidence for reality includes their visibility in scattergrams; that all occur in a single sex (females) and in a measurement possibly influenced by sexual development with growth; and that the possible break in the belly regression in the Atka-Bering region has a near complement in the hind-trunk ventral measurements, which extend from the belly to the tail. Also, as discussed in a succeeding paragraph, mild inflections probably are hidden in variability of the data. Evidence against reality includes the extreme rarity of visible indications of possible breaks (none in 16 of 18 measurements and only 3 in the remaining 24 regressions), and the extreme goodness of fit ( $R^2$ ) to a straight line shown by the regressions with possible inflections (Table 2). The measures for goodness of fit for belly are the best among regions in the two regressions with possible inflections, and both measures are higher than those for corresponding male regressions, which show no indications of inflection. The weight of evidence seems to side with the visible breaks being artifacts. Yet, even if the breaks represent real inflections, the morphometric data seem to fit linear criteria well as far as conventional measures are concerned.

The regressions for sexes, within measurements and regions (Table 2), diverge with increasing SL, indicating that sexual dimorphism increases with growth. The sexes are slight, however, as evidenced by the similarity in regression parameters between sexes, and on average, characters will differ in size between sexes by only a few millimeters in the standard 260 mm SL fish (Fig. 2). Given normal variation, the differences should not be obvious or reliable in differentiating sexes by gross examination of even the largest Pacific ocean perch.

However, divergent sexual-regression pairs pose an apparent contradiction when they intersect within their data domain. Such intersections infer 1) sexual differences in fish on the juvenile side of the intersection, 2) differences on the juvenile side the reverse of those on the adult side, and 3) differences between sexes in juveniles that increase as SL's become smaller. In the morphometric data, the regressions for sexes do intersect, and the intersections form a symmetrical unimodal distribution with a strong peak near 230 mm SL. By itself, crossover need not be a problem; e.g., the symmetrical confidence limits about regression (Sokal and Rohlf 1969) are evidence that crossover within these limits is normal in samples from a single population. Yet, differences in measurements for sexes on the juvenile side of the modal point for sexual crossovers apparently are greater than can be accommodated by confidence limits based on the regressions. In 108 comparisons of mean estimates for measurements and their confidence limits at 170 mm SL, 18 have significant differences, when only about 5 are expected with 95% confidence limits. Apparently, sexually associated crossover is slightly too severe in the morphometric data to be adequately contained by confidence limits for single populations.

The evidence is strong that most of the measurement regressions do not fit their data perfectly and, because of the nature of the error, that slight growth inflections likely are concealed by variation. The three apparent inflections mentioned previously might indicate the size at inflection, but the evidence is weak. It is apparent, however, that significant sexual differences in measurements at SL's below the crossover mode should not be taken literally. (Assuming that measurement regressions may incorporate hidden inflections, most reliable estimates of juvenile measurements among sexual pairs within their data domains will be from the regression whose slope is nearest unity, particularly if the sample number is large and the slope not significantly different from unity.) Because the bulk of specimens were larger than 230 mm SL, and the regressions fit their data closely, conclusions regarding adult relationships in the present data, particularly trends, should be reliable.

## Strength of Geographic and Sexual Variation Shown in the Characters

Analysis of morphological diversity is most use-

ful where assigned components of variation can be maximized relative to unassigned components. I compared indices of variation assignable to measurement size (standard specimens), geographic, and sexual causes in the 18 characters by means of the alternate standard deviation (see Methods). First, I investigated relationships between variation and the size of a character. When mean responses for measurements in standard-sized fish from the Kodiak region were used as a basis of comparison, variability was positively related to size of the character, with the two variates significantly correlated (Fig. 4).

Size accounted for about 62% ( $R^2$ ) of the variation between characters. To remove its effect in further comparisons, I used an alternate version of the coefficient of variation; i.e., the alternate standard deviation for each character divided by a size index (Kodiak) for that character  $\times 100$ . Although the alternate coefficient of variation reduced the unassigned variability, some sizable differences remained between characters (Table 3)—major dimensions of the head and dorsum varied least, fin spines and small features of the head varied most, and the symphyseal knob varied considerably more than any other character. With the exception of belly, the major trunk

TABLE 3.—Evidence for unassigned variation in measurements in Pacific ocean perch after correction for measurement size. Measurements ( $\bar{Y}$ ) are related to a standard-sized fish of 260 mm SL from the Kodiak region by regressions in Table 2. Relative variation for each measurement is indexed by the alternate coefficient of variation (ACV) (see text) pooled over all regions and expressed as a percentage. Measurements arranged by increasing alternate coefficient of variation in the last column.

Measurement	Males		Females		Both sexes	
	$\bar{Y}$ , mm	ACV	$\bar{Y}$ , mm	ACV	$\bar{Y}$ , mm	ACV
Nape	88.66	2.50	88.36	2.29	88.52	2.40
Head	88.22	3.32	87.07	2.53	87.66	2.94
Pelvic insertion	103.03	3.20	101.42	3.01	102.24	3.11
Body-depth pelvic	78.75	3.53	78.27	3.04	78.52	3.29
Hind-trunk dorsal	95.62	3.01	95.46	3.72	95.54	3.36
Spinous dorsal-fin length	92.01	3.43	91.92	3.63	91.97	3.53
Body-depth anal	63.31	4.19	62.52	3.51	62.92	3.86
Caudal peduncle	21.43	4.08	21.06	3.65	21.25	3.87
Longest						
pectoral-fin ray	64.91	4.43	63.82	4.10	64.38	4.27
Hind-trunk ventral	91.22	4.98	89.07	4.69	90.07	4.84
Upper-jaw length	36.60	6.43	36.89	5.43	36.74	5.94
3d anal-fin spine	28.99	6.68	28.87	6.61	28.93	6.64
6th spinous ray						
in dorsal fin	30.36	7.92	29.78	7.58	30.08	7.76
Belly	75.97	8.82	79.66	7.87	77.77	8.36
Upper-jaw width	12.15	9.86	12.17	7.54	12.16	8.73
13th spinous ray						
in dorsal fin	22.11	9.45	21.81	10.05	21.96	9.74
Orbit	22.73	9.57	22.46	10.32	22.60	9.94
Symphyseal knob	5.05	13.51	5.04	14.59	5.04	14.04

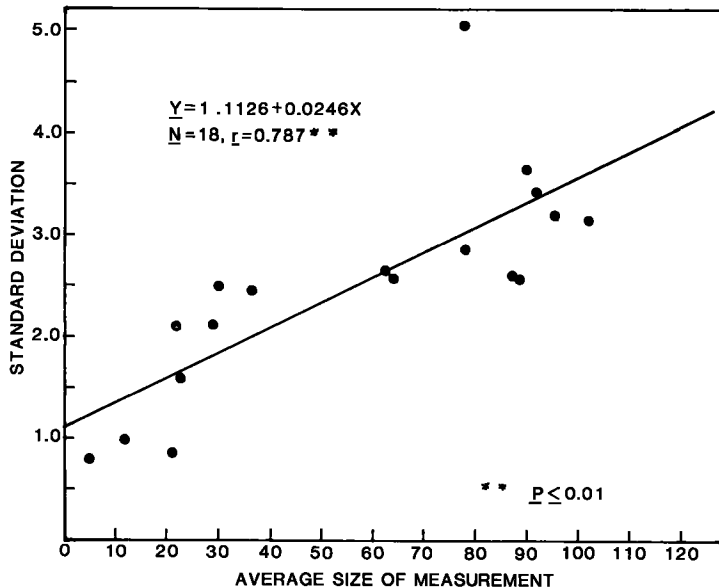


FIGURE 4.—Relationship between absolute size and variability of measurements in Pacific ocean perch. Character sizes are mean responses for hypothetical 260 mm SL fish from the Kodiak region as estimated from the regressions of Table 2; variability is estimated by alternate standard deviations for each character (see Methods) pooled over all regions.

dimensions had the lowest unassigned variability when corrected for size.

As would be expected from the plots of character measurements (Fig. 2), sexual and geographic variation were important components after the size effects were removed (Table 4). For sexual variation, the hind-trunk dorsal, spinous-dorsal fin, and body-depth pelvic measurements were the poorest discriminators, and belly, hind-trunk ventral, and longest pectoral-fin ray the best. For geographic variation, 3d anal-fin spine, symphyseal knob, and 6th spinous ray in dorsal fin were the poorest discriminators, and belly, hind-trunk ventral, and head measurements the best.

### Present Nominal Subspecies are Questionable

Barsukov (1964) synonymized the nominal species *Sebastes alutus* (Gilbert) and *S. paucispinosus* (Matsubara) but suggested that the eastern and western Pacific representatives may be separate subspecies: *S. a. paucispinosus* ranging from Honshu to Olyutorskii Bay and

along the northern Bering Sea slope, perhaps to Bristol Bay; and *S. a. alutus* ranging from California to the Gulf of Alaska and along the Aleutian Arc to, and including, the Commander Islands. Barsukov morphologically distinguished the subspecies by "Alaskan *Seb. alutus* longer than 23 cm are quite noticeably distinguished from *Seb. alutus* from other parts of the range by body depth", and in a key gives the principal subspecies discriminator as whether the ratio SL/body depth of 170-360 mm SL fish is greater than 3.2 (*S. a. alutus*) or less (*S. a. paucispinosus*).

The question of eastern and western subspecies in *S. alutus* seems more complex than Barsukov (1964) suggested. The weight of present evidence, although preliminary, does not seem to justify the nominal subspecies. First, there is the problem of how populations sympatric over a distance as great as the Aleutian Arc could maintain reproductive isolation adequate to insure genetic distinctiveness. There is no evidence for isolating mechanisms in the species—on the contrary, the larvae are pelagic (Hart 1973), which should promote rapid genetic exchange over major distances

TABLE 4.—Relative degree that measurements in standard-sized Pacific ocean perch of 260 mm SL reveal geographic and sexual variation. In the variation sections, variation not related to character size was indexed by alternate coefficients of variation that were pooled over all samples, sexual variation was indexed by differences between sexes as a percentage of their mid-size in each region (positive if males averaged larger than females and negative if males were smaller, but only absolute values were used in calculations), and geographic variation was indexed by the maximum difference between regions as a percentage of mean-estimate size of measurements from the Kodiak region (Table 3). In the discrimination section, indices indicate relative magnitudes of sexual and geographic variation relative to variation not related to character size. Low values or ranks (in parentheses) indicate that variation not related to character size was high relative to sexual (data column 4) or geographic (data column 5) variation; hence, the measurement is a poor indicator of sexual or geographic variation, and vice versa. Kendall Coefficient of Concordance (Siegel 1956) between ranks for sexual and geographic variation was not significant.

Character	Variation not related to character size	Relative variation		Discrimination	
		Sexual	Geographic	(Sexual ÷ col. 1) × 10	Geographic ÷ column 1
Nape	2.91 (1)	0.493 (4)	4.60 (7)	1.69 (10)	1.58 (13)
Spinous dorsal-fin length	3.73 (6)	(-)0.088 (2)	4.39 (5)	0.24 (2)	1.18 (9)
Hind-trunk dorsal	3.35 (4)	(-)0.019 (1)	3.80 (2)	0.06 (1)	1.13 (7.5)
Hind-trunk ventral	4.05 (9)	2.038 (17)	9.57 (15)	5.03 (17)	2.36 (17)
Belly	6.45 (11)	(-)3.873 (18)	16.47 (18)	6.00 (18)	2.55 (18)
Pelvic insertion	3.08 (3)	0.875 (11)	6.53 (12)	2.84 (14)	2.12 (15)
Head	3.07 (2)	1.104 (13)	6.69 (13)	3.60 (15)	2.18 (16)
Body-depth pelvic	3.63 (5)	(-)0.104 (3)	4.32 (4)	0.29 (3)	1.19 (10)
Body-depth anal	4.21 (10)	0.628 (8)	6.19 (11)	1.49 (9)	1.47 (11)
Caudal peduncle	4.02 (7.5)	0.828 (9)	4.53 (6)	2.06 (13)	1.13 (7.5)
Orbit	7.01 (13)	0.503 (5)	13.39 (17)	0.72 (6)	1.91 (14)
Longest pectoral-fin ray	4.02 (7.5)	1.663 (16)	6.03 (10)	4.14 (16)	1.50 (12)
Upper-jaw length	6.68 (12)	1.305 (14)	4.93 (8)	1.95 (12)	0.74 (4)
Upper-jaw width	8.09 (15)	0.970 (12)	9.03 (14)	1.20 (8)	1.12 (6)
Symphyseal knob	15.49 (18)	0.873 (10)	11.29 (16)	0.56 (4)	0.73 (2.5)
6th spinous ray in dorsal fin	8.21 (16)	1.410 (15)	5.97 (9)	1.72 (11)	0.73 (2.5)
13th spinous ray in dorsal fin	9.54 (17)	0.589 (6)	0.94 (1)	0.62 (5)	0.99 (5)
3d anal-fin spine	7.31 (14)	0.602 (7)	3.87 (3)	0.82 (7)	0.53 (1)

and erase local differentiation. Further, the species appears to be genetically nearly homogeneous over as great, and environmentally variable, a distance in the eastern part of its range—Seeb and Gunderson (in press) demonstrated “very high similarity” among populations from Washington State to the Bering Sea and found no evidence for a barrier at the Aleutian Chain. Second, as already mentioned, morphological (including morphometric) differences can be environmentally induced through modification of growth rate. The growth differences Quast (fn. 2) found, which appeared to conform more closely to latitude than ocean temperatures, resemble geographic trends in some measurements examined in the present study, including body-depth pelvic (Fig. 2H). Last, Barsukov’s criteria for the subspecies can be called into question. When referred to fish of two standard sizes, 260 and 300 mm SL, my data on body-depth pelvic (Barsukov’s “body depth”) indicate that only representatives from the Kodiak region have 95% confidence limits for mean population values that lie consistently on the *S. a. alutus* (the nominal eastern subspecies)

side of Barsukov’s criterion—confidence limits for most measurement means for other regions indicate ambiguous or improper identification (Table 5), and that a majority of specimens will be improperly identified. Further, neighboring populations in the eastern subspecies’ range frequently differ significantly in one or more measurements (Fig. 2, Table 2). If significant geographic variation were a sole criterion for subspecies then a number might need be named.

Barsukov (1964) gave further criteria for separating the nominal eastern and western subspecies, but the criteria seem subjective and impractical: Prominence and apparent squamation of occipital crests do not seem of value; as I have observed, development of crests may be highly variable within regions, and evidence for squamation can be altered in specimens collected by bottom trawl. His analysis of variation in the occipital crests is too short and subjective to be useful. Size of symphyseal knob (“larger at similar body lengths in the eastern subspecies”) is not reliable because the character has considerable

TABLE 5.—Mean, upper, and lower 95% confidence limits for the mean of body-depth pelvic (BDP) measurements and their derived proportions of standard length (SL) for Pacific ocean perch of 260 and 300 mm SL. Ratios of SL divided by body depth are categorized according to Barsukov’s (1964) criterion of 3.2 for the ratio as follows: Ratios rounding to greater than the interval 3.15-3.24 (3.2 expanded to its inclusive values with two decimal points) are followed by a blank, those within the interval are followed by an “A”, and those lower are followed by an “I”. Ratios followed by a blank would identify the eastern nominal subspecies (*S. a. alutus*) by the 3.2 criterion, those followed by an “A” would give an ambiguous identification (*S. a. alutus* or *S. a. paucispinosus*), and those followed by an “I” would identify the western nominal subspecies (*S. a. paucispinosus*).

Region (limit)	260 mm SL				300 mm SL			
	Males		Females		Males		Females	
	BDP	SL/BDP	BDP	SL/BDP	BDP	SL/BDP	BDP	SL/BDP
Atka-Bering								
Lower	81.909	3.17 A	82.665	3.15 A	94.715	3.17 A	95.717	3.13 I
Mean	81.422	3.19 A	82.258	3.16 A	94.006	3.19 A	95.183	3.15 A
Upper	80.957	3.21 A	81.853	3.18 A	93.302	3.22 A	94.652	3.17 A
Atka-Gulf								
Lower	80.115	3.25	80.145	3.24 A	92.859	3.23 A	93.687	3.20 A
Mean	79.666	3.26	79.708	3.26	92.044	3.26	92.964	3.23 A
Upper	79.219	3.28	79.274	3.28	91.236	3.29	92.247	3.25
Kodiak								
Lower	79.214	3.28	78.662	3.31	91.513	3.28	91.554	3.28
Mean	78.753	3.30	78.269	3.32	90.928	3.30	90.870	3.30
Upper	78.295	3.32	77.878	3.34	90.346	3.32	90.389	3.32
Yakutat								
Lower	81.560	3.19 A	81.271	3.20 A	94.997	3.16 A	94.278	3.18 A
Mean	80.828	3.22 A	80.600	3.23 A	93.877	3.20 A	93.236	3.22 A
Upper	80.102	3.25	79.934	3.25	92.770	3.23 A	92.186	3.25
Southeastern								
Lower	81.125	3.20 A	81.878	3.18 A	94.906	3.16 A	95.531	3.14 I
Mean	80.655	3.22 A	81.239	3.20 A	94.224	3.18 A	94.540	3.17 A
Upper	80.187	3.24 A	80.605	3.23 A	93.547	3.21 A	93.559	3.21 A
Vancouver								
Lower	83.391	3.12 I	82.356	3.16 A	97.376	3.08 I	97.027	3.09 I
Mean	82.304	3.16 A	80.629	3.22 A	96.616	3.11 I	95.938	3.13 I
Upper	81.231	3.20 A	78.958	3.29	95.861	3.13 I	94.861	3.16 A



unassigned variation for its size (Table 3), as well as high positive allometry (Table 2).

The possibility exists, since Barsukov (1964) measured body depth directly on preserved specimens, a method different from that used in the present paper, that the two methods give biased measurements relative to the other. The question cannot be fully resolved; Barsukov gave sparse collection information (e.g., his conclusions on Bristol Bay representatives were based on eight or fewer specimens between 30 and 340 mm SL), and he gave no data on statistical parameters or data peculiarities. Although the body depth measurement at pelvic fins is simple to perform, high accuracy and undistorted material are necessary because geographic variation is slight but significant (e.g., maximum geographic difference between means for body-depth pelvic at 260 mm SL is around 4 mm in Figure 2H).

Indirect evidence indicates that the combination of photogrammetry and fresh specimens used in the present study probably gave more precise measurements than the hand methods and museum specimens used by Barsukov (1964), but likely that bias between methods was unimportant relative to other factors. Barsukov stated that body depth in specimens attributed by him to *S. a. paucispinosus*, presumably including those from Bristol Bay, averages 3.05 into SL, and that his specimens of *S. a. alutus* average 3.42. In contrast, in the present study, the extreme regional confidence limits for means lie between 3.08 and 3.34 (Table 5), well within the span of Barsukov's means (my data for Bristol Bay are nearly central between his values, with confidence limits of 3.12 and 3.22).

Rather than methods bias, the wide range of mean values for body depth given by Barsukov (1964) relative to those in Table 5 may have been caused in part by chance overweighting of extreme data values because of his relatively small sample sizes. His 124 specimens were relatively few for a considerable geographic range—82 from Bristol Bay to Washington and 42 from Olyutorskii Bay and the Commander Islands. Perhaps, body-depth variation was falsely indicated as bimodal in Aleutian Arc representatives, leading to the interpretation that the data represented shallow- and deep-bodied populations.

Finally, Barsukov may have been misled by variable distortion and shrinkage of his specimens owing to conditions of preservation and storage. Although he stated that his specimens shortened 0.3-4.0% after "several" months of

preservation in alcohol, and that 200 mm SL fish lost 1% and 300 mm fish lost 2% on average, he apparently did not try to compensate for this loss in length and apparently did not measure corresponding changes in body depth at the pelvic fins. Some of his material had been preserved much longer than several months and may have been even less representative of fresh material—the Olyutorskii Bay and Commander Island specimens were collected by A. P. Andriyashev in 1932 and 1950-52, indicating probable 9-30 yr storage in alcohol before measurement.

## CONCLUSIONS

Because geographic variation was expressed in all parts of the morphology of Pacific ocean perch that I investigated, I conclude that the variation pervades body growth in the species. Over the eastern Bering Sea and eastern Pacific Ocean, adult measurements usually vary as V-shaped clines. Here, representatives of the same SL from the extremes of the sampling range (Vancouver Island and the eastern Bering Sea) resemble each other more than they resemble fish from near the midrange (Kodiak and Yakutat regions), where measurements often are smallest.

Only measurements of belly size and neighboring parts of the body have single, monotonic clines over the regions. Belly size increases dramatically from Vancouver Island to the eastern Bering Sea accompanied by corresponding size decreases in neighboring body measurements. The anterior and posterior boundaries of the belly, pelvic girdle (given by pelvic insertion), and anal-fin spines (given by body-depth anal) move relationally farther apart to give progressively larger bellies in populations farther from Vancouver Island and closer to the Bering Sea. Length of the spinous dorsal fin generally increases from southeast to northwest and length of the nape decreases, both apparently because of a relationally forward shift in the anterior insertion of the dorsal fin.

Nearly all morphometric characters apparently grow allometrically in Pacific ocean perch, but average body form does not change markedly with growth because allometric coefficients of most characters are near unity. Often, measurements vary between apparent slight but significant positive and negative allometry, depending on the sampling region. The symphyseal knob and 3d anal-fin spine (allometric coefficients were 1.52 and 0.73, respectively, including both sexes)

may be sufficiently allometric for the symphyseal knob to seem exceptionally prominent and the 3d anal-fin spine exceptionally small in some large specimens.

Most body dimensions average smaller in females than in males, but bellies are larger in females. The same mechanism, opposing relational movements of the pelvic girdle and the anal-fin spines, is responsible for sexual and geographic variation in belly size. Although sexual dimorphism increases with growth, sexual differences are not prominent and have broadly overlapping distributions. As a result, sexes probably cannot be reliably identified by gross examination of any of the 18 characters.

Neither geographic nor sexual variation is quantitatively similar between measurements in Pacific ocean perch—characters tend to vary with their absolute size. Overall, geographic variation is most poorly discriminated by the measurements of the 3d anal-fin spine, symphyseal knob, and 6th spinous ray in dorsal fin, and best discriminated by the belly, hind-trunk ventral, and head. Sexual dimorphism is most poorly discriminated by the measurements of the hind-trunk dorsal, spinous dorsal-fin length, and body-depth pelvic, and best discriminated by the belly, hind-trunk ventral, and pelvic insertion. Measurements that have been used for taxonomy of Pacific ocean perch in the past are relatively poor discriminators of geographic variation or possible genetic stocks or subspecies. Although body form changes significantly with geographic region, sex, and growth, differences are too small and unexplained variation too large for differences to be of value for distinguishing single specimens geographically.

Because of questions concerning validity and importance of published morphological information supporting supposed subspecies of Pacific ocean perch, it seems prudent that further claims for subspecies based on morphology be postponed until variation is reliably assessed over the entire species' range and definitive characteristics are known to be genetically based.

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