

MERISTIC VARIATION IN THE HEXAGRAMMID FISHES

BY JAY C. QUAST, *Fishery Biologist (Research)*

BUREAU OF COMMERCIAL FISHERIES Biological Laboratory, Auke Bay, Alaska

ABSTRACT

Meristic characters of 300 to 800 specimens of eight hexagrammid fish species are examined for geographic and local variation, and the characters are analyzed for relative variation within and between species. Significant geographic variation occurs frequently and generally is most pronounced in those species with extensive north-south distributions. Sample variation, as measured by the coefficient of variation, is quite consistent for each character both within and between species. Frequency distributions of coefficients enable

a general ranking of the characters, with counts of total vertebrae showing the lowest variation and counts of gill rakers the highest. Character variation is comparable with that reported in the literature for other fishes. Geographic variation, where pronounced, appears to be positively correlated with local variation. Character variation probably is affected both by time of embryonic fixation and structural peculiarities of the part.

Students of variation in fishes have usually described, for each population, the fluctuations in range, mode, or mean that are correlated with changes in such environmental factors as geography, temperature, and salinity. A few students have analyzed the correlation between variation of different characters within populations of a species. Both approaches have yielded valuable information. A third approach has been neglected; prior to this study, little attempt has been made to measure the variation of meristic characters within regional samples for the purpose of comparing fish species or populations of fishes. For works of this nature, one must turn to such papers as those on ammonites (Simpson, 1953) and on oreodonts (Baker, 1955).

The term "meristic" has at least two interpretations in the ichthyological literature. A general usage is synonymous with "numerical" or "capable of being counted." A restricted usage applies to those countable characters that

appear to be anatomically associated with body somites. Gill raker counts are "meristic" in the general sense, but not in the restrictive. In this paper the more general usage is employed except where otherwise stated.

Data utilized in my analysis became available during taxonomic studies on the nine extant species of the family Hexagrammidae. The family is allied to the Cottidae, and is in the same percoid suborder, Cottoidei. Distributions of the nine species fall within an arc of the North Pacific Ocean above lat. 30° N. (fig. 1). Only eight species are analyzed for geographic variation because insufficient material is available to analyze the ninth species, the Atka mackerel (*Pleurogrammus monopterygius*). The adults of all but one species are demersal and frequent rocky areas to depths of 60 m. or more. The adults of *P. monopterygius* appear largely to have retained the pelagic existence that characterizes hexagrammid larvae.

The three subfamilies that the family may be divided into are the Hexagramminae and the

NOTE.—Approved for publication January 6, 1964.

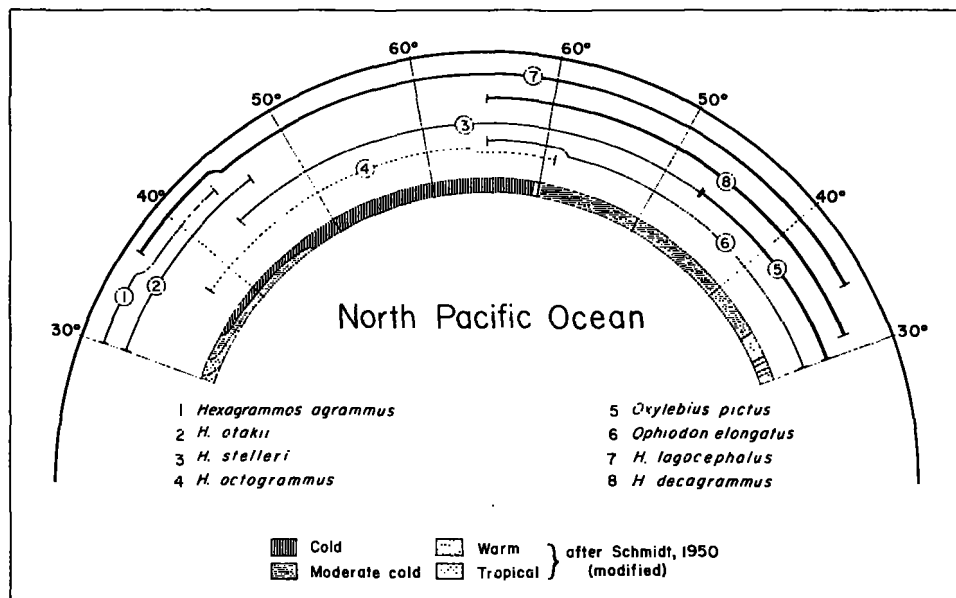


FIGURE 1.—Schematic diagram of geographic ranges in the hexagrammids that are analyzed for geographic variation. Numbers outside the semicircle indicate intersections of lines of latitude with the coastline. Species distributions are indicated by numbered arcs, and the weight of each line is roughly proportional to the degree of geographic variation (as indicated by analyses in figures 2 and 11 and discussed in the text) shown by the species. Limited inshore regions of colder upwelled water are indicated for some lower latitudes of the eastern Pacific Ocean. (Temperature data from Schmidt (1950); slightly modified.)

monotypic Oxylebiinae and Ophiodontinae. The convictfish (*Oxylebius pictus*), sole representative of the Oxylebiinae, is judged to be the most primitive member of the family because of its low meristic counts and the absence of specializations that characterize other representatives of the family. Almost all of the Hexagramminae have multiple lateral lines. In general, the evolutionary trend in the family has been toward the occupation of cold-water niches.

The names of two species depart from conventional usage, in accordance with Quast (1960): *Agrammus agrammus* is called *Hexagrammos agrammus*, and *Hexagrammos superciliosus* is synonymized with its Oriental counterpart, *H. lagocephalus*.

The family Hexagrammidae was judged ideal for meristic analysis because of the limited number of species and the high degree of overlap in their ranges, the ease with which the species could be arranged in phyletic sequence, the meristic diversity of the species, and the relative abundance of specimens in collections.

MATERIAL AND METHODS

The analysis is based on counts of vertebrae, fin rays, lateral line scales, and gill rakers of between 300 and 800 specimens, depending on the character involved. To facilitate comparisons, the geographic ranges are divided arbitrarily, and meristic data from individual localities are lumped for each division. Nearly all specimens available were examined. In most instances the collection localities range over the divisions, and in only a few are divisions represented by a single locality. A detailed listing of collection localities appears in the taxonomic section of Quast (1960). Other than gill rakers in *Ophiodon elongatus*, discussed below, there appears to be no association of meristic number with sex or size.

The methods of counting are usually those described by Hubbs and Lagler (1949). Terminal dorsal and anal rays are counted as recommended by these authors except for rare specimens that have the last two elements separated by a space

at their base approximately equal to the spacing of the preceding rays; in these, a count one unit higher is assigned. Pectoral rays and lateral line pored scales are counted on the left side unless that side is damaged. Pores in the skin over the cleithrum and pored scales on the caudal fin posterior to the hypural fan are excluded from the counts of lateral line pored scales. Gill rakers are counted on the first arch of the right side and include rudimentary rakers. (In *Ophiodon elongatus* the anteriormost rakers on the hypobranchial become so indistinct with fish growth that they cannot be counted accurately.) In vertebral counts the urostyle is included as one element, and the first caudal vertebra is identified on X-ray pictures as the anteriormost centrum with a simple haemal spine.

In regard to the analysis of meristic data, frequency distributions approximated the normal in nearly all instances. Cochran's test (Dixon and Massey, 1951) was used for general evaluation of homogeneity of variance for the *t* and analysis of variance tests. The variances appeared excessively different in an insignificant percentage of the comparisons.

GEOGRAPHIC VARIATION IN THE MEANS OF COUNTS

The means of counts (figs. 2 to 11)¹ vary geographically to some degree in all eight of the hexagrammid species examined. Of 73 species characters analyzed, approximately one-half show geographic variation. The three species with extensive north-south distributions, *Oxylebius pictus*, *Hexagrammos lagocephalus*, and *H. decagrammus*, show the greatest geographic variation both on the criterion of degree of change of counts (discussed in the section on within-sample variation) and on the criterion of the proportion of the counts that vary (fig. 1). Probably *Ophiodon elongatus* also should be included with these species because considerable geographic variation is shown despite

¹ In figures 2 to 11 the number of specimens in each sample follows the geographic designation. The mean of each sample is bracketed by a black bar that indicates its 95-percent confidence interval (with *t* correction). The light bar on each side of the mean indicates one standard deviation; the range of counts is given by the heavy lower line. Probabilities shown to the right of each species character are obtained by a *t*-test where two samples are compared, or by analysis of variance where more than two samples are compared. Coefficients of variation for the samples are indicated in the right-hand column. In the discussion, deviations between paired samples are termed "prominent" when the sample mean with the smaller confidence interval falls outside the 95-percent confidence interval of the mean for the distribution with the larger confidence interval.

only a partial sampling of its range. The other species, which have restricted Oriental distributions or distributions limited to an arc across the North Pacific, show considerably less geographic variation.

In general, the number of meristic elements declines to the south, in agreement with the latitudinal trends commonly reported for fishes in the literature. Numerous deviations from consistent geographic gradients may be noted, however, and the proportions of exceptions vary considerably from species to species.

In *Oxylebius pictus* the highest average for pre-caudal vertebrae is in the sample from northern and central California, the middle of the geographic range (fig. 2). The average for the northernmost sample is prominently (see footnote 1 for explanation of term) lower than that for the central sample, but the aggregate variation among the samples does not test as significant. The highest average for caudal vertebrae is in the northernmost sample, which is responsible for the high statistical significance of the caudal comparison; and no important differences are apparent between the two southern samples (fig. 3). Similarly, the highest average for total vertebrae occurs in the northernmost sample (fig. 4), where the high average for caudal vertebrae more than compensates for the relatively low average for pre-caudal vertebrae. No important differences in total vertebrae are demonstrated between the two southern localities. Dorsal fin spines show a definite cline of decreasing counts to the southward (fig. 5). The Puget Sound-Washington sample averages are prominently higher, and the southern-Baja California averages prominently lower than the intermediate samples. A similar trend is shown in the averages of dorsal soft rays (fig. 6), and the trends in spinous and soft rays summate to produce a very definite cline of decreasing total counts to the southward (fig. 7). The northernmost sample of anal fin rays gives the highest count, but the remaining samples show no important differences (fig. 8). Counts of lateral line pored scales shift to lower averages to the south, but the trend is slight and of borderline significance (fig. 9). Counts of pectoral rays show no definite geographic variation in means, but the southern samples appear to have greater ranges (fig. 10). Counts of gill rakers also show no definite geographic variation in means, although the range in

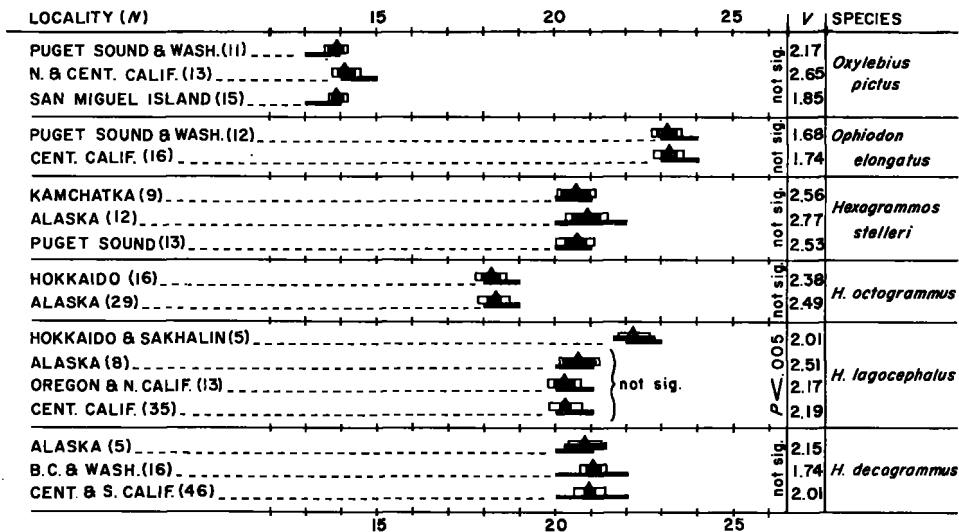


FIGURE 2.—Geographic variation in precaudal vertebrae.

counts is greater in the southern samples (fig. 11).

In *Ophiodon elongatus* no geographic trends are indicated for precaudal, caudal, or total vertebra counts (figs. 2, 3, 4). In contrast, total dorsal ray counts decrease to the southward (fig. 7), apparently because of the decrease in the soft ray portion between the northern and central samples (fig. 6) (where spine counts remain constant) and the decrease in the spinous portion between the central and southern samples (fig. 5) (where soft ray counts remain practically constant). The anal rays follow the pattern of the dorsal fin spines, and a southward decrease in counts is limited to the

southern part of the range (fig. 8). No geographic variation is apparent for the averages of lateral line pored scales, but the sample from the central portion of the range is the most variable (fig. 9)—the reverse of the situation for anal rays. Pectoral rays show no important variation. Gill raker variation is not assessed because gill raker counts change with growth in this species.

Specimens of *Hexagrammos agrammus* were available in limited quantity, and the samples are lumped into two groups. Vertebral comparisons are not made. Counts of spinous dorsal rays are prominently higher in specimens from the

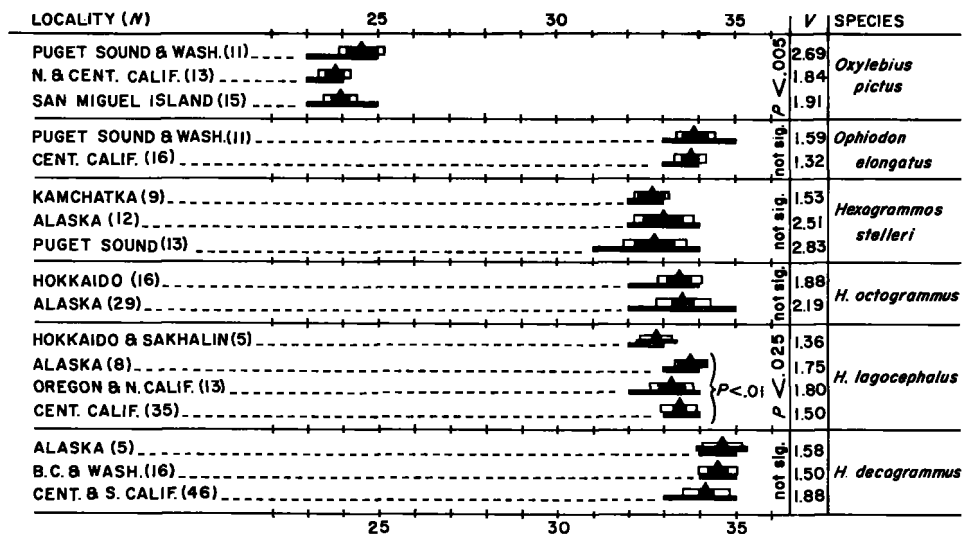


FIGURE 3.—Geographic variation in caudal vertebrae.

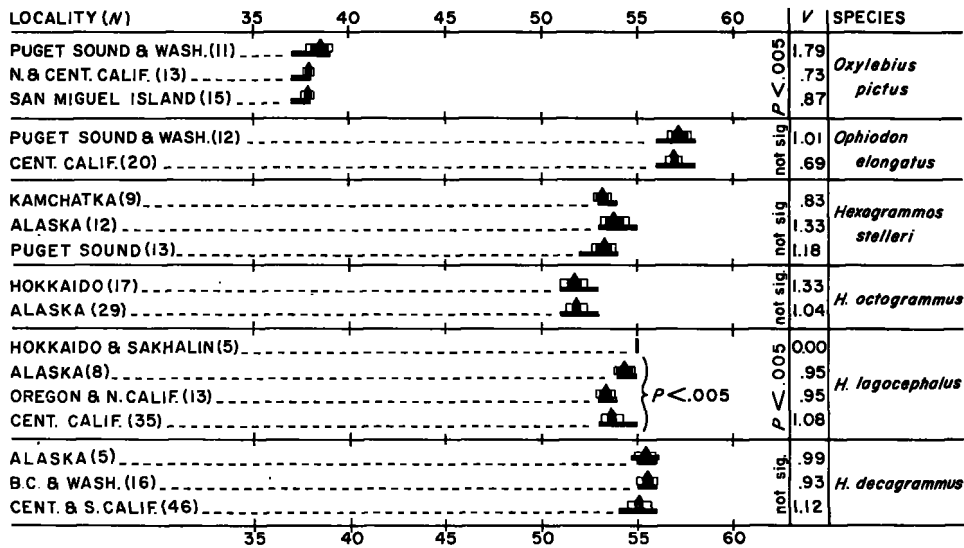


FIGURE 4.—Geographic variation in total vertebrae.

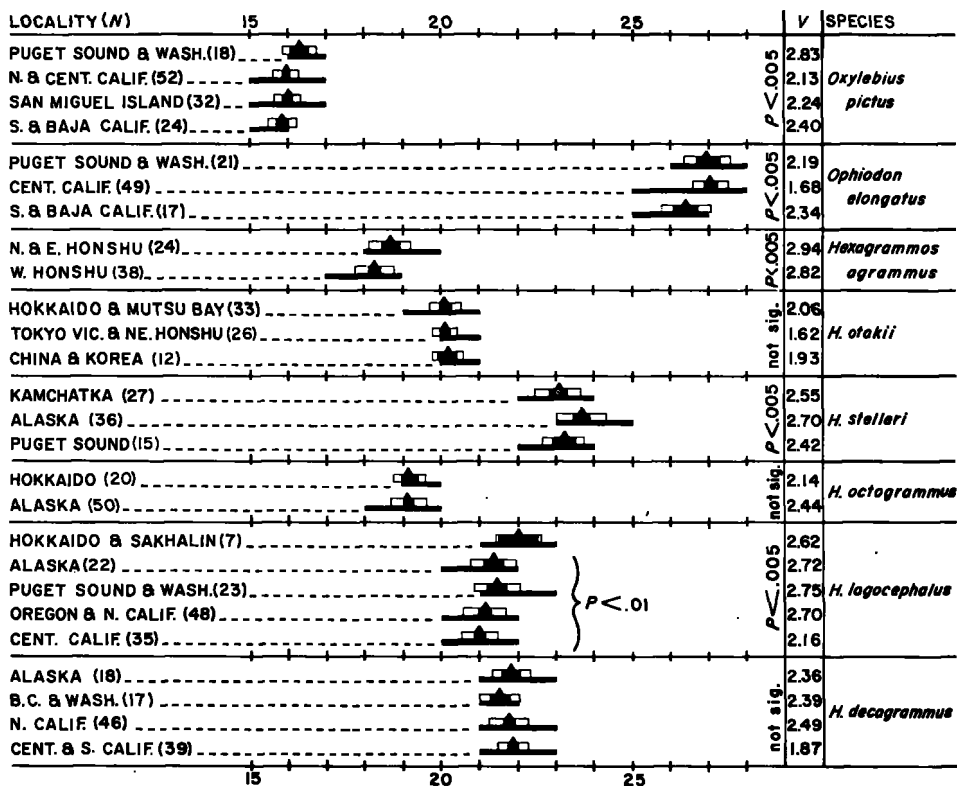


FIGURE 5.—Geographic variation in dorsal fin spinous rays.

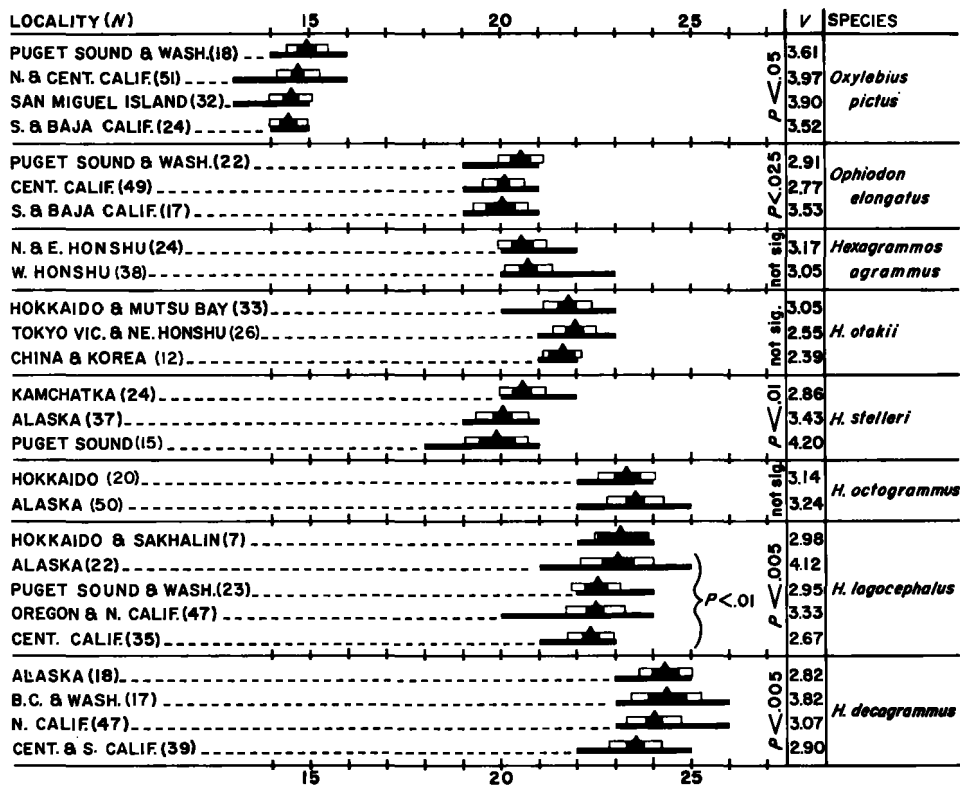


FIGURE 6.—Geographic variation in dorsal fin soft rays.

oceanic side of Honshu (fig. 5), but no differences of corresponding magnitude are apparent for dorsal soft rays or total dorsal rays (figs. 6, 7). Although anal rays are more numerous in the sample from the oceanic side (fig. 8), the difference is not significant. Counts of pectoral rays are prominently lower on the oceanic side of Honshu (fig. 10). No important variation is indicated for lateral line pored scales (fig. 9) or for gill rakers (fig. 11).

Vertebral comparisons are omitted also for *H. otakii*. Counts of dorsal fin rays show no variation worthy of note (figs. 5, 6, 7). Counts of anal rays show significant variation, however, and the mean for counts from the eastern coast of Honshu is prominently higher than the mean for Hokkaido or the mainland (fig. 8). (Although similar in mean value, the counts from the mainland and Hokkaido differ markedly in coefficient of variation.) Lateral line pored scales show a definite shift toward lower counts in the regions from Hokkaido through Honshu to China and southern Korea (fig. 9). Counts of pectoral rays show no significant differences (fig. 10). Counts of gill

rakers are prominently higher in the Hokkaido-Mutsu Bay sample than in the northeastern Honshu sample (fig. 11).

The three geographic samples of *H. stelleri* differ relatively little in latitude. No significant overall differences are indicated for counts of precaudal, caudal, or total vertebrae (figs. 2, 3, 4), although the total counts for Alaska average prominently higher than those for Kamchatka and Puget Sound. Averages for counts of total dorsal fin rays from Kamchatka and Alaska (fig. 7) are similar, although there are prominently opposing trends in spines and soft rays between the two localities (figs. 5, 6). The Puget Sound sample has prominently lower total dorsal ray counts than either Kamchatka or Alaska. No important differences are evident in the averages for anal fin rays or lateral line pored scales (figs. 8, 9). In pectoral rays, the Alaska sample has the prominently highest average (fig. 10). Gill raker counts are prominently lower in the Alaska sample than in the one from Kamchatka, but the three samples of this character do not differ significantly in the aggregate (fig. 11).

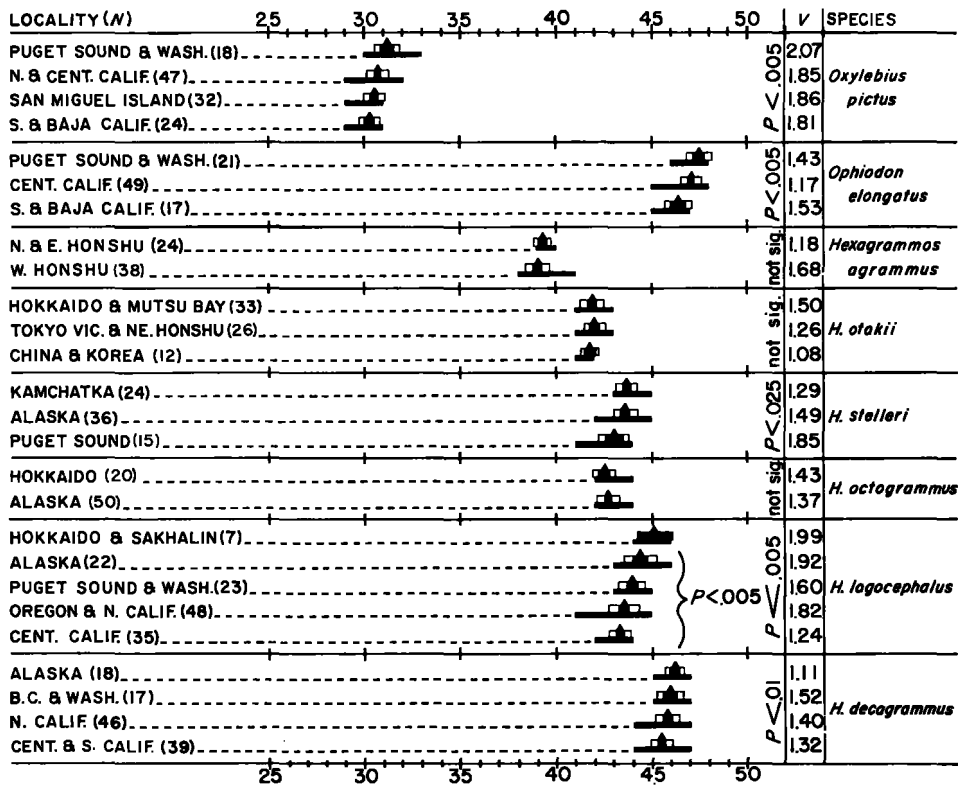


FIGURE 7.—Geographic variation in total dorsal rays.

Samples of *H. octogrammus* from the Orient and Alaska show few important meristic differences. Average counts for vertebrae (figs. 2, 3, 4), dorsal fin rays (figs. 5, 6, 7), lateral line pored scales (fig. 9), and gill rakers (fig. 11) are quite similar in the two samples. Only counts of anal and pectoral rays show differences of possible significance, and the Oriental sample gives the highest average in each instance (figs. 8, 10).

In *H. lagocephalus*, a sharp discontinuity is shown between samples of counts of precaudal vertebrae from Hokkaido-Sakhalin and Alaska (fig. 2). The dramatic difference may warrant subspecific recognition of the eastern and western Pacific representatives. Adequate data are not available from intermediate points, however, and a cline actually may exist between the two regions. In contrast, no important differences are apparent between samples of precaudal counts from the northeastern Pacific. A reciprocal relationship between precaudal and caudal counts, similar to that noted for *Oxylebius pictus*, is apparent in the Oriental and eastern Pacific samples (figs. 2, 3). Prominent differences exist between all samples of

total vertebral counts, with the Oriental counts the highest and the Alaskan specimens second highest (fig. 4). Definite clines of decreasing counts from Hokkaido to central California are apparent in dorsal fin rays (figs. 5, 6, 7), and the clines remain significant whether the Oriental samples are included or not. Anal fin rays show a similar cline except for a slight increase in means between the Oregon-northern California sample and the central California sample (fig. 8); the variation in anal fin rays is also significant whether the Oriental sample is considered or not. Averages for lateral line pored scales show a variation pattern similar to that of anal fin rays, with the highest average in the Orient (fig. 9). Pectoral rays also have the highest average in the Oriental sample, and the Oriental counts are nearly disjunct from the distributions obtained from the eastern Pacific, where no variation is apparent (fig. 10). Little variation is visible in the numbers of gill rakers (fig. 11).

In *H. decogrammus* vertebral counts show a low degree of geographic variation, but caudal and total vertebral counts are prominently lower from

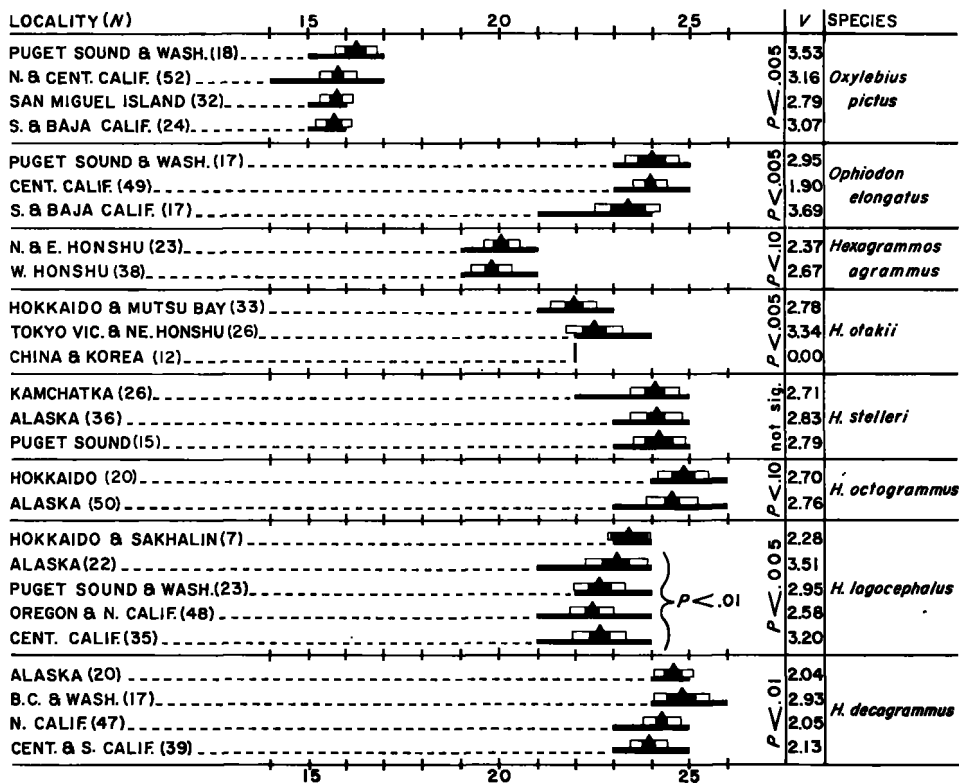


FIGURE 8.—Geographic variation in anal fin rays.

California than from British Columbia and Washington (figs. 2, 3, 4). Numbers of dorsal fin spinous rays show no differences worthy of emphasis, but the dorsal soft rays show a prominent decrease in number in the southern part of the species geographic range (figs. 5, 6). Total dorsal fin ray counts show a cline of numerical decrease to the south (fig. 7); the shift apparently is caused by a slight decline in spinous ray counts in the northern part of the geographic range (where soft ray counts remain constant) and a prominent decrease in soft ray counts in the southern part (where the shift in spinous counts opposes but does not completely compensate for the shift in the number of soft rays). Anal fin rays follow the dorsal soft ray pattern and show a decrease in counts only in the southern half of the geographic range (fig. 8). A general north-south cline of decreasing numbers of lateral line pored scales is evident, although the differences between adjacent samples are slight (fig. 9). Similar clines are noticeable in numbers of pectoral rays and gill rakers, but the aggregate variation in gill rakers does not test as significant (figs. 10, 11).

The foregoing examination of meristic variation in the hexagrammids demonstrates that the manifestation of this variation is quite complex and that shifts in means and ranges of counts between geographic samples are not always predictable. The tendency for meristic counts to be greater in the more northern and more western Pacific localities is obvious. Sampling error may be responsible for some of the contradictory trends noted between neighboring samples and, in part, for the poor correspondence in details of variation found between the species over shared portions of their geographic ranges. Numerous instances of poor correspondence between trends in counts of total elements and the numbers of elements in their sections also are noted. For example, a southward decrease in total vertebrae in *Oxylebius pictus* over the two northernmost localities (fig. 4) reflects a considerable decrease in the average number of caudal vertebrae (fig. 3), and the average number of precaudal vertebrae may actually vary in the opposite direction over the same region (fig. 2). As a corollary, the apparent lack of geographic variation in a total count may mask

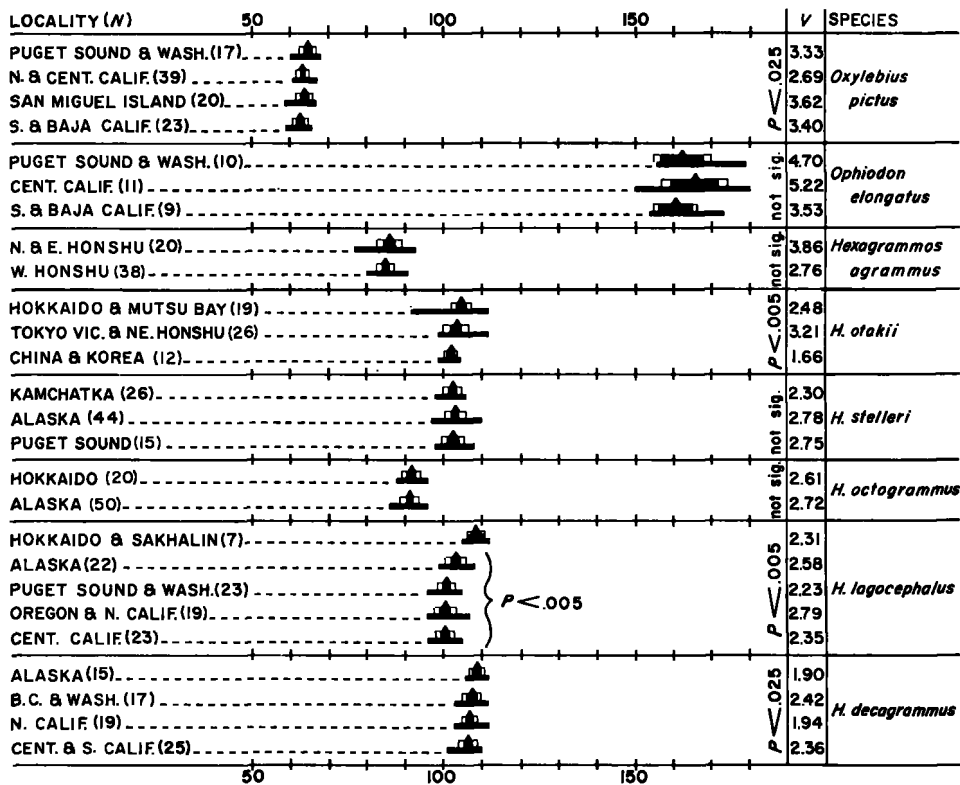


FIGURE 9.—Geographic variation in lateral line pored scales.

significant opposing geographic trends in its sections such as, for example, the pattern of dorsal fin variation in *H. stelleri* between Kamchatka and Alaska (figs. 5, 6, 7). Significant geographic variation is most frequent in the dorsal fin, second most frequent in the anal fin, and least frequent in the gill rakers.

WITHIN-SAMPLE VARIATION OF MERISTIC CHARACTERS

In addition to the mean, a measure of dispersion is necessary to characterize fully a normal frequency distribution, and the study of variation in organisms is not complete without some such estimate of the variation of characters about their sample averages. This estimate provides an index to the stability of the processes that lead to the mean values of anatomical features used to characterize populations or species. Statistics on meristic characters in fishes have the advantage that these characters are easily counted and their frequency distributions commonly approximate normal.

Simpson (1953) raised an important question

concerning the role of variation in evolution without arriving at any definite conclusions. He asked whether a highly variable population would offer more materials for evolution of new species than one that is less variable. This and other questions regarding variation in phyletic lines of animals are responsible for the following analysis. In order to examine the hexagrammid fishes in this respect, coefficients of variation are calculated for meristic characters from the available geographic samples of the species. This coefficient gives the standard deviation of a sample as a percentage of the mean. For a discussion of its use, see Simpson, Roe, and LeWontin (1960).

Interspecific and Intraspecific Similarities in Variation Coefficients of a Character

A comparison of the character coefficients of variation for all hexagrammid samples (see figs. 2 to 11 and table 1) demonstrates that for each character (e.g. total vertebral count) there is a remarkable consistency in the degree of variation shown (1) between geographic samples of a species and (2) between the species themselves. Also,

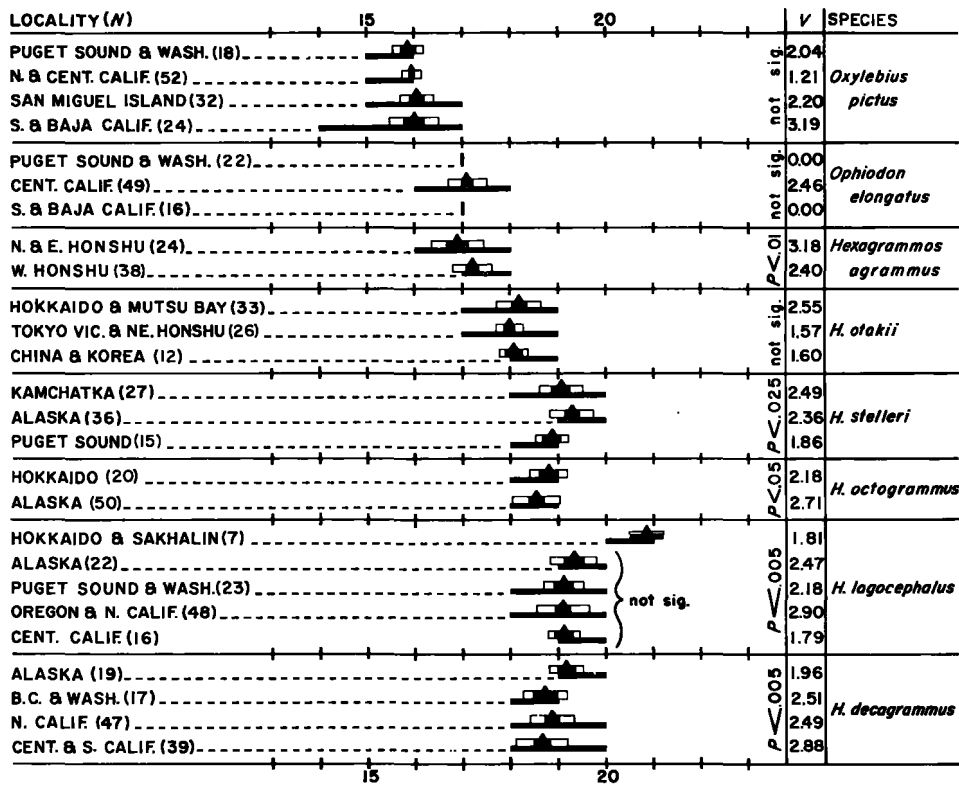


FIGURE 10.—Geographic variation in pectoral rays.

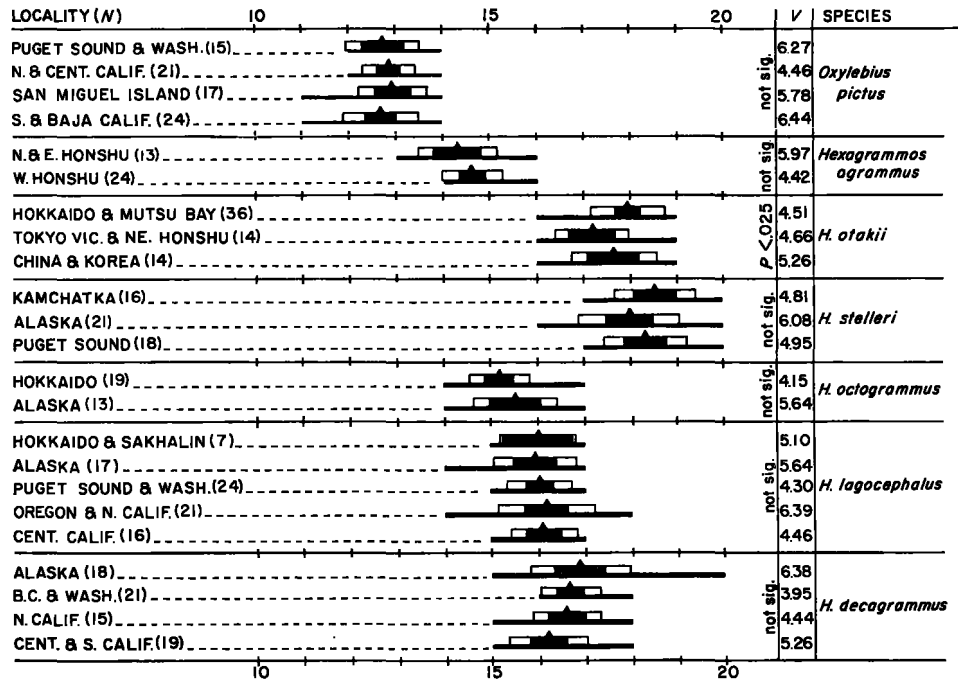


FIGURE 11.—Geographic variation in gill rakers.

each of the characters (e.g. number of anal fin rays, number of caudal vertebrae) appears to have a characteristic modal value for variation that usually differs in some degree from that for each of the other characters. Because of the consistency in variation between similar counts and the difference in variation between different counts, the samples form a hierarchical pattern when plotted on a frequency diagram (fig. 12). Similar results are obtained by ranking for each species, in order of numerical value, the averages of each set of character coefficients. In nearly all rankings, vertebral values are lowest, and total dorsal rays adjoin; whereas gill raker values are consistently highest.

The study shows an interesting relationship between the variation of entire counts, namely total dorsal spines and total vertebrae, and that of their serial components. In each comparison of this type (fig. 12), the range of coefficients for the whole count is distinctly lower than for either of its sections. The greater variation shown by components of the whole counts may be explained in part by an apparent variability in the developmental fate of the transitional elements; that is, whether a given element will develop into the type characteristic of the anterior or the posterior section. This instability, mentioned above as introducing some exceptions to the general geographic trends of the means, is presumably not linked to body metamerism, but rather to the processes that influence the fate of the boundary

TABLE 1.—Variation data on hexagrammid species not presented in figures 2 to 11¹

Species and character	Number	Mean and range of counts	Coefficient of variation
<i>Hexagrammos agrammus:</i>			
Precaudal vertebrae.....	32	18.81 (18-20)	2.84
Caudal vertebrae.....	32	29.22 (28-30)	2.26
Total vertebrae.....	32	48.03 (46-50)	1.45
<i>Hexagrammos atakii:</i>			
Precaudal vertebrae.....	32	20.08 (20-21)	1.44
Caudal vertebrae.....	12	31.58 (31-32)	1.63
Total vertebrae.....	12	51.67 (51-52)	0.95
<i>Pleurogrammus monopterygius:</i>			
Dorsal spines.....	34	22.18 (24-28)	3.42
Dorsal soft rays.....	33	26.61 (24-28)	3.75
Total dorsal rays.....	33	48.79 (47-50)	1.43
Total anal rays.....	31	26.10 (25-27)	2.68
Pectoral rays.....	34	25.09 (24-26)	2.67
Precaudal vertebrae.....	8	26.62 (26-27)	1.95
Caudal vertebrae.....	8	33.62 (33-35)	2.21
Total vertebrae.....	8	60.25 (60-61)	0.77
Lateral line pored scales.....	38	152.08 (139-166)	4.13
Gill rakers.....	31	24.90 (22-27)	4.79

¹ Data are from collections from single geographic locations only: *Hexagrammos agrammus*, Kyogo Misaki, Japan; *H. atakii*, "Tokyo," Japan; *Pleurogrammus monopterygius*, Alaska.

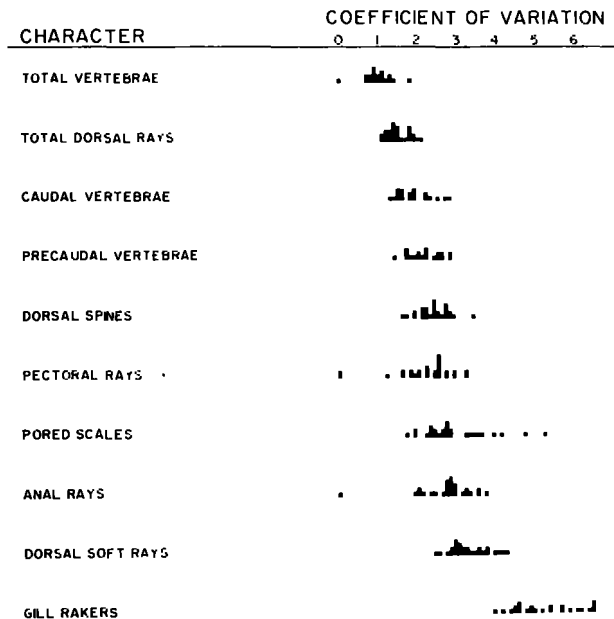


FIGURE 12.—Frequency diagram of variation coefficients for samples of hexagrammid meristic counts. Characters arranged in order of increasing variability.

elements. Although according each section of entire counts high values for variation, the instability of transitional elements has no effect on the variability of entire counts because the total number of elements is not affected. As an example, the frequency with which a boundary element becomes either a dorsal spine or a dorsal soft ray, or a precaudal or a caudal vertebra, has no effect on the total number of elements in the dorsal fin or in the vertebral column. Gosline (1947) described a negative correlation between the number of anterior and posterior elements for *Etheostoma exile*, and Hubbs and Hubbs (1954) described it for the kelp perch, *Brachyistius frenatus*.

The values for the variation of meristic characters of the same body region are not necessarily similar. Although the caudal vertebrae and the anal and soft dorsal fins are of similar extent and occupy the same body region in hexagrammid fishes, an overall comparison of the frequency distributions of the character variation coefficients (fig. 12) demonstrates that variation in the numbers of caudal vertebrae throughout the family generally is less than in anal rays and dorsal soft rays.

Meristic Variation of Hexagrammids Compared With That of Other Fishes

In general, meristic variability in characters of the hexagrammid fishes agrees with or is lower than that for the same characters in fishes of several other families and orders randomly selected from the literature (table 2). Coefficients of variation (V) for vertebral counts are relatively uniform and low among all samples of the various families, with two exceptions: In *Fundulus*, especially in laboratory-reared samples, and in some samples of the flatfish *Parophrys vetulus*, the coefficients are unusually high. Variation in the number of dorsal spines, as compared with the hexagrammids, is lower in five families and higher in two. The range of coefficients for numbers of dorsal fin soft rays in hexagrammids approximates that of herring, flatfishes, some scorpaenids, one cottid, and one goby, but is considerably lower than that of one serranid, two percids, and two scorpaenids. Variation in numbers of anal rays, lateral line pored scales, pectoral rays, and gill rakers in hexagrammids generally is below that of the other examples.

Overall Variation in the Hexagrammids and Its Relationship to Evolution Within the Family

A crude estimate of general meristic variability was attempted for each of the nine species of Hexagrammidae by calculating character by character the number of positive and negative deviations of all samples of each species from the family averages for variation. It was assumed that any species having overall high or low values for variation also will have unusually high or low totals of values above or below the family means. When the frequencies of positive and negative deviations were tested with the chi-square distribution, a significant departure from the distribution of values expected in a homogeneous sample was found at the 95-percent level, indicating that some species probably have greater allotments of variation coefficients above or below the family means than would be expected by chance alone. The data indicate that the values for *Oxylebius pictus* and *Hexagrammos decagrammus* are in large part responsible for the high chi-square value. The two species depart strongly from the family averages for meristic variation, but in different directions: In *O. pictus*, 12 out of 15 coefficients are above the family means; in *H. decagrammus*, 13 out of 15 coefficients are below.

Because the average counts for meristic characters in the two species are markedly dissimilar, another interpretation of the differences in variation between the two species, as indicated by V , would be necessary if the standard deviations of character samples of *O. pictus* and *H. decagrammus* were the same. In this instance, the divisor of the variation equation would be larger for characters of *H. decagrammus* because of the higher counts in this species, and hence would accord this species lower values for variation. The data disclose, however, that the standard deviations for characters of *O. pictus* are not the same as for those of *H. decagrammus*, and that the latter are consistently higher (table 3). The lower values for V in *H. decagrammus* are the result of the disproportionate differences in means and standard deviations of the two species: the increase in standard deviations of character samples between *O. pictus* and *H. decagrammus* does not quite keep pace with that of the mean values of their meristic characters.

The differences in variation between *O. pictus* and *H. decagrammus* suggest that the more highly evolved form may be less variable. *Oxylebius pictus* is interpreted as being the most primitive living species in the family because of its low meristic counts and single lateral line. In contrast, *H. decagrammus* has these characters in an apparently more derived condition. However, since it is not known to what extent the differences in variability between the two species are due to environmental rather than to genetic causes, the significance of the differences is questionable. In addition, other hexagrammid species that contrast nearly as strongly in subjective estimates regarding their evolutionary status show no corresponding general differences in their variation. It must be concluded that any relationships between variation and evolution in the Hexagrammidae are too subtle or too complex to be reliably indicated by such gross numerical analyses.

Relationship Between Variation Within Samples and Geographic Variation of a Character

Considerable taxonomic significance may pertain to the possible relationships between the variation within regional or local samples of a character, as measured by the coefficient of variation, and the variation between samples taken over the entire geographic range of a species. A

TABLE 2.—Comparison of coefficients of variation (V) for hexagrammids with those for other fishes, as calculated from data randomly selected from the literature

Character, family, and species	Samples (specimens)	Sample averages	Range of V
Vertebral elements:			
Hexagrammidae:-----	20 (327)	38-60	0.7- 1.8
Clupeidae:			
<i>Clupea pallasii</i> (Hubbs, 1925).....	5 (847)	52-53	1.2- 1.5
<i>Sardinops caerulea</i> (Hubbs, 1925).....	2 (494)	52	1.1- 1.2
Engraulidae:			
<i>Engraulis mordax</i> (Hubbs, 1925).....	2 (729)	46	1.3- 1.5
Cyprinodontidae:			
<i>Fundulus heteroclitus</i> (Gabriel, 1944):			
Laboratory-reared specimens.....	3 (932)	32-33	2.3- 2.9
Wild population.....	1 (105)	32	2.0
Bothidae:			
<i>Citharichthys stigmaeus</i> (Taylor, 1957).....	25 (1,988)	37-38	.9- 1.8
Pleuronectidae:			
<i>Eopsetta jordani</i> (Taylor, 1957).....	15 (1,486)	43	.8- 1.9
<i>Microstomus pacificus</i> (Taylor, 1957).....	5 (266)	52	1.2- 1.7
<i>Parophrys vetulus</i> (Taylor, 1957).....	27 (2,130)	42-44	1.1- 2.8
Percidae:			
Fourteen species (Bailey and Gosline, 1955).....	14 (405)	36-43	.7- 1.5
<i>Etheostoma exile</i> (Bailey and Gosline, 1955).....	1 (1,000)	37	1.9
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (1,938)	36-38	1.1- 1.8
Dorsal spines:			
Hexagrammidae:-----	27 (799)	16-27	1.6- 3.4
Serranidae:			
<i>Roccus saxatilis</i> (Raney, 1957).....	12 (1,320)	9	3.0- 6.0
Percidae:			
<i>Etheostoma exile</i> (Gosline, 1947).....	1 (1,000)	10	7.9
<i>Percina nigrofasciata</i> (Crawford, 1956).....	19 (1,720)	12	4.1- 5.9
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	15-16	3.4
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (283)	12	.7-1.4
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (1,754)	7-8	4.6-8.6
Gobiidae:			
<i>Clevelandia ios</i> (Prasad, 1958).....	4 (188)	4-5	.9-1.2
Dorsal soft rays:			
Hexagrammidae:-----	27 (795)	14-27	2.4-4.2
Clupeidae:			
<i>Clupea pallasii</i> (Hubbs, 1925).....	2 (390)	18	3.7-4.1
Serranidae:			
<i>Roccus saxatilis</i> (Raney, 1957).....	4 (294)	11	4.3-5.0
Percidae:			
<i>Etheostoma exile</i> (Gosline, 1947).....	1 (1,000)	11	6.0
<i>Percina nigrofasciata</i> (Crawford, 1956).....	19 (1,698)	11-12	4.2-6.1
Bothidae:			
<i>Citharichthys stigmaeus</i> (Taylor, 1957).....	25 (2,268)	82-88	2.5-5.8
Pleuronectidae:			
<i>Eopsetta jordani</i> (Taylor, 1957).....	16 (1,337)	90-93	2.2-3.4
<i>Microstomus pacificus</i> (Taylor, 1957).....	5 (255)	103-105	3.2-4.6
<i>Parophrys vetulus</i> (Taylor, 1957).....	27 (2,083)	77-83	3.2-5.6
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	8-9	5.6-7.7
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (283)	10	.7-3.4
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (1,753)	16-18	3.0-4.0
Gobiidae:			
<i>Clevelandia ios</i> (Prasad, 1958).....	4 (188)	16-17	3.0-3.6
Anal rays, total or soft rays only:			
Hexagrammidae:-----	27 (816)	16-26	1.9-3.7
Clupeidae:			
<i>Clupea pallasii</i> (Hubbs, 1925).....	2 (390)	16-17	5.0-5.4
Cyprinodontidae:			
<i>Fundulus</i> , 2 spp. (Brown, 1958).....	15 (368)	10	2.6-6.1
Serranidae:			
<i>Roccus saxatilis</i> (Raney, 1957).....	4 (294)	10-11	3.8-5.0
Percidae:			
<i>Etheostoma exile</i> (Gosline, 1947).....	1 (1,000)	8	8.6
Bothidae:			
<i>Citharichthys stigmaeus</i> (Taylor, 1957).....	25 (2,265)	63-70	2.1-4.1
Pleuronectidae:			
<i>Eopsetta jordani</i> (Taylor, 1957).....	15 (1,331)	70-73	2.6-5.4
<i>Microstomus pacificus</i> (Taylor, 1957).....	5 (258)	85-87	3.3-4.5
<i>Parophrys vetulus</i> (Taylor, 1957).....	27 (2,058)	57-62	3.1-6.0
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	6	5.7-6.4
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (283)	5	2.3-2.4
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (1,752)	15-18	3.1-4.1
Gobiidae:			
<i>Clevelandia ios</i> (Prasad, 1958).....	4 (188)	16	3.5-3.8

TABLE 2.—Comparison of coefficients of variation (V) for hexagrammids with those for other fishes as calculated from data randomly selected from the literature—Continued

Character, family, and species	Samples (specimens)	Sample averages	Range of V
Blenniidae:			
<i>Istiblennius edentulus</i> (Strasburg, 1955).....	3 (280)	22	2.2-2.8
Acanthuridae:			
Three species (Randall, 1955, 1956).....	6 (249)	20-26	2.0-3.0
Lateral line scales or pored scales:			
Hexagrammidae:-----	27 (620)	63-165	1.7-5.2
Cyprinidae:			
<i>Notropis spilopterus</i> (Gibbs, 1957a).....	16 (1,157)	36-39	1.7-2.7
<i>Notropis venustus</i> (Gibbs, 1957b).....	19 (1,149)	36-42	1.7-4.3
Percidae:			
<i>Etheostoma exile</i> (Gosline, 1947).....	1 (1,000)	53	5.1
<i>Percina nigrofasciata</i> (Crawford, 1956).....	19 (1,745)	52-63	4.1-6.1
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	15	6.9-11.6
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (278)	25-26	5.2-5.4
Pectoral rays:			
Hexagrammidae:-----	27 (803)	16-25	1.2-3.2
Cyprinidae:			
<i>Notropis spilopterus</i> (Gibbs, 1957a).....	22 (2,757)	14	3.0-6.1
<i>Notropis venustus</i> (Gibbs, 1957b).....	23 (2,575)	14-16	3.1-8.8
Percidae:			
<i>Percina nigrofasciata</i> (Crawford, 1956).....	19 (1,702)	28-29	2.5-4.5
Bothidae:			
<i>Citharichthys stigmaeus</i> (Taylor, 1957).....	25 (2,330)	11-12	4.6-7.2
Pleuronectidae:			
<i>Eopsetta jordani</i> (Taylor, 1957).....	16 (1,441)	12-13	2.3-7.9
<i>Microstomus pacificus</i> (Taylor, 1957).....	5 (272)	10	5.8-7.9
<i>Parophrys vetulus</i> (Taylor, 1957).....	21 (1,704)	12	4.3-7.1
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	12	2.6-3.7
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (278)	22	2.7
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (4,256)	18-19	2.5-3.2
Gobiidae:			
<i>Clevelandia ios</i> (Prasad, 1958).....	4 (188)	19	3.6-4.9
Gill rakers:			
Hexagrammidae:-----	24 (611)	13-25	3.9-6.4
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (85)	8-10	10.8-13.1
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (283)	13	5.5-6.9

¹ Hubbs, Carl L., and L. C. Hubbs. Analysis of meristic variation in *Leptocottus armatus*, a fish of western North America. Manuscript being prepared for publication, Scripps Institution of Oceanography, La Jolla, Calif.

character that varies little within regional or local samples assumes greater significance when associated with extensive geographic variation. An index of variation within samples of species characters is available in the form of averaged coefficients of variation of the samples. An index of geographic variation may be obtained by dividing the maximum difference between sample means of a species character by the midrange of the character means. The value obtained, like the coefficient of variation, expresses the difference as a percentage of the mean or central value. To determine what relationships may exist between these two types of variation, averaged values of the coefficient of variation were compared with the index of geographic variation for each of nine strictly meristic counts in the four species that display marked geographic variation—*Oxylebius*

TABLE 3.—A comparison of mean values for the standard deviation in samples of *Oxylebius pictus* and *Hexagrammos decagrammus*

Character	<i>O. pictus</i>			<i>H. decagrammus</i>			Proportionate increase	
	Standard deviation		Mid-range of count	Standard deviation		Mid-range of count	Standard deviation	Mid-range of count
	Number	Mean		Number	Mean			
Dorsal spines.....	4	0.387	16.0	4	0.487	22.0	1.26	1.37
Dorsal soft rays.....	4	.550	14.5	4	.760	24.0	1.38	1.65
Total dorsal rays.....	4	.585	31.0	4	.612	45.5	1.06	1.47
Anal rays.....	4	.498	15.5	4	.560	24.5	1.12	1.58
Pectoral rays.....	4	.341	15.5	4	.462	19.0	1.35	1.23
Precaudal vertebrae.....	3	.310	14.0	3	.407	21.0	1.31	1.60
Caudal vertebrae.....	3	.520	24.0	3	.470	34.0	1.09	1.42
Total vertebrae.....	3	.430	38.0	3	.564	55.0	1.31	1.45
Lateral line pored scales.....	4	2.080	63.5	4	2.310	107.5	1.11	1.69
Gill rakers.....	4	.735	12.5	4	.832	17.5	1.13	1.40
Average increase.....							1.21	1.47

pictus, *Ophiodon elongatus*, *Hexagrammos lagocephalus*, and *H. decagrammus* (table 4). The comparison by means of the rank-correlation test (Dixon and Massey, 1951) indicates a probable positive correlation between the two types of variation for *H. decagrammus* and *Ophiodon elongatus*, and *H. lagocephalus* if the Oriental sample is excluded. A positive correlation may also exist in *Oxylebius pictus*. The pooled data for all four species show a high level of significance. It seems, therefore, that the two types of variation are positively associated in the hexagrammid fishes and that characters exhibiting the greatest shift in means geographically, by the above criteria, also tend to have the highest average values for the coefficient of variation in the regional samples. This conclusion suggests that the other species of hexagrammids, whose characters exhibit comparable variation on a local basis, have a potential for geographic variation that is unrealized.

The eight species contrast markedly in the total amount of geographic variation they demonstrate relative to their local variation. A comparison is possible if the index of geographic variation of each species character is divided by the corresponding index of local variation and all the quotients are averaged for each species (table 5). The four species with extensive north-south distribution, *Oxylebius pictus*, *Ophiodon elongatus*, *Hexagrammos lagocephalus*, and *H. decagrammus*, generally show the highest values for character

TABLE 4.—Rank correlation between local and geographic variation in meristic characters in four species of *Hexagrammidae*

[Meristic characters are ranked for both types of variation (see text) within the four species and also over the four species (overall ranking in parentheses). Highest values represent lowest ranks. Significance levels of within-species data: 5-percent=0.600; 1-percent=0.783. Significance levels of overall data: 5-percent=<0.306; 1-percent=<0.432. (From Dixon and Massey, 1951)]

Character	<i>Oxylebius pictus</i>		<i>Ophiodon elongatus</i>		<i>Hexagrammos lagocephalus</i>		<i>Hexagrammos decagrammus</i>	
	Local	Geographic	Local	Geographic	Local	Geographic	Local	Geographic
Precaudal vertebrae.....	5(17)	7(25)	5(26)	9(36)	6(18)	1(1)	6(23)	8(31)
Caudal vertebrae.....	7(20)	3(12)	6(29)	7(34)	8(28)	9(17)	7(27)	7(29)
Total vertebrae.....	9(32)	8(28)	8(34)	8(35)	9(38)	8(16)	9(33)	9(32)
Dorsal spines.....	4(13)	6(18)	4(22)	5(23)	3(10)	4(4)	4(15)	6(27)
Dorsal soft rays.....	1(2)	2(11)	2(7)	3(21)	1(4)	7(10)	1(5)	2(9)
Total dorsal rays.....	8(24)	5(15)	7(30)	4(22)	7(26)	6(6)	8(31)	5(26)
Anal rays.....	3(6)	1(7)	3(9)	2(20)	2(8)	5(5)	3(14)	1(8)
Pectoral rays.....	6(19)	9(30)	9(35)	6(33)	5(16)	2(2)	2(11)	3(19)
Lateral line pored scales.....	2(3)	4(13)	1(1)	1(14)	4(12)	3(3)	5(21)	4(24)
Rank correlation coefficient within species.....	0.567		0.683		0.300 ¹		0.800	
Rank correlation coefficient over the four species.....	0.598							

¹ Rank correlation coefficient=0.783 if Oriental sample is excluded.

variation geographically. This finding is schematized in figure 1. The ranking of species is similar whether the sectional counts are used or not. The variation data for *H. lagocephalus* emphasize, once again, the meristic differences between representatives from the eastern Pacific (formerly *H. superciliosus*) and those from the Orient (table 5). East-west variation accounts for much of the very high values attributed to *H. lagocephalus*, and the values correspond much more closely to those of the other species when the Oriental sample is excluded.

DISCUSSION

Meristic variation in fishes apparently has its basis in a number of processes, the relationships between some of which are not clear. Variations in the process of body segmentation during ontogeny are probably the basic source of variation in those counts that may be termed meristic in the strict sense. Vertebrae are laid down relatively early in life and are subject to fewer extraneous influences than meristic characters fixed later in ontogeny. Counts of total vertebrae, therefore, reasonably may be expected

TABLE 5.—Geographic variation relative to local variation for all hexagrammid species assessed

[Degree of geographic variation relative to local variation averaged over all characters of each species (see text). Data for total counts column excludes the sectional counts (precaudal and caudal vertebrae; dorsal spines and soft rays). I=index of geographic variation for each species character divided by the corresponding index of local variation]¹

Species	All counts				Total counts only			
	Z I	Number characters	Average I	Rank	Z I	Number characters	Average I	Rank
<i>Oxylebius pictus</i>	10.27	10	1.03	2	5.95	6	0.99	3
<i>Ophiodon elongatus</i>	6.82	9	.76	4	4.52	5	.90	4
<i>Hexagrammos agrammus</i>	3.56	7	.51	7	2.50	5	.50	6
<i>H. otakii</i>	4.96	7	.71	5	4.24	5	.85	7
<i>H. stelleri</i>	5.87	10	.59	6	2.94	6	.49	5
<i>H. octogrammus</i>	2.86	10	.29	8	2.11	6	.35	8
<i>H. lagocephalus</i> ²	24.09	10	2.41	1	15.22	6	2.54	1
(<i>H. lagocephalus</i>) ³	(8.21)	(10)	(.82)	(3)	(4.66)	(6)	(.78)	(5)
<i>H. decagrammus</i>	9.43	10	.94	3	6.44	6	1.07	2

¹ Arrangement of species-character indices about the median for all indices in a 2 x 8 table indicates that the species distributions are highly unlikely on the basis of chance (chi square=27.4; 99.5 percentile=20.3) and that ranking is justified. Rank correlation analysis between the arrays in the columns all counts and total counts only indicates close correlation ($r_s=0.96$; 1 percent critical value=0.83). (Tests and confidence levels from Dixon and Massey, 1951.)

² All samples.

³ Oriental sample excluded.

to be the least variable of the meristic characters, a conclusion borne out not only by the hexagrammid variation coefficients (fig. 12) but also by the comparison of hexagrammid coefficients with those for fishes in other families and orders (table 2).

Hubbs (1926) suggested that increased meristic counts in northern representatives of fishes of the northern hemisphere could be caused by dissimilar effects of low temperatures on embryonic rates of growth and differentiation. He theorized that both rates were slowed by lower temperatures but that differentiation was slowed more than growth, with the result that the embryo was larger at the time that differentiation of the counts took place. In later papers Hubbs theorized that a larger number of meristic elements result in the organs of such an embryo because of the greater amount of actual tissue space available when the meristic elements are formed. This explanation is contingent on the assumption that the meristic elements are of roughly the same size in embryos developing at colder temperatures or, as stated by Hubbs and Hubbs (1945, p. 268), "that meristic elements such as vertebrae, scales, and fin rays are laid down at a relatively constant distance apart, in absolute terms, and that the number of

elements depends on the space available, up to the time when development stops."

A large number of papers have been published on the subject since Hubbs proposed his theory (for a review see Gordon, 1957), but to my knowledge no one has tested Hubbs' theory by measuring the developing segments in groups of fish embryos that have developed under differing environmental conditions. Another pertinent question is whether meristic variation finds its expression in the entire series of a meristic count or whether it is concerned mainly with variation in the occurrence of terminal elements, as indicated by Hubbs and Hubbs (1945) and McHugh (1950). Ford (1937) believed that variation in the ultimate centra in the vertebral column was the usual cause of variation in vertebral count, but he also cited some examples of variation in vertebrae at the beginning of the column, implying that in some perciform species the centra may be added either at its beginning or at its end. Seymour (1959), however, found nearly equal frequencies of abnormal vertebrae in both caudal and precaudal regions of experimentally reared chinook salmon (*Oncorhynchus tshawytscha*).

The relationship between changes in numerical counts through variation and their changes through evolution should be a fertile field for study. The hexagrammid species form a series in which increase in meristic count parallels habitation of colder waters, both intraspecifically and interspecifically. Neither interspecific increase in vertebral counts through geographic variation nor intraspecific variation in these counts is confined to the posterior region of the vertebral column. It seems likely that several processes, at least, are involved in meristic variation as expressed by vertebral number, and that the addition or loss of vertebrae through the fusion of elements at the ends of the vertebral column may sometimes be but an environment-induced change that takes place when the embryo is not developing under environmental conditions to which the population is genetically adjusted.

It appears that the variation of samples may be of value as an index of the degree to which a population has adapted to local conditions. In two examples, at least, fish populations reared in artificial situations were more variable than those reared in natural situations. In both *Fundulus*

heteroclitus (table 2) and *Etheostoma exile*,² vertebral variation was considerably higher in samples from modified environments than it was in samples of the same or closely related species from natural situations. Further support for the use of variation as an index to adaption may be found in the data of Seymour (1959). Although Seymour did not analyze his data from the standpoint of variation, such an analysis definitely indicates that batches of chinook salmon eggs reared at temperatures above or below those at which the eggs normally develop produce embryos with significantly increased variation in number of vertebrae (fig. 13).

In accordance with the large proportion of the data reported in the literature, it appears that the intraspecific geographic variation in the Hexagrammidae is temperature correlated. In general, water temperatures decline northward along the eastern and western coasts of the North Pacific Ocean and are lowest in the Bering Sea and in the Sea of Okhotsk (U.S. Navy Hydrographic Office, 1944). In some eastern temperate coastal regions, particularly off northwest-southeast coastlines and south of projecting headlands, this pattern is disturbed somewhat by the upwelling of colder waters and by the local warming of partly enclosed waters. The geographic variation in the meristic characters of the hexagrammids usually parallels this general geographic gradient in ocean temperatures, and the four species with the most extensive north-south distributions show the largest differences in their counts. Conclusive evidence of temperature-correlated variation in this family is still lacking, however, because little is known about the natural range of temperatures at which hexagrammid eggs develop. At present it only may be surmised that more northerly representatives of the species undergo lower temperatures at sensitive periods of development, such as those described by Tåning (1952). The environmental factors of salinity, oxygen tension, and carbon-dioxide tension, as listed by Gordon

² Bailey and Gosline (1955) did not refer to the artificial circumstances involved in the rearing of the *Etheostoma exile* population that they cite. These vertebral data are included in a long list of similar data on populations of other percid species that, presumably, were taken in the field. However, the *E. exile* data are the same as those analyzed by Gosline for an earlier paper (1947), and were taken on specimens (called *Poecilichthys exilis* at that time) which had been reared in a hatchery pond that was protected from predators. Gosline stated that the population was possibly not a natural one and that an unusually high percentage of abnormal specimens had been found. The unusually high variation values that I calculated from Gosline's data (table 2) support this supposition.

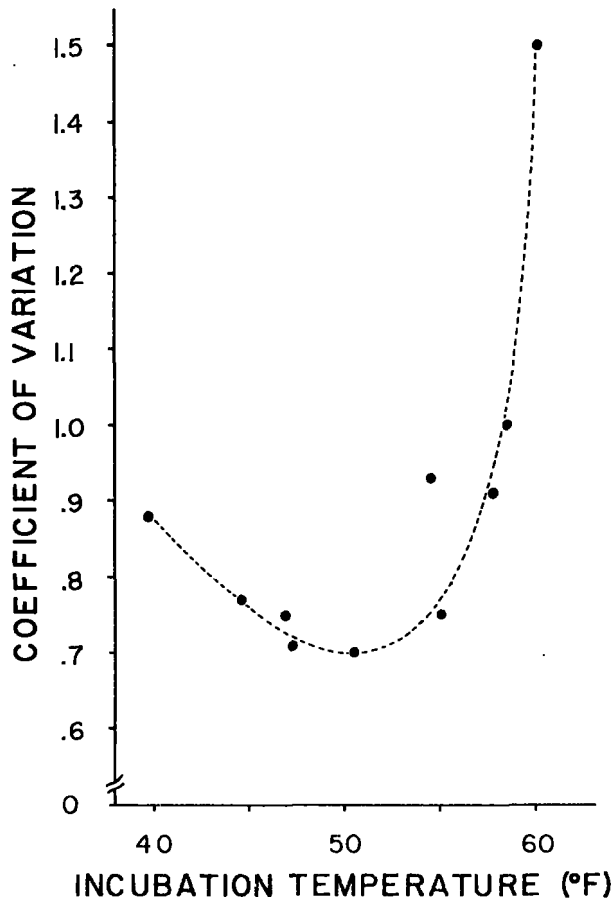


FIGURE 13.—Vertebral variation in batches of chinook salmon, *Oncorhynchus tshawytscha*, reared at different temperatures. Above and apparently below the middle range of temperatures (from 45° to 55° F.), variation increased markedly in the surviving young. Data fitted by eye. (Calculated from Seymour, 1959.)

(1957), probably can be eliminated as a cause of the variation observed in hexagrammids. Available information indicates that the larvae are pelagic and that juveniles and adults occupy rocky open-coast intertidal and subtidal habitats, both of which probably are quite uniform in salinity and dissolved gases, regardless of latitude. If temperature is proved to be directly or indirectly responsible for much of the intraspecific meristic variation in the Hexagrammidae, its role in the interspecific meristic differences in the family should also be investigated. It is possible that a part of the important meristic differences that characterize hexagrammid species also is due,

again directly or indirectly, to the range of temperatures at which a particular species develops.

Geographic variation in the Hexagrammidae differs in at least one important aspect from experimental results reported by Molander and Molander-Swedmark (1957) and Tåning (1952). These authors indicated that for a trout and a flatfish species respectively the means of all meristic counts do not vary in the same direction with higher or lower temperatures. Molander and Molander-Swedmark found that the means of vertebrae are lower in batches of larvae raised at 8° C. than in batches raised at 6° C., which is the opposite of the trend of variation in dorsal ray and anal ray means over this temperature range. Similarly, vertebra and fin ray means vary in opposite directions in Tåning's experiments. In contrast, the direction of geographic variation of these characters in the Hexagrammidae is largely consistent between characters. Similar results are reported by Hubbs and Hubbs³ in their extensive analysis of geographic variation in the cottid *Leptocottus armatus* in which the means for all meristic counts also decline toward the south. The general trend of geographic variation exemplified by the hexagrammids and *L. armatus* is commonly observed but is not universal. For example, the pattern of geographic variation reported for *Gobius* by Johnsen (1936) shows opposing trends between the means of total dorsal rays and total vertebrae on the one hand and those of pectoral counts and total vertebrae on the other. Such an inverse relationship between the total counts was shown in only one instance among the hexagrammids (pectoral and anal rays in *H. agrammus*), and the relationship may be fortuitous.

Little is known about the causal mechanism behind variation. It appears, however, that numerical characters other than somites and their functionally associated vertebrae probably have at least two sources of variation in addition to those to which vertebrae are subject. On the one hand, these characters follow the vertebrae in time of differentiation, and the formative tissues are therefore susceptible to environmental influence for a greater period of time before the number

³ Hubbs, Carl L., and L. C. Hubbs. Analysis of meristic variation in *Leptocottus armatus*, a fish of western North America. Manuscript being prepared for publication, Scripps Institution of Oceanography, La Jolla, Calif.

of elements is fixed. As an extreme example, the number of gill rakers, which appears to be the latest count to be fixed in many fishes (and rakers may continue to be added or lost with growth into adult life), is the most variable numerical character assessed in the Hexagrammidae. On the other hand, variability of a count also seems highly dependent on the anatomical relationships of the elements making up the count. The relationship seems somewhat analogous to the statistical concept of degrees of freedom. The number of vertebral elements corresponds closely to the number of somites and may be described as having but one source of variation (with the somites), or one degree of freedom. The total count of dorsal rays has additional possible sources of freedom in many perciform fishes because elements may be either added or lost at both the anterior and posterior ends of the fin. In the hexagrammid fishes, however, the dorsal fin gains only one degree of freedom over the vertebrae, because the fin spines and their inter-neurals occupy all available spaces at the insertion of the fin, and the number of spines corresponds closely to the number of anterior interneural spaces. In these fishes there is little opportunity for variation at the fin's anterior insertion. Similarly, the hexagrammids show no variation in addition or loss of fin elements with respect to the number of vertebral elements within the fin (in *Ophiodon elongatus* one element seems to be consistently lacking). The one additional source of variation in number of total dorsal elements over number of vertebrae in these fishes lies in the addition or deletion of elements at the posterior end of the fin. The total elements in the dorsal fin of hexagrammids thus may be characterized as having two degrees of freedom. Because of the variable fate of adjoining rays separating the spinous and soft portions, the spinous dorsal fin of these fishes also has two degrees of freedom. The soft-rayed fin, however, like the anal fin, probably is able to gain or lose elements at either end, and thus may be characterized as having three degrees of freedom.

Hubbs and Hubbs (1945) held that the pectoral rays vary entirely at the lower part of the fin in *L. armatus*. Carl L. Hubbs states (personal communication, 1961), "I believe that it is usually not true that elements may be added at both ends, as in the dorsal and anal. It does

seem that this does occur in the first dorsal of darters (as *E. exile*), in which the front of the fin slopes down, with no specialized elements But usually the front ray(s) is (are) specialized and fixed as in an anal fin with I, II, or III spines (depending on the species) or in the pectoral fin with the uppermost ray specialized (one short; the next long, thick, unbranched). The anal fin is usually fixed in front of the posterior of the anus and by vertebral connections." He adds. "If the variation in pectoral rays was at either end, then it wouldn't be the almost universal rule that the lowest (i.e., morphologically most posterior) ray is the shorter on the side with the higher number of rays." However, an unstable forward position of a fin's anterior formative tissue may have little to do with the later formation of the specialized anterior fin elements, which merely will appear one or more somites removed from their usual position. The insertions of dorsal and anal fins certainly have changed materially in the evolution of the various perciform fishes; a strong argument that the somites of insertion are subject to variation as well as the other morphological characteristics of fishes. Furthermore, specialized elements such as anal fin spines do vary in number in some perciform fishes, in eight of nine hexagrammid species, for example, anal spines vary over two or three units. Also, the variation in the number of the first vertebral element bearing the first haemal spine (presumably one cause of reciprocal variation in numbers of precaudal and caudal vertebrae) argues against the specialized anterior portion of the anal fin being fixed completely serially in respect to the vertebral column. Although Hubbs' argument concerning the last element in the pectoral fins seems persuasive, it applies mainly to the length of the formative tissue at the time of meristic differentiation and may have little to do with whether the formative tissue is shifted forward or backward one or two somites or whether the tissue is "longer" because the tissue for additional elements is added anteriorly, posteriorly, or medially.

The methods of variation study utilized in my paper are admittedly crude in comparison with refinements that would have been possible were the study more limited in scope and more specimens available. It is evident from the data presented that the variation in samples is influenced by the type of sample chosen and that a hierarchy

of values may be constructed from data obtained by different sampling methods. If geographic variation occurs, it is the same as saying that the value for the variation of all samples of a character, when lumped, is greater than the variation in regional samples, which, in turn, should exceed that of local samples. Local samples should be less variable than regional assortments because the geographic component of variation should decrease as the samples are limited to a narrower geographic range. Theoretically, further reduction of variation by more restrictive sampling is possible. Local samples drawn from a single year class should reduce the amount of variation over samples drawn from several year classes, especially where environmental conditions change appreciably from year to year. In a single instance of this type available among the hexagrammids, a large sample of a single year class of *Ophiodon elongatus* from San Francisco Bay (figs. 2 to 11) yielded considerably lower values for variation in most of its meristic elements than mixed samples taken elsewhere along the species range.⁴ Even further reductions in the variation of samples may occur with more selective sampling. Significant differences between meristic counts in samples of a year class taken from individuals spawned early and late in the spawning season have been reported for numerous fishes from both fresh-water habitats (Hubbs, 1922 and 1924) and salt-water habitats (Hubbs, 1925, and Hubbs and Hubbs, 1954). Even the variation in a sample of fish spawned at the same time and place may be lessened. Mottley (1934 and 1937) demonstrated lower values for variation in samples of siblings of *Salmo* spp. than in samples of a single year class from mixed parentage. In conclusion, because of this hierarchy of values for character variation that depends on the type of sample chosen, it is important that the sampling method be kept in mind when comparisons of variation are being made.

It is difficult to assess what relationship, if any, exists between the number of lateral line pored scales and the number of somites; and the hexagrammids are not analyzed in this regard. Scales are laid down late in ontogeny, and their number is subject to an undetermined set of influences

⁴ However, the year-class differences in variation are nearly restricted to the characters that also show geographic variation (dorsal spines, dorsal soft rays, total dorsal rays, and total anal rays). This adds weight to the foregoing observations concerning a positive relationship between local and geographic variation.

after the fixation time of the somites, with the result that nearly all mechanical correspondence between the two meristic series, such as that described for fin rays and vertebrae, may be lost.

SUMMARY AND CONCLUSIONS

The following conclusions are based on all available samples of the species. While the specimens are numerous in the aggregate, some samples were necessarily small and inadequate for conclusive testing of the hypotheses. Therefore these are provisional conclusions that must await intensive examination of large series of specimens for final substantiation.

1. There is significant geographic variation in the means of some meristic counts in all eight of the hexagrammid species investigated.

2. The species differ in the number of meristic characters that vary geographically; even similar species differ in this respect in overlapping portions of their geographic ranges.

3. Geographic variation in meristic counts probably is related directly or indirectly to environmental temperatures over the geographic ranges.

4. Geographic variation in the number of gill rakers does not appear to be correlated with the variation of those characters associated with the body somites.

5. The variation shown by meristic characters is remarkably consistent for each character, not only for the different regions occupied by a single species but also between the eight hexagrammid species studied.

6. Meristic variation in the Hexagrammidæ usually is as low as or lower than that calculated from the data for other fishes randomly selected from the literature.

7. Despite the general consistency of variation shown by each character within and between hexagrammid species, two species differ significantly in overall variation (as measured by the coefficient of variation) from the family averages. The most primitive representative, *Oxylebius pictus*, generally is the most variable, whereas the highly specialized *Hexagrammos decagrammus* is less variable than the average of species of the family in 13 out of 15 characters. However, no other examples of correlation were found between overall variation in the hexagrammid

species and subjective estimates of their specializations.

8. In species exhibiting marked geographic variation, the variation of different meristic characters within regional samples is positively correlated with the degree of geographic variation.

9. The coefficient of variation may be of some value in assessing how well fish populations are adapted to environmental conditions during embryonic stages.

10. The hypothesis is presented that both the time of fixation and the structural relations of the meristic parts are operative in creating differences in variation in meristic characters.

ACKNOWLEDGMENTS

Many individuals and institutions cooperated by furnishing specimens for this investigation. Boyd W. Walker, University of California at Los Angeles; Carl L. Hubbs, Scripps Institution of Oceanography; F. E. J. Fry, University of Toronto; and Garth I. Murphy, California Academy of Sciences, all gave help and advice.

LITERATURE CITED

- BADER, ROBERT S.
1955. Variability and evolutionary rate in the oreodonts. *Evolution*, vol. 9, No. 2, pp. 119-140.
- BAILEY, REEVE M., AND WILLIAM A. GOSLINE.
1955. Variation and systematic significance of vertebral counts in the American fishes of the Percidae. University of Michigan, Ann Harbor, Museum of Zoology, Miscellaneous Publication 93, 44 pp.
- BROWN, JERRAM L.
1958. Geographic variation in southeastern populations of the cyprinodont fish, *Fundulus notti* (Agassiz). *American Midland Naturalist*, vol. 59, No. 2, pp. 477-488.
- CRAWFORD, RONALD W.
1956. A study of the distribution and taxonomy of the percid fish, *Percina nigrofasciata* (Agassiz). Tulane University, New Orleans, Tulane Studies in Zoology, vol. 4, No. 1, 55 pp.
- DIXON, WILFRID J., AND FRANK J. MASSEY, JR.
1951. Introduction to statistical analysis. McGraw-Hill Book Company, Inc., New York, 370 pp.
- FORD, E.
1937. Vertebral variation in teleostean fishes. *Journal of Marine Biological Association of the United Kingdom*, vol. 22, No. 1, 60 pp.
- GABRIEL, MORDECAI L.
1944. Factors affecting the number and form of vertebrae in *Fundulus heteroclitus*. *Journal of Experimental Zoology*, vol. 95, No. 1, pp. 105-147.

- GIBBS, ROBERT H., JR.
 1957a. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. II. Distribution and variation of *Notropis spilopterus*, with the description of a new subspecies. *Lloydia*, vol. 20, No. 3, pp. 186-211.
 1957b. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. III. Variation and subspecies of *Notropis venustus* (Girard). Tulane University, New Orleans, Tulane Studies in Zoology, vol. 5, No. 8, pp. 175-203.
- GORDON, MYRON.
 1957. Physiological genetics of fishes. In the physiology of fishes. Margaret E. Brown (editor), vol. 2. Academic Press, New York, 526 pp.
- GOSLINE, WILLIAM A.
 1947. Some meristic characters in a population of the fish *Poeciliichthys exilis*: their variation and correlation. University of Michigan, Ann Arbor, Museum of Zoology, Occasional Papers, No. 500, 23 pp.
- HUBBS, CARL L.
 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of water during development. *American Naturalist*, vol. 56 (July-August), pp. 360-372.
 1924. Seasonal variation in the number of vertebrae of fishes. *Papers of the Michigan Academy of Science, Arts, and Letters*, vol. 2 (1922), pp. 207-214.
 1925. Racial and seasonal variation in the Pacific herring, California sardine and California anchovy. State of California Fish and Game Commission, Fish Bulletin No. 8, 23 pp.
 1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. *American Naturalist*, vol. 60 (January-February), pp. 57-81.
- HUBBS, CARL L., AND LAURA C. HUBBS.
 1945. Bilateral asymmetry and bilateral variation in fishes. *Papers of the Michigan Academy of Science, Arts, and Letters*, vol. 30, 310 pp.
 1954. Data on the life history, variation, ecology, and relationships of the kelp perch, *Brachyistius frenatus*, an embiotocid fish of the Californias. *California Fish and Game*, vol. 40, No. 2, pp. 183-198.
- HUBBS, CARL L., AND KARL F. LAGLER.
 1949. Fishes of the Great Lakes region. Cranbrook Institute of Science, Bloomfield Hills, Mich., 186 pp.
- JOHNSON, SIGURD.
 1936. On the variation of fishes in relation to environment. Bergens Museums Årbok Naturvidenskapelig Rekke, 4 hefte, 26 pp.
- MATSUBARA, KIYOMATSU.
 1943. Studies on the scorpaenoid fishes of Japan (II). *Transactions of Sigenkagaku Kenkyusyo*, No. 2, pp. 171-486.
- McHUGH, JOHN L.
 1950. Variations and populations in the clupeoid fishes of the North Pacific. Ph.D. Thesis, University of California at Los Angeles, 116 pp.
- MOLANDER, ARVID R., AND MARTHA MOLANDER-SWEDMARK.
 1957. Experimental investigations on variation in plaice (*Pleuronectes platessa* Linne). Reports Lysekil Institute of Marine Research (Biology) No. 7, 44 pp.
- MOTTLEY, C. McC.
 1934. The effect of temperature during development on the number of scales in the Kamloops trout, *Salmo kamloops* Jordan. Contributions to Canadian Biology and Fisheries (A, general, No. 41), vol. 41, No. 8, pp. 255-263.
 1937. The number of vertebrae in trout (*Salmo*). *Journal of Biological Board of Canada*, vol. 3, No. 3, pp. 169-176.
- PRASAD, RAGHU R.
 1958. Racial analysis of *Clevelandia ios* (Jordan and Gilbert) in California waters. *American Midland Naturalist*, vol. 59, No. 2, pp. 465-476.
- QUAST, JAY C.
 1960. The fishes of the family Hexagrammidae: their classification, variation, and osteology. Ph.D. Thesis, University of California at Los Angeles, 380 pp.
- RANDALL, JOHN E.
 1955. A revision of the surgeon fish genus *Ctenochaetus*, family Acanthuridae, with descriptions of five new species. *Zoologica*, vol. 40, part 4, pp. 149-166.
 1956. A revision of the surgeon fish genus *Acanthurus*. *Pacific Science*, vol. 10, No. 2, pp. 159-235.
- RANEY, EDWARD C.
 1957. Subpopulations of the striped bass, *Roccus saxatilis* (Walbaum), in tributaries of Chesapeake Bay. In U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries, John C. Marr (editor), No. 208, pp. 85-107.
- SCHMIDT, P. U.
 1950. Fishes of the Sea of Okhotsk. *Akademiia Nauk, SSSR, Moscow*, 370 pp.
- SEYMOUR, ALLYN.
 1959. Effects of temperature upon the formation of vertebrae and fin rays in young chinook salmon. *Transactions of the American Fisheries Society*, vol. 88, No. 1, pp. 58-69.
- SIMPSON, GEORGE GAYLORD.
 1953. The major features of evolution. Columbia University Press, New York, 434 pp.
- SIMPSON, GEORGE GAYLORD, ANNE ROE, AND RICHARD D. LEWONTIN.
 1960. Quantitative zoology. Harcourt, Brace and Company, Burlingame, New York, 440 pp. [Revised edition.]
- STRASBURG, DONALD W.
 1955. North-south differentiation of blennioid fishes in the central Pacific. *Pacific Science*, vol. 9, No. 3, pp. 297-303.

TÅNING, Å. VEDEL.

1952. Experimental study of meristic characters in fishes. Biological Reviews of the Cambridge Philosophical Society, vol. 27, No. 2, pp. 169-193.

TAYLOR, FREDERICK H. C.

1957. Variations and populations of four species of

Pacific Coast flatfish. Ph.D. Thesis, University of California at Los Angeles, 351 pp.

UNITED STATES NAVY HYDROGRAPHIC OFFICE.

1944. World atlas of sea surface temperatures.

Publication 225, 2d edition.