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Title: THE RELATIONSHIP BETWEEN MORPHOLOGY AND ECOLOGY IN THE SPATANGOID URCHIN Brisaster latifrons

Abstract approved: Redacted for Privacy
Dr. James E. McCauley

The variability exhibited by the common spatangoid B. latifrons has been considered by several authors, but until now, no systematic attempts have been made to link it causally with particular aspects of its habitat.

Up to 12 measurements were made on each of 368 specimens collected off the Oregon coast from depths of 100-840 m. The bathymetric range of the species was divided, for comparative purposes, into four zones: two on the continental shelf, two on the slope. Allometric growth equations of nine structures were calculated for specimens from each of the four zones and were used to correct original measurements for the effects of disproportionate growth. This manipulation permits one to directly compare individuals of different sizes.

It was noticed that specimens from the slope, particularly those from 600 m and deeper, demonstrated consistent morphological differences from shelf specimens. Generally, characteristics of the slope-inhabitants are those originally ascribed to Brisaster (=Schizaster) townsendi; characteristics of the shelf-inhabitants are those ascribed to B. latifrons.

The several environmental factors known to form a gradient with depth (particle size and organic carbon concentration of the sediment, temperature, dissolved oxygen concentration) were each considered as agents responsible for influencing test development. None was wholly rejected as a possible source of variation. Attention was directed toward the oxygen minimum at the deeper end of the urchin's bathymetric range, however, and to the likelihood that hypoxious conditions are inducing differential growth of the plates that bear the respiratory apparatus. Most of the other differences between the two principal variants can be attributed to disproportionate enlargement of the petaloid portion of the ambulacra.

The Relationship Between Morphology and Ecology in the Spatangoid Urchin Brisaster latifrons

by

Charles Lawrence Brownell

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Associate Professor of Oceanography
in charge of major

Redacted for Privacy

Chairman of Department of Oceanography

Redacted for Privacy

Dean of Graduate School

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Several friends cordially volunteered their linguistic talents: Ernesto Ducca, former roommate from Costa Rica, now teaching in Honduras, translated Spanish; Hank Tyler, fellow biological oceanography student, and Coryl Christenson, fellow employee at Corvallis Taxi Service, now at Arizona State University, translated French; and Mrs. Jon Kangas, my sister, translated Russian.

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THE RELATIONSHIP BETWEEN MORPHOLOGY AND ECOLOGY IN THE SPATANGOID URCHIN *Brisaster latifrons*

INTRODUCTION

The U. S. Fish Commission steamer *Albatross*, under the direction of Alexander Agassiz, dredged the first specimens of this common irregular echinoid from the Gulf of Panama in 1888. In a preliminary report on the echinoids collected on the expedition, Agassiz (1898) included descriptions of what he believed to be two distinct species of spatangoids: *Schizaster latifrons* and *S. townsendi*. Clark (1917) transferred both names to the genus *Brisaster*. This nomenclature was perpetuated, though sometimes hesitatingly, until 1967 when McCauley reported his inability to find a single character that justified distinguishing the two at the species level. By recommending suppression of the name *townsendi*, McCauley cleared up confusion that had been accumulating since 1898. A history of that confusion was given in the introduction to his paper and need be mentioned only briefly here.

Problems started when Agassiz (1898) labeled photographs of a specimen he had identified as *S. townsendi* with the name *S. latifrons*. The mistake was corrected in the final Albatross report (Agassiz, 1904) but somehow reappeared intact in a 1937 publication by H. L. Clark. Errors in plate labeling were not the only

source of disorder; contradictions appeared in published texts as well. The width of the posterior petals, found to be an important character in this study, supplies the example:

Agassiz (1898, p. 82) wrote of townsendi: "It is marked by. . . the great width of all the lateral ambulacra." His photograph (mislabeled) confirms his statement (Pl. XI, Figure 2). He made no claims as to the value of posterior petal width in separating latifrons from townsendi. Nevertheless, the character was adopted by later authors and has created some discord. Clark (1917, p. 179) included Brisaster latifrons among those species with "petals smaller and narrower" than B. townsendi (note: Clark referred former Schizaster species with three genital pores to the genus Brisaster Gray). Mortensen (1951, p. 290) contradicted Clark when he wrote of B. latifrons: "... the posterior petals are broader than those of townsendi; . ." Mortensen (1951, p. 288) summarized his concept of B. townsendi's posterior petals by stating: "They are relatively narrow."

I suspect that the misunderstanding about posterior petal width originated from ambiguities in Agassiz's description and figures of latifrons. The figures he published (1904, Pl. 102, Figures 1-4) were of an immature specimen, only 17 mm long, and decidedly morphologically neanic. Clark never published a photograph of latifrons . . . the ones he labeled as such (1937, Pl. XXIV, Figures

7, 8) were none other than the ones Agassiz mislabeled in 1898 but corrected in 1904 . . . and was probably unsure as to the characters Agassiz originally intended that name to designate. Mortensen (1951, Pl. XXIII, Figures 2, 3, 9) supplied the only published photographs of correctly-labeled B. latifrons in existence (excluding Koehler's monstrosities: 1924, Pl. III, Figures 5, 6, 10, 11, 15). Since the specimen he photographed bore wide posterior petals, it is only natural that he favored a corresponding text description, even at the risk of contradicting earlier statements by Agassiz and Clark.

It is now clear that all these descriptions, figures, and photographs are of a single species of animal: Brisaster latifrons. Their diversity demands study.

The first step in this project was to accurately quantify the variation that exists among populations off Oregon; the second, to determine whether the variation is non-random; and the third, to correlate it, if possible, with known features of the submarine environment.

MATERIALS AND METHODS

Collecting and Handling

The present study is based on specimens of B. latifrons collected from 1960 to 1969 by Oregon State University students and staff. The animals were taken by otter trawl, Smith-McIntyre grab, beam trawl, and anchor dredge from OSU research vessels Acona, Yaquina, and Cayuse.

Since B. latifrons is found in abundance off the Oregon coast, no attempt was made, particularly in large catches, to preserve all the specimens taken. Most were simply counted and thrown back. Those that were kept are here assumed to be a representative sample of the population, though selection of exceptionally small or large specimens may bias the collection. McCauley (1967), speaking of Oregon specimens, noted that the heart-urchins taken in any one sample tended to be of a similar size. This phenomenon would seem to lessen the selection bias mentioned above: the sorter is not given much of an opportunity to make a choice. Unbroken individuals are definitely selected over broken ones and this may partially explain the paucity of the more fragile, immature specimens in the collection.

Aboard ship, the urchins were preserved in 10% buffered formalin. It was later replaced with 70% isopropanol in Corvallis.

Each whole specimen was rinsed of mud and other debris and weighed. Specimens in very good condition were weighed and measured and set aside for study of their spines, pedicellariae, and tube feet. The spines of the others were removed with a stiff-bristled test-tube brush under running water. Their tests were then opened along the ambitus with a fine-toothed jeweler's-saw blade attached to a 60-cycle electric vibrator. A routine examination was made for parasites and any irregularities in anatomy. Gonads and gut were then removed and preserved in 70% isopropanol. Both halves of the test were rinsed, labeled, and dried.

Hawkins (1913) and Chesher (1963) described methods of making the sutures of the echinoid test more visible. Another method, very simple and quite satisfactory, was employed here. After the test halves dried completely, glycerine, stained red with ordinary stamp-pad ink, was brushed onto one surface. Two or three minutes later, enough acetone was poured onto the test to saturate it. The test was then allowed to dry. The sutures, best observed on the inside of the test, appeared as deep red lines.

Bathymetric Grouping of Stations

It was noticed early in the study that the morphology of specimens of certain depths differed consistently from specimens of other depths. In order to compare this variation, some guidelines had to be

devised to define bathymetric limits for grouping stations. Ideally, each station should be treated independently and fitted with its own allometric lines of growth. This would require large samples from each station, however, which, with two or three exceptions, were not available.

The 368 specimens were divided among four arbitrary bathymetric zones: 100-155 m, 200-245 m, 400-600 m, and 800-840 m. Depths not included by these four zones were not represented by collections. The distribution of specimens among the four depth zones is reported in Table 1. A photograph of four dried tests, one from each of the zones, is included as Figure 1.

Table 1. Summary of sample sizes

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
No. specimens examined TOTAL 368	204	61	64	39
No. specimens opened TOTAL 216	84	50	45	37
No. specimens used in biometrical analysis TOTAL 117	43	31	19	24
No. stations represented TOTAL 39	9	13	5	12

The ranges were dictated more by collecting patterns established by OSU benthic cruises than by choice. Nevertheless, they are somewhat relevant to the biological and physical realities of the

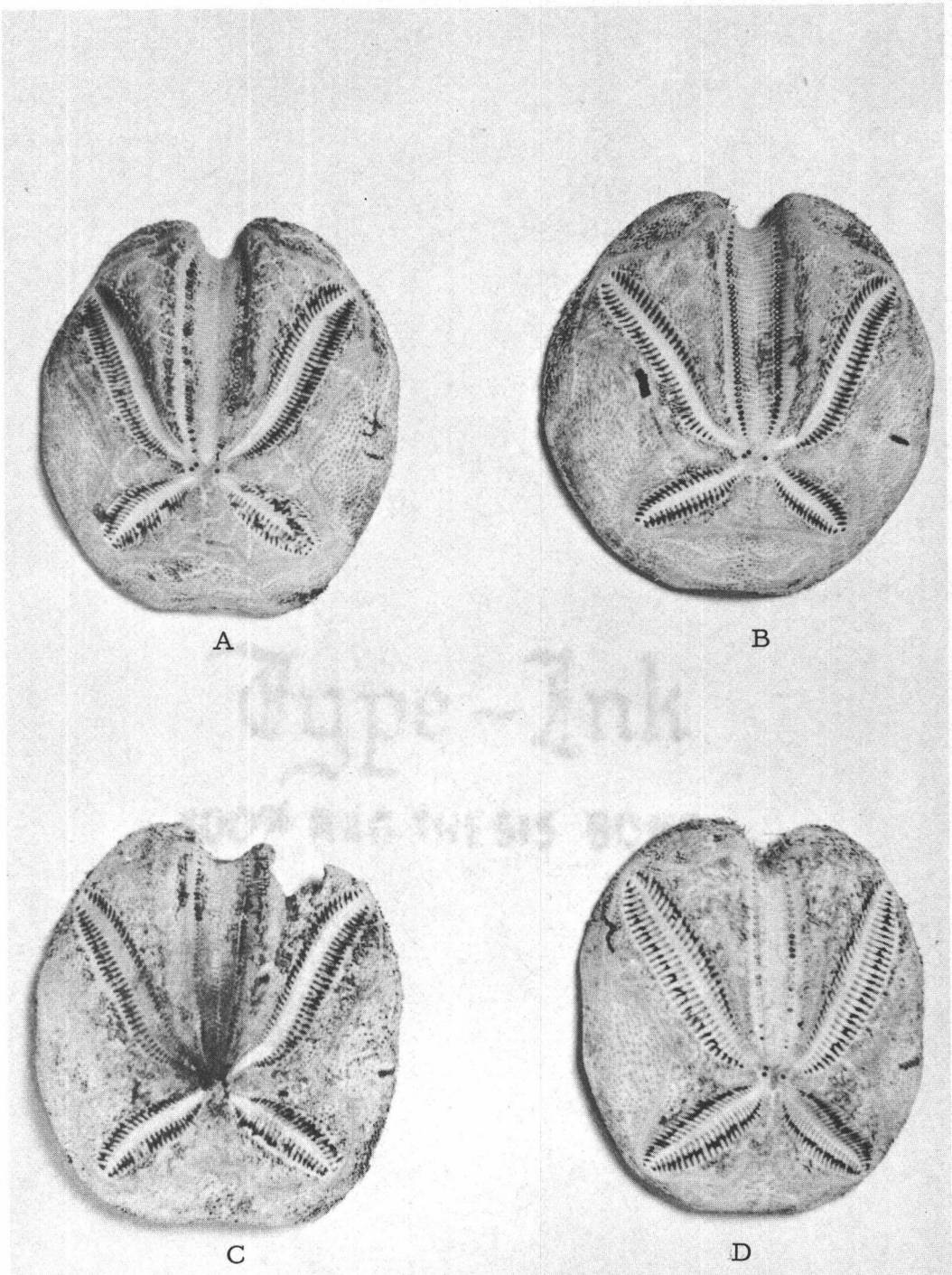

Figure 1. Photograph of four specimens, one from each of the depth zones. Natural size. A. 150 m, B. 200 m, C. 512 m, D. 800 m.

area. The populations within any single zone are, as a rule, morphologically similar. The shallower two depth zones lie primarily on the continental shelf; the deeper two, on the continental slope. (All the stations from depths of 245 m and less are hereafter referred to as shelf stations, although strictly speaking, the shelf extends only to depths of about 180 to 200 m.)

Measurements

While opening the urchins in the above manner, certain reappearing variations in test morphology were noted. Some of the variations were strictly qualitative. Others lended themselves quite readily to measurement. Each measurement, denoted by a small Latin letter by which it will be addressed throughout this paper, is shown in Figure 2. Definitions of technical terms may be found in the glossary published by Durham & Wagner (1966). Plating is according to Lovén (1874).

Length (a): This measurement was obtained by placing the specimen on a piece of millimeter-ruled graph paper and reading the projection to the nearest 0.1 mm.

Width (b): This was measured in the same manner as a.

Height (c): This was measured to the nearest 0.1 mm with vernier calipers.

Length of petal I (d): This was defined as the distance from the

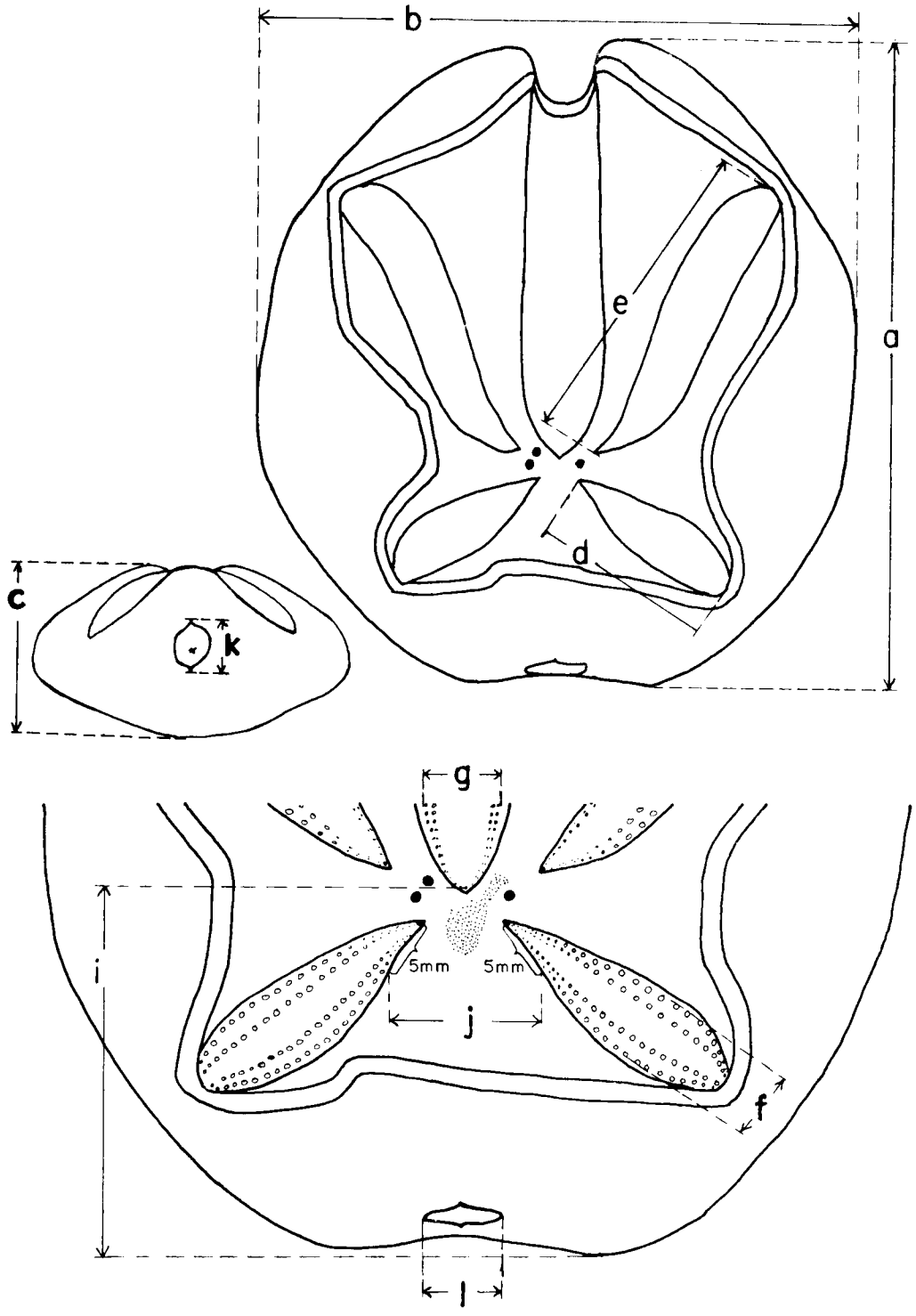

Figure 2. Diagrammatic representation of Brisaster latifrons showing the measurements.

center of the terminal pore to the apical margin of the peripetalous fasciole where it crosses the ambulacrum. It was measured with vernier calipers.

Length of petal II (e): This was defined and measured in the same manner as d.

Width of petal I (f): This was defined as the distance from the outer edge of one abradial pore to the outer edge of the opposing abradial pore measured at the petal's widest point. It was measured with the 6X ocular micrometer of a binocular dissecting microscope to the nearest 1/2-unit (0.08 mm.).

Width of the anterior ambulacrum (g): This was defined and measured in the same manner as f.

Distance from the anterior margin to the level of maximum width (h): This was measured by aligning the urchin's antero-posterior axis to the y-axis of a piece of millimeter-ruled graph paper and adjusting it until the x-axis intersected the level of maximum width. The distance between the anterior margin and the x-axis was then read to the nearest 0.1 mm off the graph paper. This measurement was later rejected (see below).

Distance from the posterior margin to the apical system (i): This was defined as the distance between the terminal pore of ambulacrum III and the posterior margin. It was measured by lining up, by eye, the terminal pore of ambulacrum III with the

x-axis of a piece of millimeter-ruled graph paper and reading the distance between the x-axis and the posterior margin to the nearest 0.1 mm off the graph paper.

Separation of the posterior petals (j): This is a rather arbitrary measurement designed to quantify the divergence of the posterior margins of petals V and I. The ocular micrometer of the 6X binocular microscope was used to first find the point on the posterior margin of each petal that was exactly five millimeters from its corresponding terminal pore. The distance between these two points (j) was then measured with the same microscope to the nearest 1/2-unit (0.08 mm).

Height of the periproct (k): This was measured with the binocular microscope to the nearest 1/2-unit (0.08 mm).

Width of the periproct (l): This was measured in the same manner as k.

As many of these 12 measurements as possible were made on each test, depending on its condition. Because the level of maximum width has been given taxonomic importance in differentiating B. latifrons and B. townsendi (Clark, 1917; Djakonov, 1949; Baranova, 1955, 1957), it was disconcerting to discover the reproducibility of measurement h to be unsatisfactory. The measurement was rejected for two reasons: (1) There was a tendency for some tests to have straight and parallel margins for a distance. In such cases,

the alignment of the test to the graph paper used in the measurement became very critical, and too often irreproducible. (2) Many tests were slightly asymmetrical, such that the right side would yield one "level of maximum width" and the left side another. Rather than design artificial rules to govern such cases, the parameter was abandoned entirely.

Several variates in addition to the above were considered, namely, the course of the peripetalous fasciole (Figure 2), the flexure of the antero-lateral petals, the size of the respiratory tube feet, the development of the gonads, the fullness of the gut, and several aspects of the anterior ambulacrum.

Several respiratory podia (those of the lateral petals) were removed from individuals from ten stations. The base and height of each podium was measured to the nearest 0.05 mm with the ocular micrometer of a binocular dissecting microscope. Since a respiratory tube foot is very nearly triangular, the area of its two sides can be approximated by doubling the familiar expression for the area of a triangle:

$$\text{Minimum surface area} = 2(1/2 \text{ base} \times \text{height}). \qquad (1)$$

Because this approach completely neglects the numerous flaps and papillae born by the podia, it is here termed the "minimum surface area." It is used for comparative purposes as an index of tube foot

size, only.

The three gonads were removed from each of 216 specimens and placed in 70% isopropanol. Wet weights were made following a 60-second blotting period on a folded dry paper towel. Gonad index was calculated so:

$$\text{Gonad Index} = \frac{\text{gonad wet weight}}{\text{total wet weight}} \times 100. \qquad (2)$$

Total wet weights were made following a 5-minute blotting period. They were unobtainable in those instances where coelomic fluid had leaked from breaks in the test. In such cases, total wet weights were estimated by multiplying the product of the dimensions length, width, and height, in centimeters, by a suitable factor (0.53 gm/cm^3). The factor is simply the slope of the regression of length x width x height on weight for all unbroken specimens.

Gut fullness was measured in a small number of specimens by taking alcoholic wet weights of intestinal contents.

No attempt was made to quantify the length and depth of the anterior ambulacrum. The number of plates comprising that structure, however, was determined for 63 specimens.

Ratios

Published metrical data on echinoids are usually in the form of ratios--of one structure to another, or of one structure to the

whole. Doderlein (1906) reported the size of echinoid structures as a percentage of the length. Clark (1917) related the width of a petal to its length, or the height of the test to its total length, etc. By way of conformity, the same procedure was followed here.

Six of the nine ratios listed below have the letter s in the denominator. Instead of basing proportions on total length (suggested by Chesher, 1968), it was decided to follow Kermack's (1954) suggestion to calculate an "overall size" for each specimen, that is, the geometric mean of its dimensions: "size" (s) = $\sqrt[3]{\text{length} \times \text{width} \times \text{height}}$. The value s, hereafter simply termed the size of the specimen, provides a more comprehensive measure of its magnitude. The specimens off Oregon of size $\geq$ 30 are proportioned such that s is between 73% and 85% (mean = 78%) of the length. A specimen of size 30 would typically have a length of between 37 and 40 mm.

The measurements made on each test were combined in various straightforward ways to yield the following nine ratios:

c/a ratio of height to length

d/s relative length of petal I

e/s relative length of petal II

f/s relative width of petal I

g/s relative width of ambulacrum III

i/a level of the apical system

j/s relative separation of the posterior petals

$\sqrt{kl}/s$ relative size of the periproct

e/d ratio of petal II to petal I

It will be noted that three of the nine ratios, namely, c/a, i/a, and e/d, differ from the others in the nature of their denominator. These particular ratios have been given taxonomic importance (Clark, 1917; Mortensen, 1951) and are therefore left in a form which permits direct comparison with data of earlier investigators.

All computations were performed on an Olivetti Underwood Programma 101 desk computer at the Dept. of Oceanography, OSU. Programs for statistical analysis were taken from an Olivetti Underwood manual prepared by Williams (1968).

Calculation of Corrected Ratios

Expressing sizes of specific structures as ratios eliminates, to a first approximation, errors resulting from attempting to compare individuals of different sizes. Total reliance on ratios, however, requires the assumption that the ratios remain constant throughout the animal's ontogeny. Mortensen's (1951, p. 291) comment on Brisaster latifrons (and B. townsendi) makes the validity of this assumption highly questionable: ". . . but it would have no sense that all the large specimens should be one species, all the small specimens from the same locality another species." The present study indicates that uncorrected ratios may be used only for

gross comparisons, and even this breaks down if very immature specimens are taken into consideration.

Nine variates are expressed in ratio form; the denominator of the ratio is the "standard" in each case. In order to compare the same structure from different sized specimens, it is desirable to first determine whether that structure grows at a rate directly proportional to the rate of the standard. If so, growth is isometric, and the ratios can be compared directly. If not, growth is allometric and the ratios must first be corrected for the effects of the disproportionate growth before specimens of different sizes can be compared. Following is a sample calculation which demonstrates how the corrections were made in this study. An actual specimen, taken at 150 m. off Oregon, serves as the example:

length ($\underline{a}$) = 59.0 mm.

width ($\underline{b}$) = 56.5 mm.

height ($\underline{c}$) = 31.0 mm.

size ($\sqrt[3]{\underline{abc}}$) = 46.9

length of petal I ($\underline{d}$) = 19.0 mm.

relative length of petal I ($\underline{d}/\underline{s}$) = 0.405

A corrected value for the relative length of petal I ($\underline{d}/\underline{s}$) will be calculated for this specimen. The first step involves the calculation of the slope of the line which best approximates the rate of change of the ratio ($\underline{d}/\underline{s}$) with respect to test size ($\underline{s}$) for all specimens of size

$\geq$ 30 at that depth range. Specimens of size less than 30 were not considered in the calculation of any of these lines.

The approximation most commonly used for data of this type is least squares. Some investigators (Kermack, 1954; Raup, 1956) have substituted the reduced major axes of Kermack and Haldane (1950) for least squares. Cock (1966, p. 145) discussed the advantages of these and other methods and concluded: "The simple regression estimate will usually be adequate for comparative purposes. . ." In this study it was assumed that the simplicity of the least squares approach would outweigh the additional accuracy that reduced major axes might introduce.

A line, then, was calculated by method of least squares: The regression of $\underline{d}/\underline{s}$ on $\underline{s}$. It has the formula

$$d/s = ms + b, \tag{3}$$

where $\underline{m}$ is the slope of the line and $\underline{b}$, the $\underline{y}$-intercept. (The letter $\underline{b}$ here is not to be confused with the test measurement denoted by the same letter.) In the example the slope was calculated to be 0.0024; the $\underline{y}$-intercept, 0.2925 (Table 3).

The slope ($\underline{m}$) from equation (3) was incorporated into the following equation used to correct the original ratio for allometric growth:

$$R_c = R_o + m(\bar{s} - s_i), \tag{4}$$

where $\underline{R}_c$ is the corrected value for the ratio; $\underline{R}_o$ is the original value for the ratio; $\underline{m}$ is the slope of the regression line fitted to the plot of $\underline{R}_o$ versus $\underline{s}$ for all specimens in that depth zone; $\overline{\underline{s}}$ is the mean size of all specimens of size ≥ 30 from all four depth zones; and $\underline{s}_i$ is the size of the specimen whose $\underline{R}_o$ is being corrected. Substituting the numerical values from our example into equation (4) yields

$$R_c = 0.405 + 0.0024\ (42.2 - 46.9) \tag{5}$$

$$R_c = 0.405 - 0.011 \tag{6}$$

$$R_c = 0.394 \tag{7}$$

This corrected ratio approximates the $\underline{d}/\underline{s}$ value our example would have if it were of average size (42.2). The mean size of all specimens included in the biometrical analysis (the $\overline{\underline{s}}$ in equation 4), although arbitrary, was chosen to keep extrapolation error to a minimum, and to provide corrected values which were reasonably close to the original ratios.

Corrected ratios for all specimens of size 30 or greater were plotted against depth and the graphs are presented in the results section. Growth lines for six of the structures measured ($\underline{d}$, $\underline{e}$, $\underline{f}$, $\underline{g}$, $\underline{j}$, $\sqrt{\underline{kl}}$) are also presented in the results. The lines were obtained by multiplying equation (3) through by $\underline{s}$, and graphing the resultant quadratic expression:

$$d = ms^2 + bs. \tag{8}$$

The graph of $\underline{d}$ versus $\underline{s}$ in this equation yields a line that approximates the rate of change of posterior petal length ($\underline{d}$) with respect to overall test size ($\underline{s}$).

In applying equation (3), one assumes that the rate of change of the original ratio relative to size remains constant once the individual has reached a size of 30. The assumption permits one to estimate the change in the ratio during growth with a straight line. In applying equation (4), one assumes that the rate of change of the original ratio relative to size is equal in all individuals from any single depth zone. This assumption permits one to extrapolate the growth curve of any individual to a desired reference point (in this case, the population mean, $\overline{\underline{s}}$); and subsequently, to permit comparison of different sized individuals.

A proper test of these assumptions would require that a series of measurements be made, at intervals in time, on the same group of growing urchins. Data collected in this manner are termed "longitudinal." The data collected in this study are of the "mixed cross-sectional" variety (Cock, 1966), and suffer from several obvious disadvantages. Uppermost is the fact that because measurements are made only once on each specimen, the element of time is lacking and attempts at deriving growth rates are severely limited. The mere fact that I have relied on the two assumptions outlined above speaks for my own faith in their validity. If they are

shown by subsequent investigators to be erroneous, the conclusions drawn in this paper would remain virtually unaffected. The more outstanding morphological trends that B. latifrons exhibits off Oregon are quite apparent, with or without the aid of correctional calculations. Lesser trends, however, would go unnoticed were it not for certain mathematical refinements (or manipulations, as the case may be) along the way.

RESULTS

Most of the results have been organized into graphical form. For six of the nine ratios, two graphs are included: (1) relative growth lines for the structure at each depth zone (taken from equation 8); and (2) the plot of the corrected ratio of each specimen versus the depth at which it was captured (taken from equation 4). For three of the ratios (c/a, i/a, and e/d) only the latter graph is included.

Observations on the other variates are presented in three additional figures and one table.

Results of the Biometrical Analysis

The Ratio of Height to Length: c/a (Figure 3, Table 2)

The graph of this ratio (corrected for allometry) plotted against depth (Figure 3) suggests that there was nearly as much variation within collections from a single depth as there was between depths. A t-test revealed, however, that differences between the 200-245 m depth zone and each of the other three zones were significant at the 1% level. The means of both corrected and uncorrected c/a for the 200-245 m specimens were lowest; that for the 800-840 m specimens, highest. The 100-155 m and 400-600 m depth zones fell in between. Data for this ratio are summarized in Table 2.

The amount of variation within the 400-600 m depth zone, as

indicated by its higher standard deviation (Table 2), exceeded that within any of the other zones. Likewise, calculated rate of change of the ratio c/a with respect to overall size (as indicated by the values labeled "slope of the regression line of uncorrected c/a on s" in Table 2), was maximal among specimens from the 400-600 m depth zone. Both of these observations can be made for most of the other ratios as well. Zones 100-155 m and 800-840 m exhibited virtually no change in relative height with increased test size (growth was isometric) through the growth period studied. This information is derived from the fact that the slopes of the regression lines for those depth zones approach zero (Table 2).

Table 2. Ratio of height to length

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
Number of specimens	43	31	19	24
Mean of uncorrected c/a	0.5187	0.4814	0.5234	0.5350
Mean of corrected c/a	0.5187	0.4872	0.5159	0.5349
Slope of the regression of uncorrected c/a on s	-0.0000	-0.0011	-0.0014	-0.0001
y-intercept of the regression of uncorrected c/a on s	0.5200	0.5339	0.5749	0.5398
Standard deviation of uncorrected c/a	0.0251	0.0258	0.0336	0.0258
Correlation coefficient	-0.0082	-0.2335	-0.2444	-0.0178

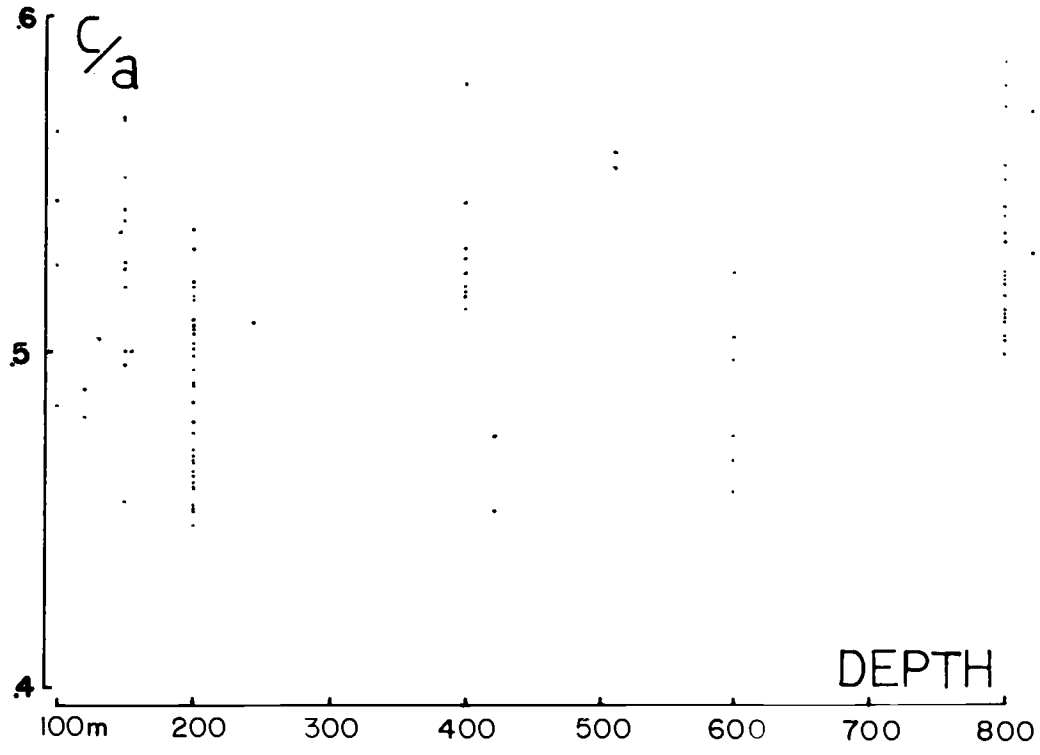

Figure 3. Graph of corrected ratio of test height to test length ($\underline{c}/\underline{a}$) for each specimen plotted against the depth at which it was taken.

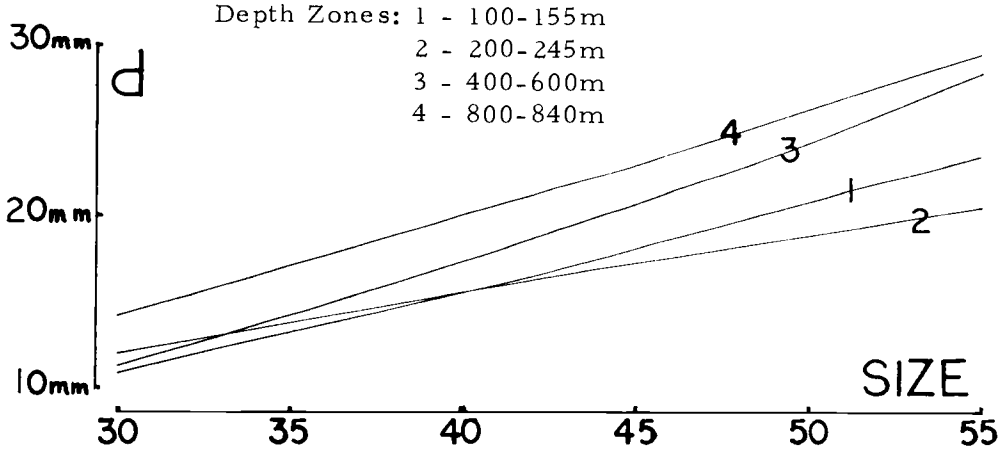

Figure 4. Growth lines of the length of petal I ($\underline{d}$) with respect to size ($\sqrt[3]{\underline{abc}}$) for each of the four depth zones. Estimated by method of least squares.

The Relative Length of Petal I: d/s (Figures 4, 5; Table 3)

Specimens from 800-840 m had relatively longer posterior petals than specimens from the two shallow depth zones; specimens taken at intermediate depths fell within the extremes set by the others (Figure 5). The differences between the two shallower depth zones were not statistically significant ($P > .05$); differences between the 200-245 m depth zone and the 800-840 m depth zone were significant at the 1% level.

The graph of growth lines (Figure 4) shows how the length of petal I increases as the animal grows. Posterior petals of specimens from 800-840 m were longer throughout the size range ($30 \leq s \leq 55$) graphed. In all zones except 200-245 m, there was a slight upward curvature of the growth lines, indicating that the relative length of petal I increased with increasing test size.

Table 3. The relative length of petal I

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
Number of specimens	43	31	19	24
Mean of uncorrected d/s	0.3944	0.3831	0.4170	0.5038
Mean of corrected d/s	0.3957	0.3894	0.4455	0.5073
Slope of the regression of uncorrected d/s on s	0.0024	-0.0012	0.0053	0.0023
y-intercept of the regression of uncorrected d/s on s	0.2925	0.4400	0.2210	0.4104
Standard deviation of uncorrected d/s	0.0392	0.0273	0.0394	0.0284
Correlation coefficient	0.3966	-0.2384	0.7931	0.3118

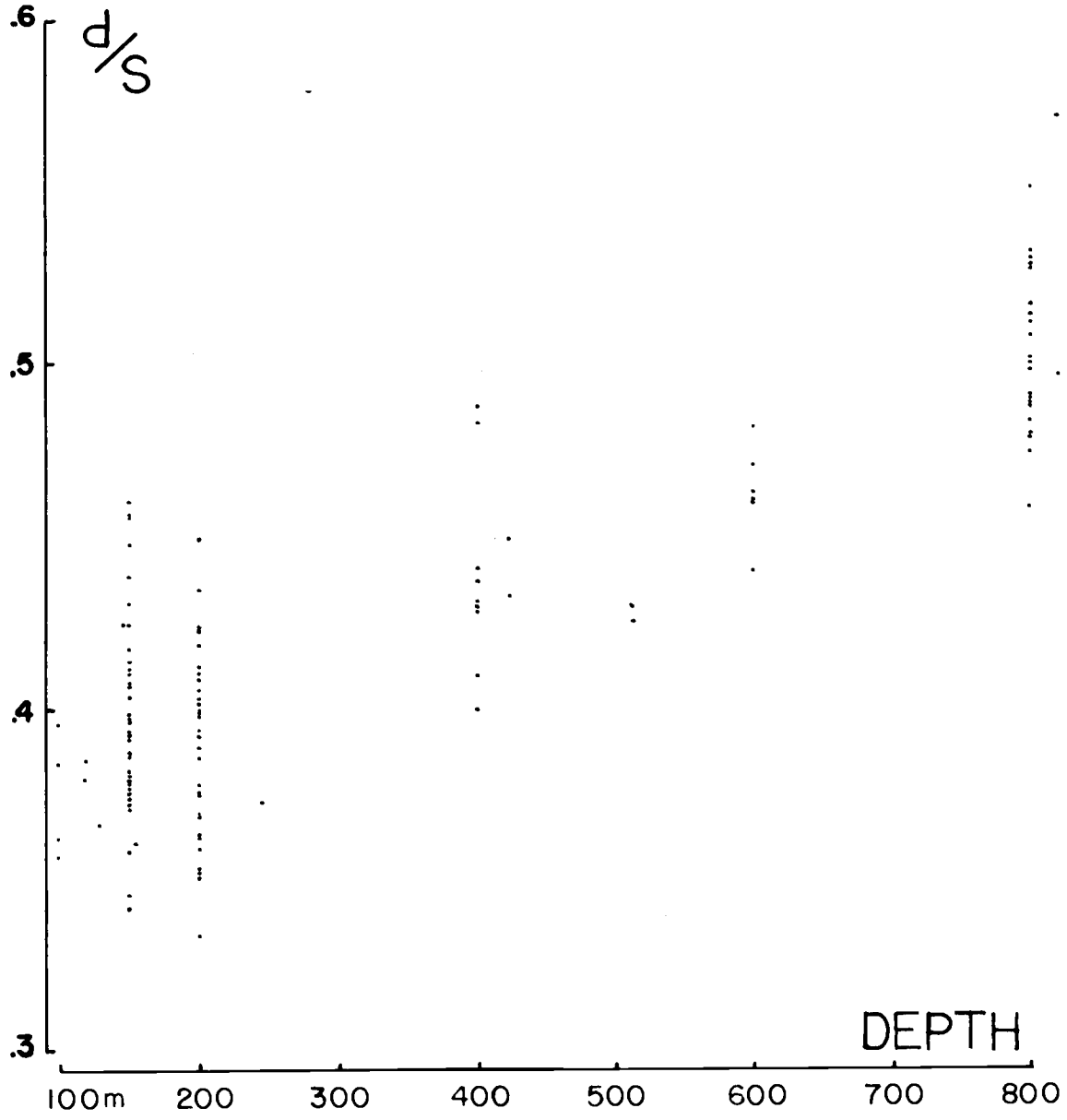

Figure 5. Graph of corrected relative length of petal I (d/s) for each specimen plotted against the depth at which it was taken.

The Relative Length of Petal II: e/s (Figures 6, 7; Table 4)

The ratio of e to s, corrected for allometry, weakly separated the two shelf zones from the two slope zones (Figure 6). Differences between the 100-155 m zone and the 200-245 m zone were not statistically significant; differences between the 200-245 m zone and each of the two slope zones were significant at the 1% level.

The direction of concavity of the growth lines resembled that of the previous ratio in that only the 200-245 m zone exhibited a decrease in relative petal length with increase in overall size (Figure 7).

Table 4. The relative length of petal II

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
Number of specimens	43	31	19	24
Mean of uncorrected e/s	0.7321	0.7268	0.7045	0.7568
Mean of corrected e/s	0.7337	0.7357	0.7614	0.7583
Slope of the regression of uncorrected e/s on s	0.0029	-0.0017	0.0039	0.0010
y-intercept of the regression of uncorrected e/s on s	0.6069	0.8090	0.5979	0.7168
Standard deviation of uncorrected e/s	0.0324	0.0304	0.0420	0.0341
Correlation coefficient	0.5770	-0.3096	0.5404	0.1112

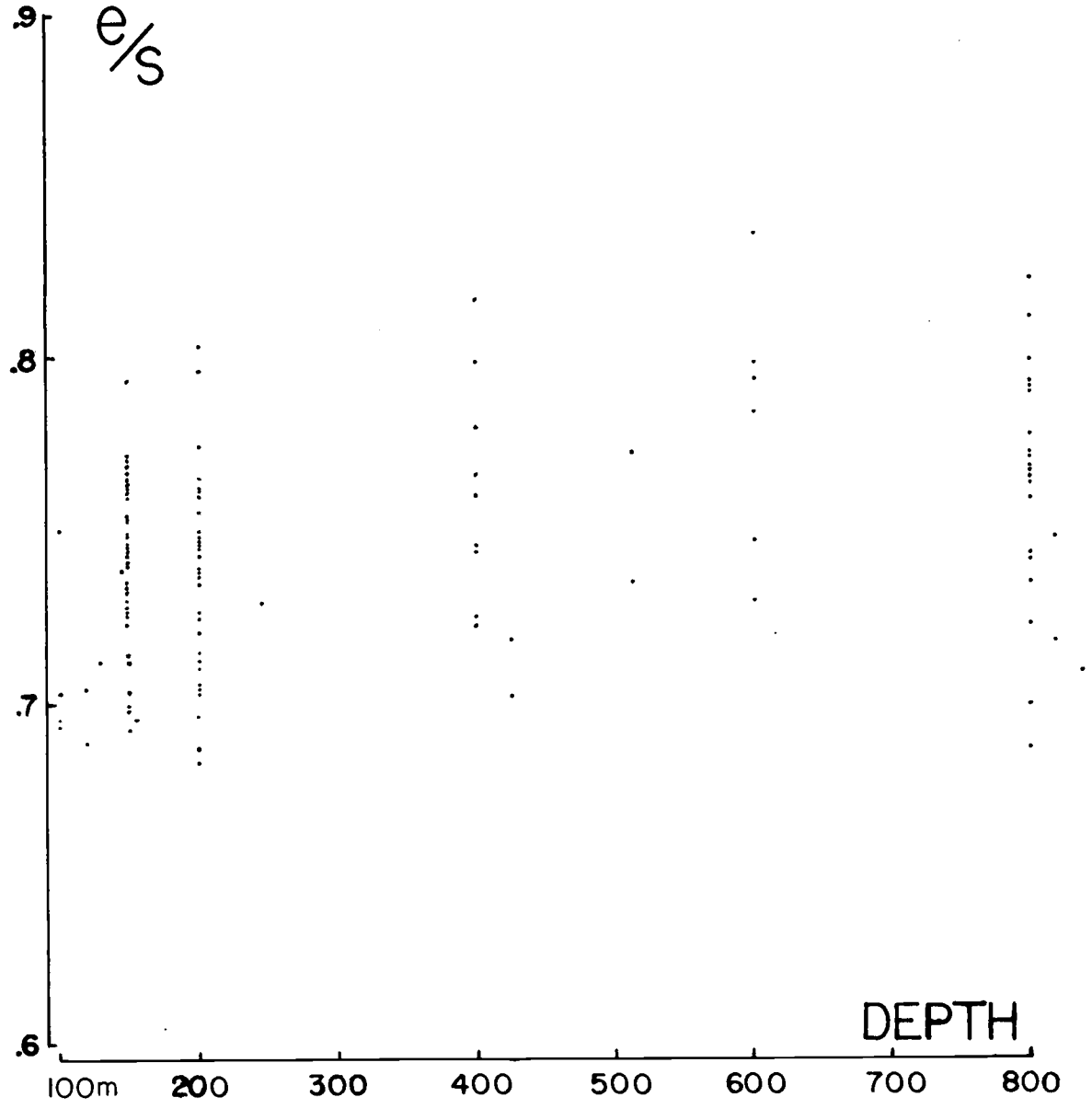

Figure 6. Graph of corrected relative length of petal II (e/s) for each specimen plotted against the depth at which it was taken.

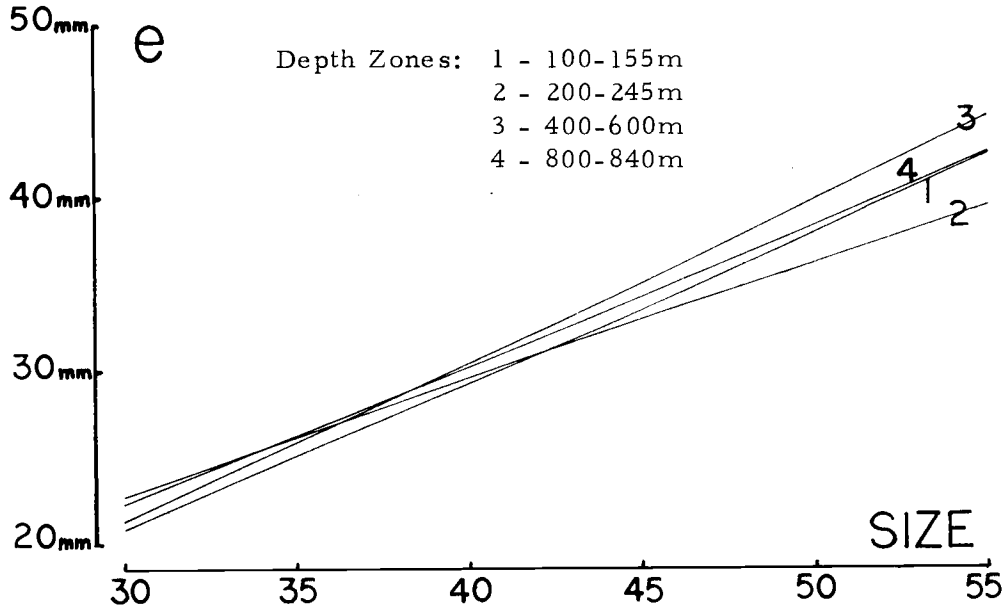

Figure 7. Growth lines of the length of petal II (e) with respect to size ($\sqrt[3]{abc}$) for each of the four depth zones. Estimated by method of least squares.

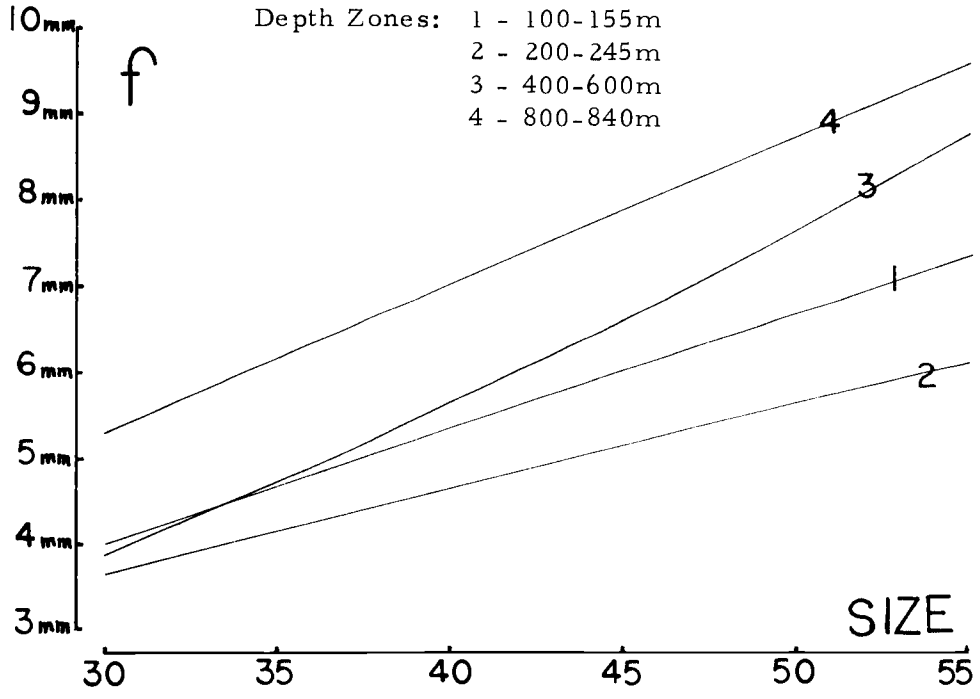

Figure 8. Growth lines of the width of petal I (f) with respect to size ($\sqrt[3]{abc}$ for each of the four depth zones. Estimated by method of least squares.

The Relative Width of Petal I: f/s (Figures 8, 9; Table 5)

The width of petal I clearly separated the 200-245 m specimens from the 800-840 m ones (Figure 8). The other two depth zones had animals distributed between the former with respect to this character. Differences between the 200-245 m depth zone and each of the other three zones were significant at the 1% level.

Growth lines for all but the 400-600 m depth zone were, for all practical purposes, straight, and very little allometric correction became necessary for those specimens (Figure 9). The concavity of the 400-600 m growthline resulted, in part at least, from the dissimilarity of populations from that depth zone combined with a disparity in their average sizes.

Table 5. Relative width of petal I

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
Number of specimens	43	31	19	24
Mean of uncorrected f/s	0.1333	0.1137	0.1361	0.1750
Mean of corrected f/s	0.1333	0.1158	0.1425	0.1748
Slope of the regression of uncorrected f/s on s	0.0000	-0.0004	0.0012	-0.0001
y-intercept of the regression of uncorrected f/s on s	0.1327	0.1331	0.0905	0.1783
Standard deviation of uncorrected f/s	0.0170	0.0161	0.0183	0.0097
Correlation coefficient	0.0052	-0.0139	0.3956	-0.0327

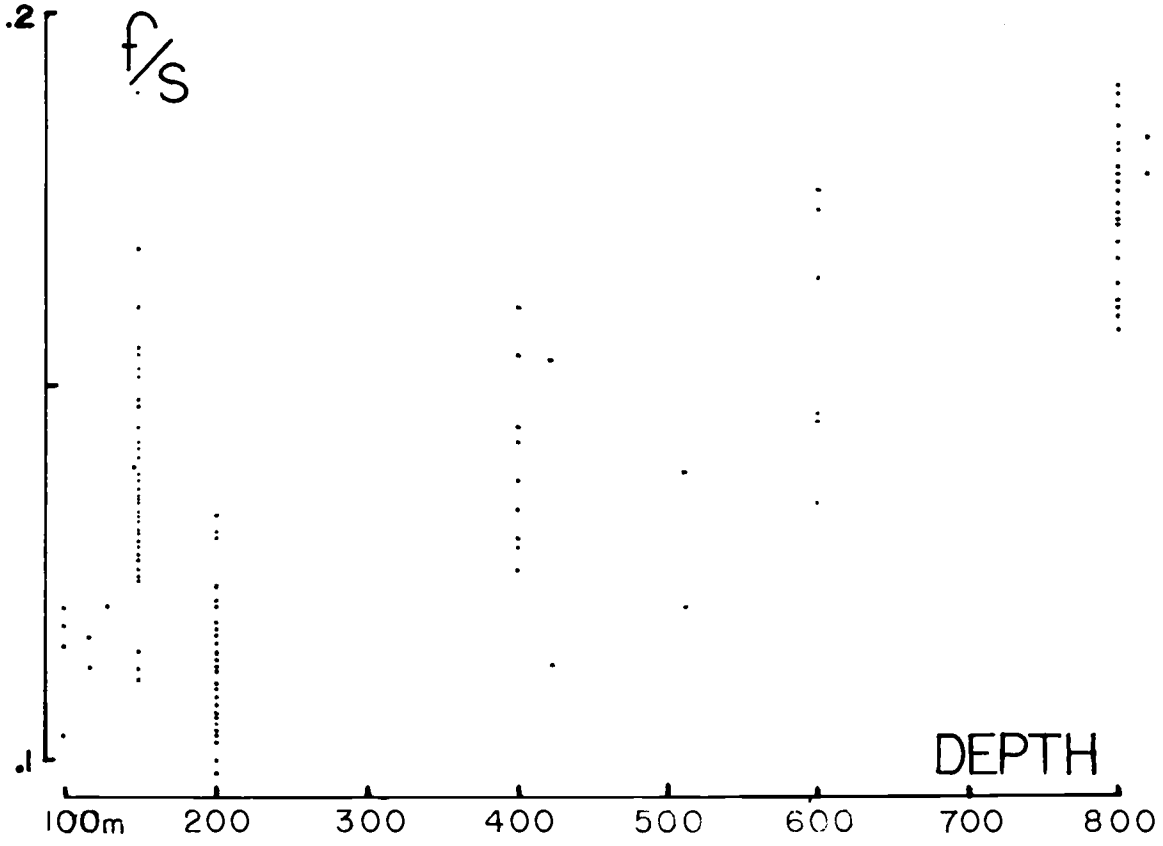

Figure 9. Graph of corrected relative width of petal I (f/s) for each specimen plotted against the depth at which it was taken.

The Relative Width of Ambulacrum III: g/s (Figures 10, 11; Table 6)

There was a tendency for the relative width of ambulacrum III to decrease as depth increases. Variate g/s is one of the three of nine ratios where depth zones 200-245 and 800-840 m were not at opposite ends of a continuum: the mean relative width of the anterior ambulacrum was greater in specimens from the 100-155 m zone than any of the other three (Figure 11). Differences (after correction) between the two shallowest zones were significant at the 5% level

only; differences between the 200-245 m and 800-840 m zones were significant at the 1% level.

The downward turning of the growth lines through the range $30 < \underline{s} < 55$ indicates that the relative width of the anterior ambulacrum decreases with increase in specimen size in all four depth zones (Figure 10). The tendency was greatest in the two slope zones (400-600 m and 800-840 m).

Table 6. Relative width of ambulacrum III

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
Number of specimens	43	31	19	24
Mean of uncorrected g/s	0.1853	0.1710	0.1807	0.1481
Mean of corrected g/s	0.1849	0.1773	0.1641	0.1458
Slope of the regression of uncorrected g/s on s	-0.0008	-0.0012	-0.0031	-0.0015
y-intercept of the regression of uncorrected g/s on s	0.2207	0.2300	0.2955	0.2075
Standard deviation of uncorrected g/s	0.0156	0.0145	0.0232	0.0141
Correlation coefficient	-0.3458	-0.4643	-0.7865	-0.3998

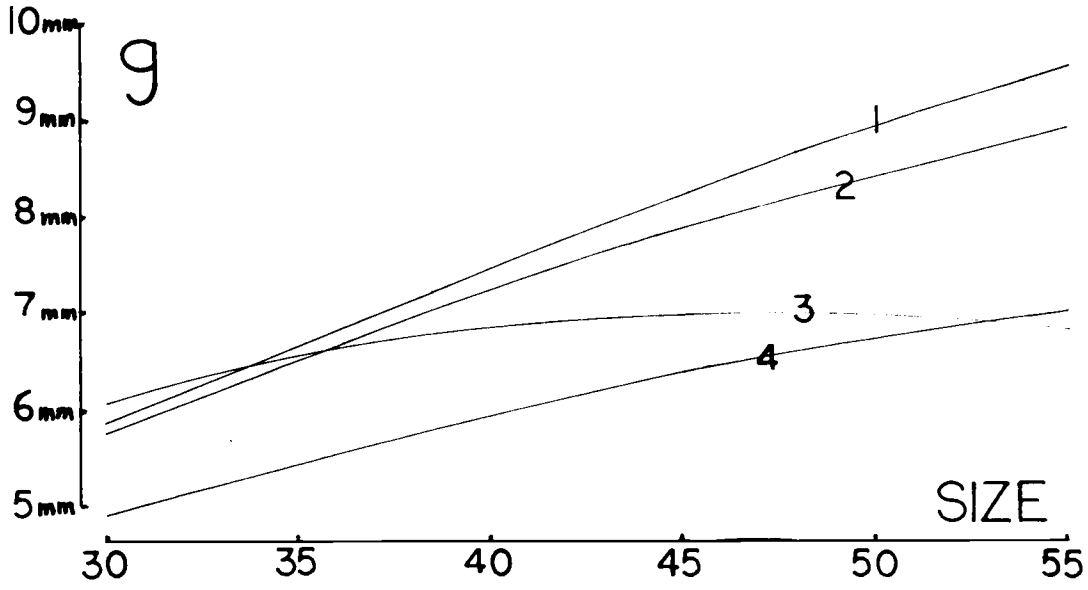

Figure 10. Growth lines of the width of ambulacrum III (g) with respect to size ($\sqrt[3]{abc}$) for each of the four depth zones. Estimated by method of least squares.

The Level of the Apical System: i/a (Figure 12, Table 7)

A high i/a value denotes a more centralized apical system, a low i/a value denotes a more eccentric apical system. The two shallower depth zones yielded specimens of slightly lower i/a values than the deeper two (Figure 12). Differences between the two shallow depth zones were not statistically significant; differences between the 200-245 m depth zone and each of the two deeper zones were significant at the 1% level.

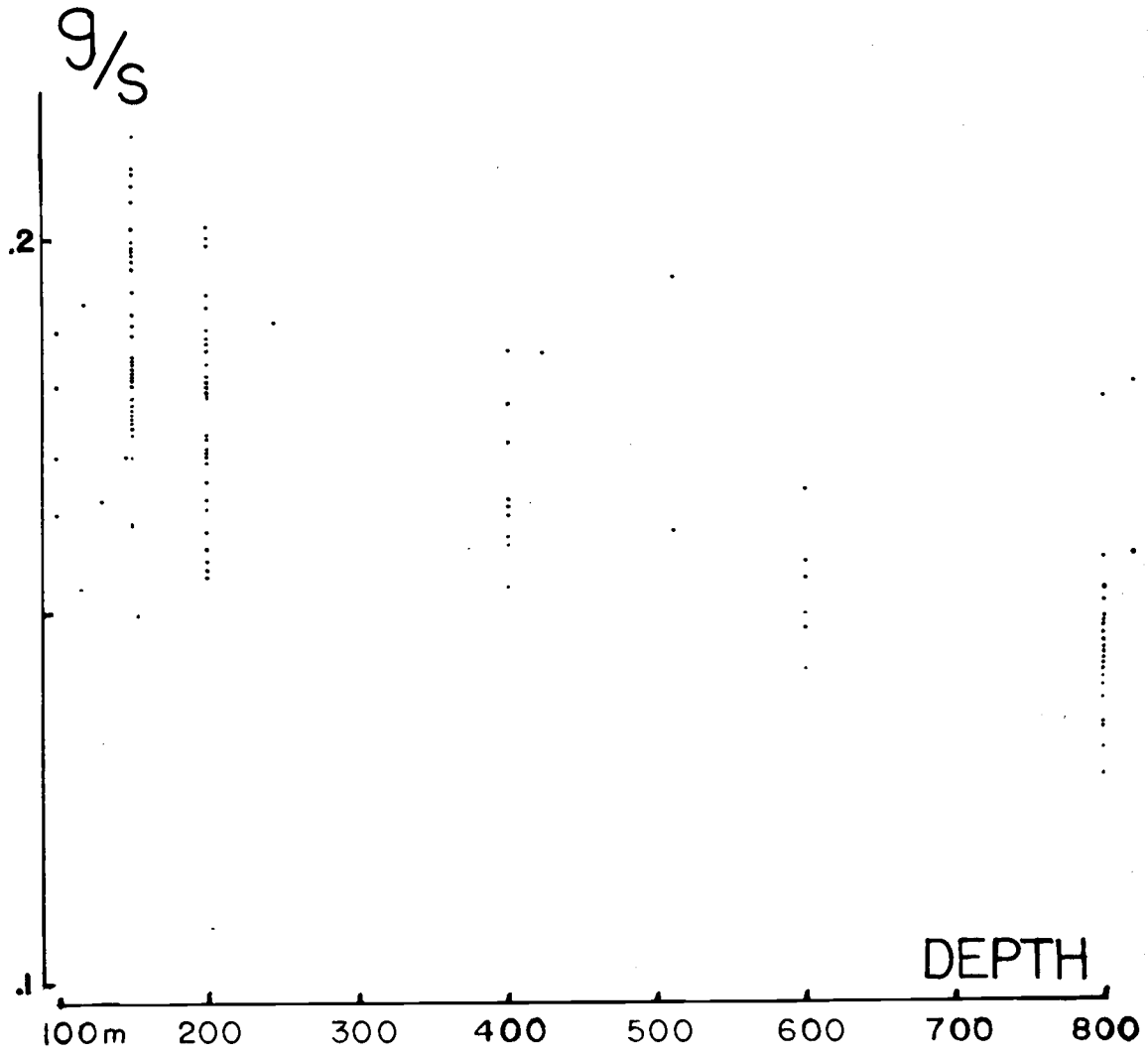

Figure 11. Graph of corrected relative width of ambulacrum III (g/s) for each specimen plotted against the depth at which it was taken.

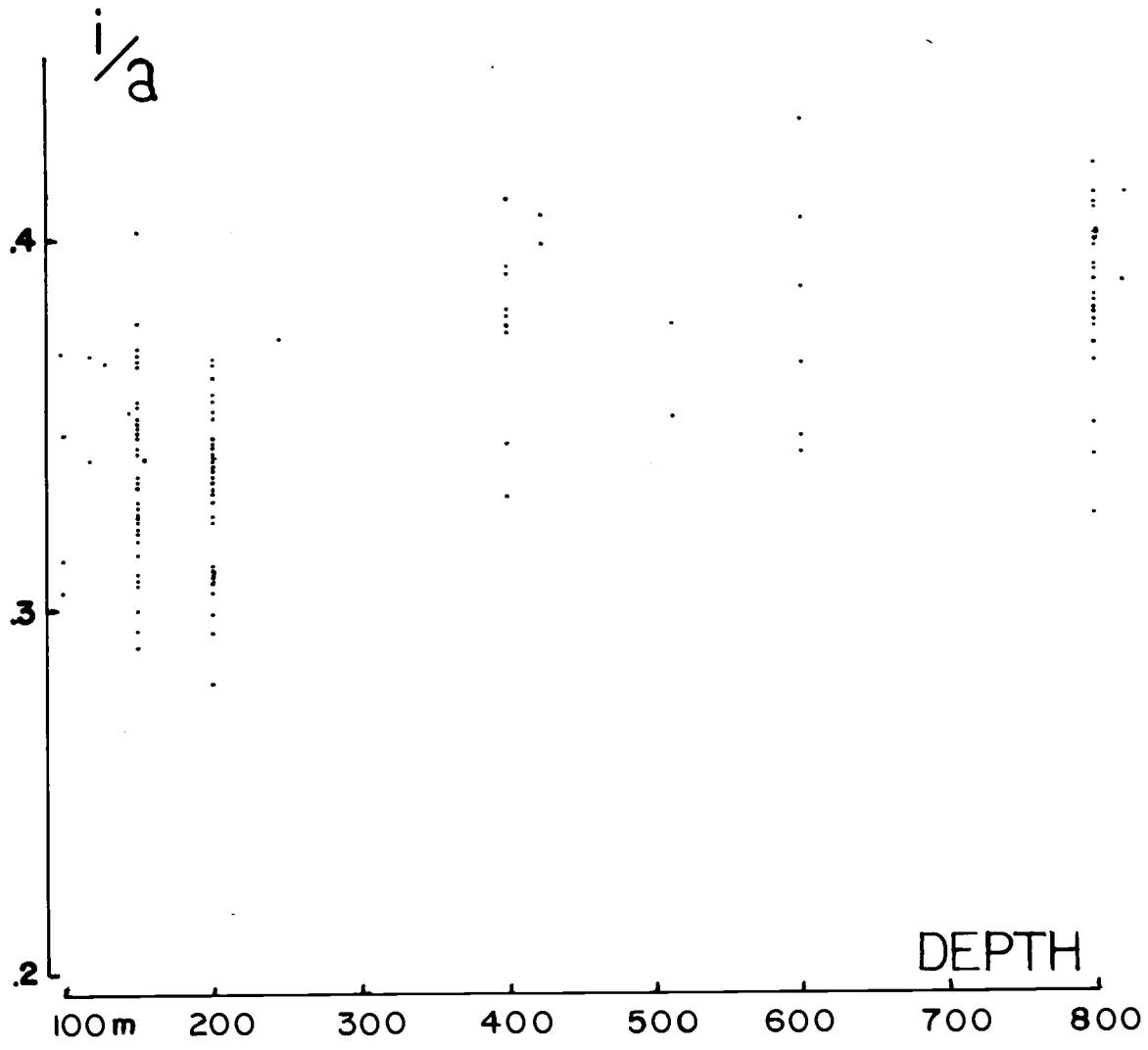

Figure 12. Graph of corrected level of the apical system (i/a) for each specimen plotted against the depth at which it was taken.

Table 7. Level of the apical system

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
Number of specimens	43	31	19	24
Mean or uncorrected i/a	0.3381	0.3381	0.3721	0.3835
Mean of corrected i/a	0.3379	0.3339	0.3791	0.3865
Slope of the regression of uncorrected i/a on s	-0.0004	0.0008	0.0013	0.0020
y-intercept of the regression of uncorrected i/a on s	0.3547	0.2998	0.3233	0.3025
Standard deviation of uncorrected i/a	0.0248	0.0233	0.0272	0.0243
Correlation coefficient	-0.1019	0.1883	0.2861	0.3163

The Relative Separation of the Posterior Petals: j/s (Figures 13, 14; Table 8)

The special nature of this measurement (it is not a definable structure or organ that is being measured) caused it to depart from simple allometry (that is, the plot of log j versus log s would not give a straight line).

The ratio of j to s decreases markedly as the animal matures and corrections for disproportionate growth were greater for this ratio than for any of the others (Figure 14).

The 800-840 m specimens yielded considerably lower j/s ratios than the shelf specimens (Figure 13). From the same graph, note the tendency for the 100-155 m specimens to have lower j/s values than the 200-245 m specimens. Differences among the three

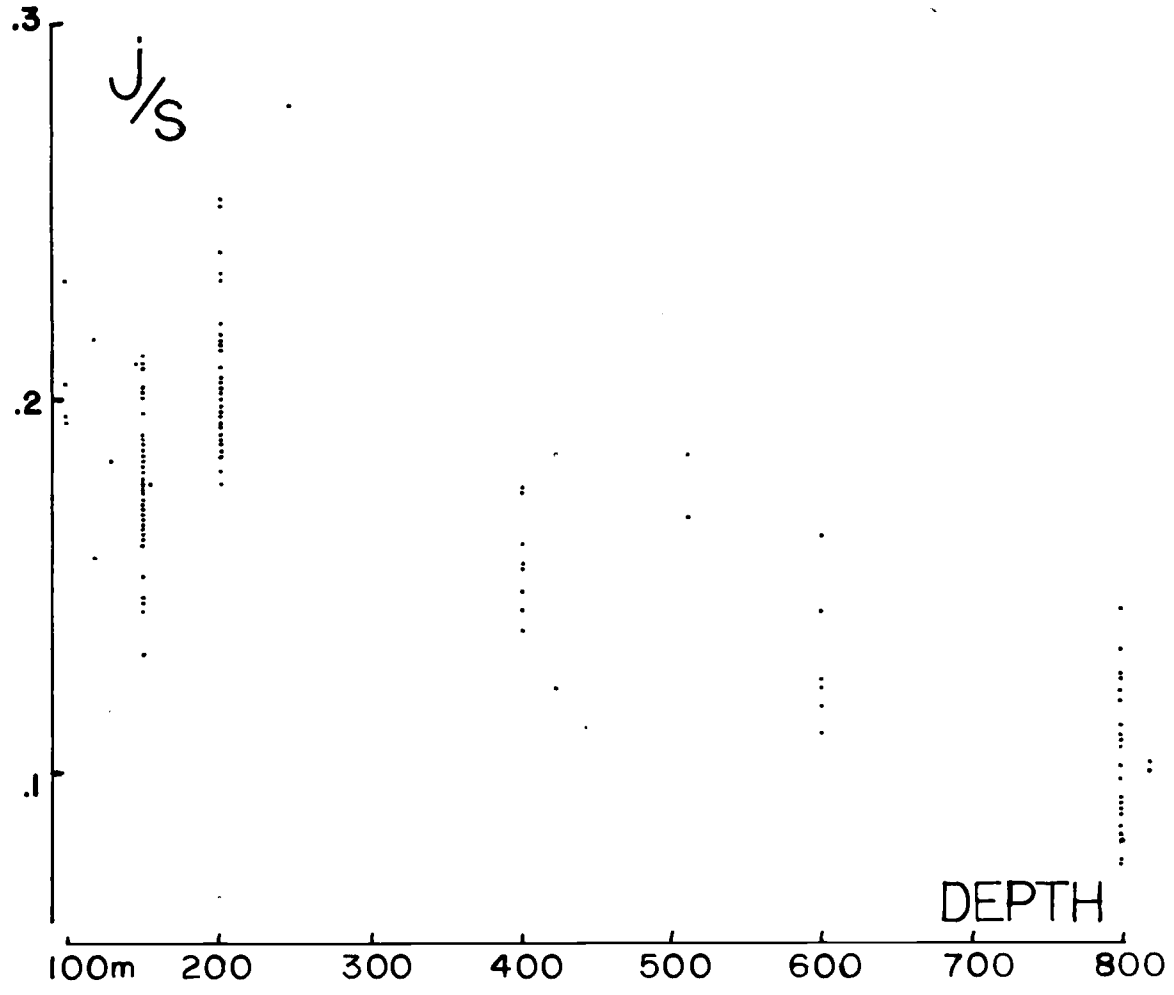

Figure 13. Graph of corrected relative separation of the posterior petals (j/s) for each specimen plotted against the depth at which it was taken.

shallowest depth zones were not statistically significant prior to allometric correction, but were significant to the 1% level following correction. Differences between the 800-840 m depth zone and each of the other zones were significant at the 1% level both before and after correction for allometry.

Table 8. Relative separation of the posterior petals

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
Number of specimens	43	31	19	24
Mean of uncorrected j/s	0.1836	0.1856	0.1838	0.1060
Mean of corrected j/s	0.1807	0.2072	0.1489	0.1024
Slope of the regression of uncorrected j/s on s	-0.0050	-0.0041	-0.0065	-0.0024
y-intercept of the regression of uncorrected j/s on s	0.3925	0.3820	0.4215	0.2027
Standard deviation of uncorrected j/s	0.0382	0.0338	0.0439	0.0199
Correlation coefficient	-0.8338	-0.6650	-0.8610	-0.4599

The Relative Size of the Periproct: $\sqrt{kl}/s$ (Figures 15, 16; Table 9)

Although the mean size of the periproct was slightly greater in specimens from 400-600 m, their individual values fell entirely within the extremes set by specimens from other depths (Figure 15).

The growth lines for all depth zones except 200-245 m very nearly parallel each other (Figure 16). In the 200-245 m specimens

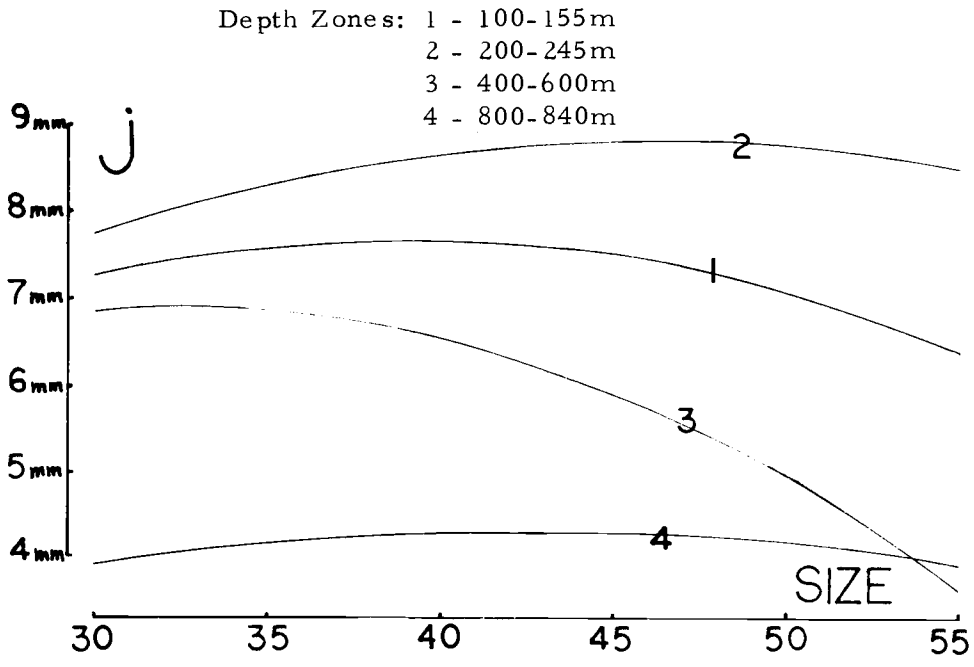

Figure 14. Growth lines of the separation of the posterior petals ($\underline{j}$) with respect to size ($\sqrt[3]{\underline{abc}}$) for each of the four depth zones. Estimated by method of least squares.

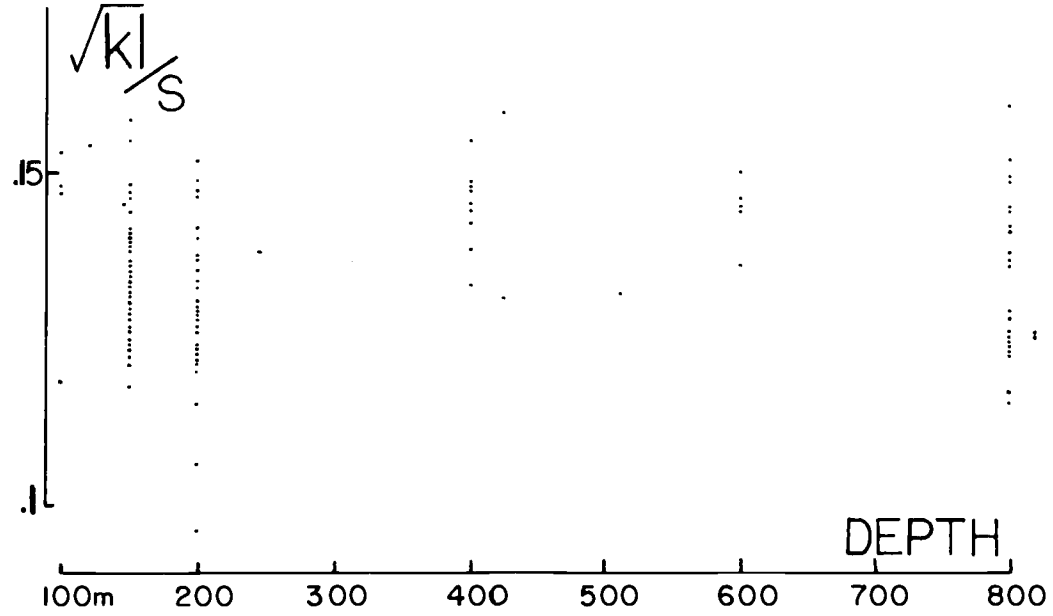

Figure 15. Graph of corrected relative size of the periproct ($\sqrt{\underline{kl}}/\underline{s}$) for each specimen plotted against the depth at which it was taken.

the tendency for overall size ($\underline{s}$) to outgrow periproct size ($\sqrt{\underline{kl}}$) was strongest.

Table 9. Relative size of the periproct

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-840 m
Number of specimens	39	28	17	24
Mean of uncorrected $\sqrt{kl}/s$	0.1365	0.1300	0.1439	0.1340
Mean of corrected $\sqrt{kl}/s$	0.1363	0.1347	0.1428	0.1339
Slope of the regression of uncorrected $\sqrt{kl}/s$ on s	-0.0004	-0.0009	-0.0002	-0.0001
y-intercept of the regression of uncorrected $\sqrt{kl}/s$ on s	0.1511	0.1705	0.1522	0.1380
Standard deviation of uncorrected $\sqrt{kl}/s$	0.0104	0.0123	0.0076	0.0115
Correlation coefficient	-0.2099	-0.3947	-0.1728	-0.0336

The Ratio of Petal II to Petal I: $\underline{e}/\underline{d}$ (Figure 17, Table 10)

Excluding the 200-245 m specimens, the ratio of the right lateral petals decreases slightly as the urchin matures; or stated another way, petal I grows faster than petal II (from slope of the regression lines, Table 9).

The 800-840 m depth zone had specimens with $\underline{e}/\underline{d}$ ratios substantially lower than the others (Figure 17). The difference was significant at the 1% level.

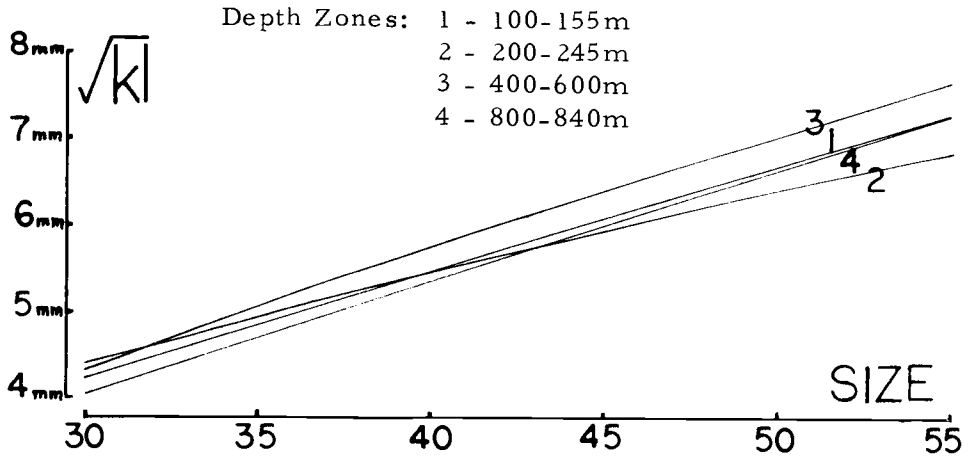

Figure 16. Growth lines of the size of the periproct ($\sqrt{kl}$) with respect to size ($\sqrt[3]{abc}$) for each of the four depth zones. Estimated by method of least squares.

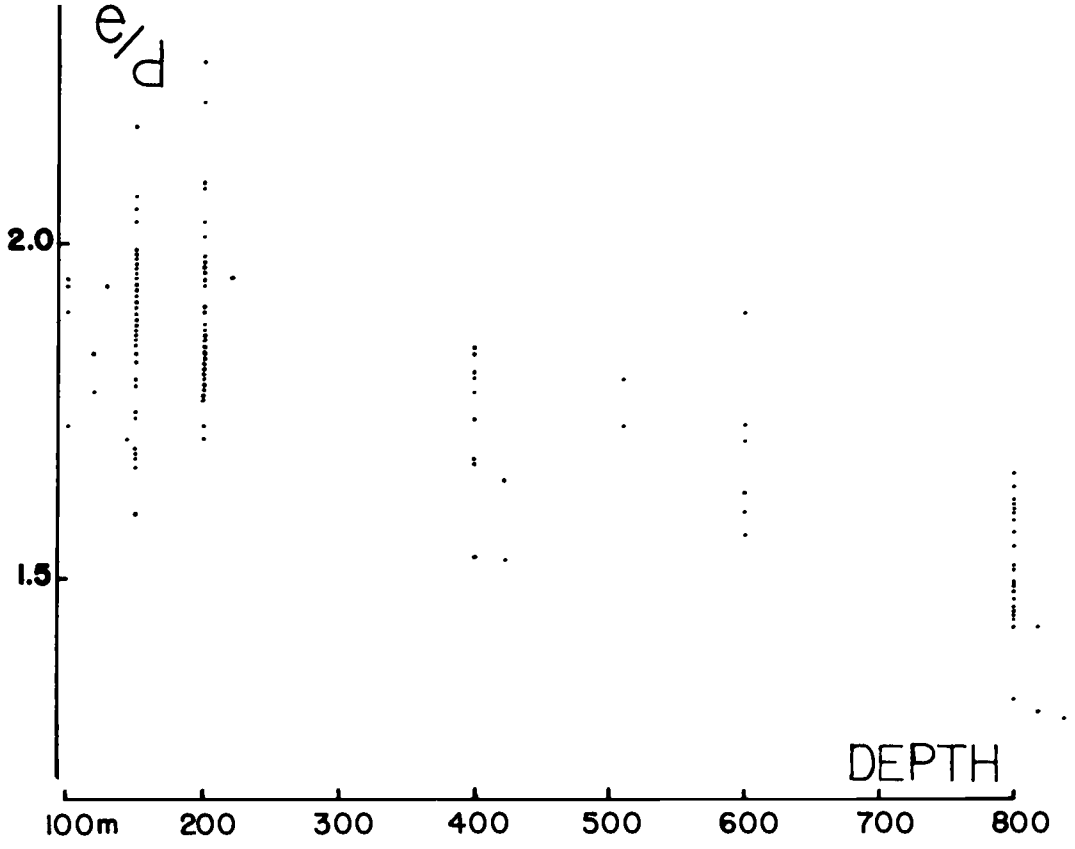

Figure 17. Graph of corrected ratio of petal II to petal I ($\underline{e}/\underline{d}$) for each specimen plotted against the depth at which it was taken.

Table 10. Ratio of petal II to petal I

	100 m-155 m	200 m-245 m	400 m-600 m	800 m-844 m
Number of specimens	43	31	19	24
Mean of uncorrected e/d	1.8765	1.9048	1.7858	1.5075
Mean of corrected e/d	1.8729	1.8985	1.7149	1.5005
Slope of the regression of uncorrected e/d on s	-0.0064	0.0012	-0.0132	-0.0046
y-intercept of the regression of uncorrected e/d on s	2.1441	1.8466	2.2736	1.6949
Standard deviation of uncorrected e/d	0.1290	0.1339	0.1318	0.1032
Correlation coefficient	-0.3112	0.0498	-0.5892	-0.1721

Additional Variates

In addition to the preceding nine measured variates, several more were discovered which do not readily lend themselves to quantification. As was the case with the preceding nine ratios, there is a tendency for the 200-245 m specimens and the 800-840 m specimens to reside at opposite ends of a continuum; the 100-155 m and 400-600 m specimens tending to fall somewhere in between.

The Peripetalous Fasciole. The course of the peripetalous fasciole across the posterior interambulacrum varies significantly from specimen to specimen. The difference may be located by following the fasciole counterclockwise around the dorsal surface of the test. It rounds the peripheral end of petal V and may then do one

of two things: (1) it may continue more or less directly across interambulacrum 5 toward the peripheral end of petal I (Figure 1, B), or (2) it may continue for a short distance, turn abruptly apicad, and then return to the peripheral end of petal I in a similar fashion (Figure 1, D). Most individuals from the 200-245 m zone and a few from the 100-155 m and 400-600 m zones conformed to the former type. All the individuals from the 800-840 m zone and many from the other zones conformed to the latter.

The Flexure of Petals II and IV. The petals in question originate from ocular plates II and IV of the apical system. Near their point of origin they are widely divergent, approaching 180°. Almost immediately, the petals bend anteriorly and may then follow a variety of routes toward the ambitus. In specimens from the 800-840 m depth zone the remainder of the petal is very nearly straight; the angle between petals II and IV remains constant. In other specimens, particularly those from the two shallow depth ranges, the petals are straight for a considerable distance but then diverge; the divergence reaches a maximum where the peripetalous fasciole intersects the ambulacra. The nature of the flexure is more clearly understood if one examines the four denuded tests in Figure 1. Only in the 800 m specimen are the two petals straight.

The Respiratory Podia. Each plate in the lateral ambulacra supports a single, highly modified tube foot, believed to function as

an organ of oxygen exchange (Cuénot, 1948). Tube feet were plucked from the central area of petals I and II of individuals from ten stations and measured. Table 11 supplies a summary of the results. The origin of the values in the column headed: "minimum surface area" is covered in the methods section.

Table 11. Number and "minimum surface area" of respiratory podia

depth	$\sqrt[3]{abc}$ "size"	No. of petal I podia	"minimum surface area" of petal I podia	No. of petal II podia	"minimum surface area" of petal II podia
118 m	31.1	19	1.65 mm^2	37	1.68 mm^2
150 m	41.7	23	2.94 mm^2	44	4.07 mm^2
150 m	46.4	20	2.80 mm^2	38	5.70 mm^2
Mean min. sfc. area 100-155 m:			2.46 mm^2		3.82 mm^2
200 m	37.0	23	1.35 mm^2	40	1.65 mm^2
200 m	42.4	26	1.60 mm^2	41	2.59 mm^2
200 m	47.1	25	3.20 mm^2	45	5.21 mm^2
Mean min. sfc. area 200-245 m:			2.05 mm^2		3.15 mm^2
423 m	34.0	23	2.00 mm^2	36	3.82 mm^2
600 m	39.2	21	3.64 mm^2	32	4.26 mm^2
Mean min. sfc. area 400-600 m:			2.82 mm^2		4.04 mm^2
800 m	36.6	27	5.44 mm^2	35	5.92 mm^2
840 m	37.7	27	5.63 mm^2	34	7.32 mm^2
Mean min. sfc. area 800-840 m:			5.53 mm^2		6.62 mm^2

Again, the 800-840 m and 200-245 m depth zones yielded the largest and smallest values, respectively; the other depths, intermediate values. The mean minimum surface area calculated for podia from the 800-840 m specimens was approximately double that

for podia from the 200-245 m specimens. The ampullae associated with the respiratory podia of the 800-840 m specimens, though not measured, also appeared to be larger. It should be noted here that these measurements are, to an undetermined extent, dependent on the degree of retraction of the podia following the death of the specimen and may only approximate the dimensions of normally functioning podia. Assuming such retraction to be uniform, one can, at least, make profitable comparative use of the data.

The Development of the Gonads. A mean gonad index was calculated for each of 39 stations. Again, only specimens of $s \geq 30$ were included. The stations were divided into two groups, those in the 100-155 m and 200-245 m depth zones, and those in the 400-600 m and 800-840 m depth zones. The station means of each group were then averaged separately. The mean gonad index of the former group was found to be about five times the mean of the latter group: 2.25: 0.42 in the females, and 3.00:0.65 in the males.

Although collections were distributed throughout the year, the possibility of error due to seasonal gonadal variation must be admitted. Such effects, however, are in no way comparable to the five-fold difference observed.

The Fullness of the Gut. The alimentary canal of a typical specimen from 800-840 m is reduced, i.e., both its diameter and length are minimal. Some individuals from that depth zone had

empty intestines and flattened ceca. Specimens from the two shallower zones typically yielded fully distended guts.

The Anterior Ambulacrum. The relative width of ambulacrum III (g/s) is one of the nine variates expressed in ratio form above. The 800-840 m specimens were found to bear narrower anterior ambulacra than shallower specimens. The length, depth, and plate density of ambulacrum III varied in a corresponding manner. On the basis of observation alone, it appeared that the anterior ambulacra of individuals from 800-840 m were shorter and shallower. A count was made of the total number of plates comprising the anterior ambulacra of all specimens of size from 40 to 50. The specimens were separated into two groups: the two shallower depth zones and the two deeper depth zones. The rate of plate production was calculated by method of least squares for each group separately. In the shallower specimens an average of seven new plates were budded off during the growth period studied ($40 \leq s \leq 50$); five new plates were budded off during the same period by deeper specimens. Plate number was plotted against depth of capture and is presented as Figure 18. The number of anterior ambulacral plates was minimal in the 800-840 m specimens, maximal in the 150 and 200 m specimens.

The density of the spines on the floor of ambulacrum III was minimal in specimens from the 800-840 m depth zone. In all specimens the number of spines born by each plate of the anterior

ambulacrum increased anteriorly away from the ocular, however, the increase was more immediate and more pronounced in individuals from the two shallower depth zones.

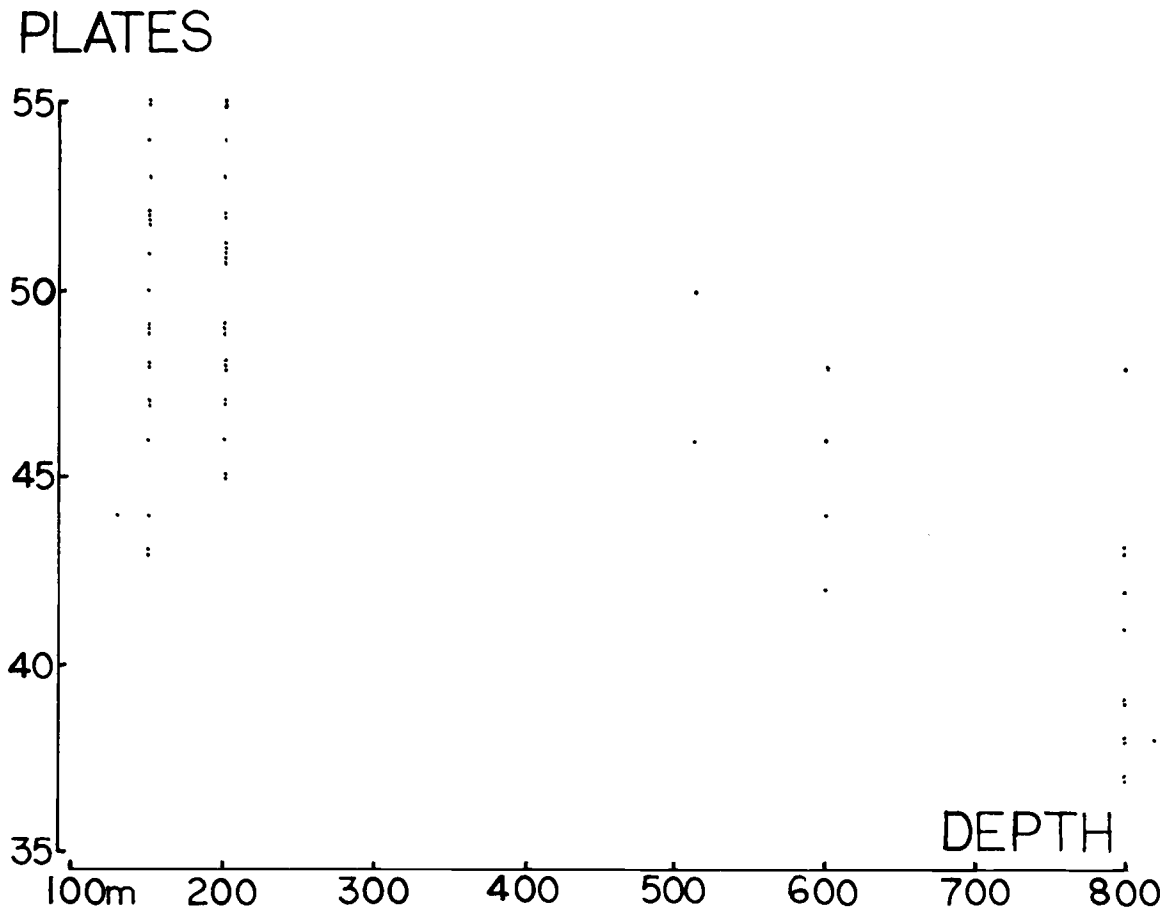

Figure 18. Graph of the number of plates in ambulacrum III for each specimen plotted against the depth at which it was taken.

Summary of Results

The analysis of the nine variates expressed in ratio form are summarized in Figure 19. The graph is designed to permit visual

comparison of the uncorrected and corrected values of the nine ratios at each of the four depth zones. The broad lines are the means of the corrected ratios; the narrow lines, the uncorrected ratios. The separation between the two gives an idea of the amount of allometric correction made on specimens from the corresponding depth zone.

The figure (19) and the following 11 points serve to summarize the results of the biometrical analysis:

(1) In six of the nine variates considered in Figure 19 the 200-245 m depth zone yielded values at one extreme, the 800-840 m depth zone yielded values at the other extreme. Zones 100-155 m and 400-600 m yielded intermediate values.

(2) Particularly outstanding differences appeared in four of the variates. The slope-inhabiting specimens, especially those from 600 m and deeper, had longer posterior petals (d/s), wider posterior petals (f/s), narrower anterior ambulacra (g/s), and less separation between posterior petals (j/s) than shelf-inhabiting specimens.

(3) The 200-245 m depth zone exhibited an ontological reduction in the relative length of both lateral petals (ratios d/s and e/s), whereas the other three depth zones showed an increase.

(4) All depth zones exhibited an ontological reduction in the relative width of ambulacrum III (g/s); the trend was especially

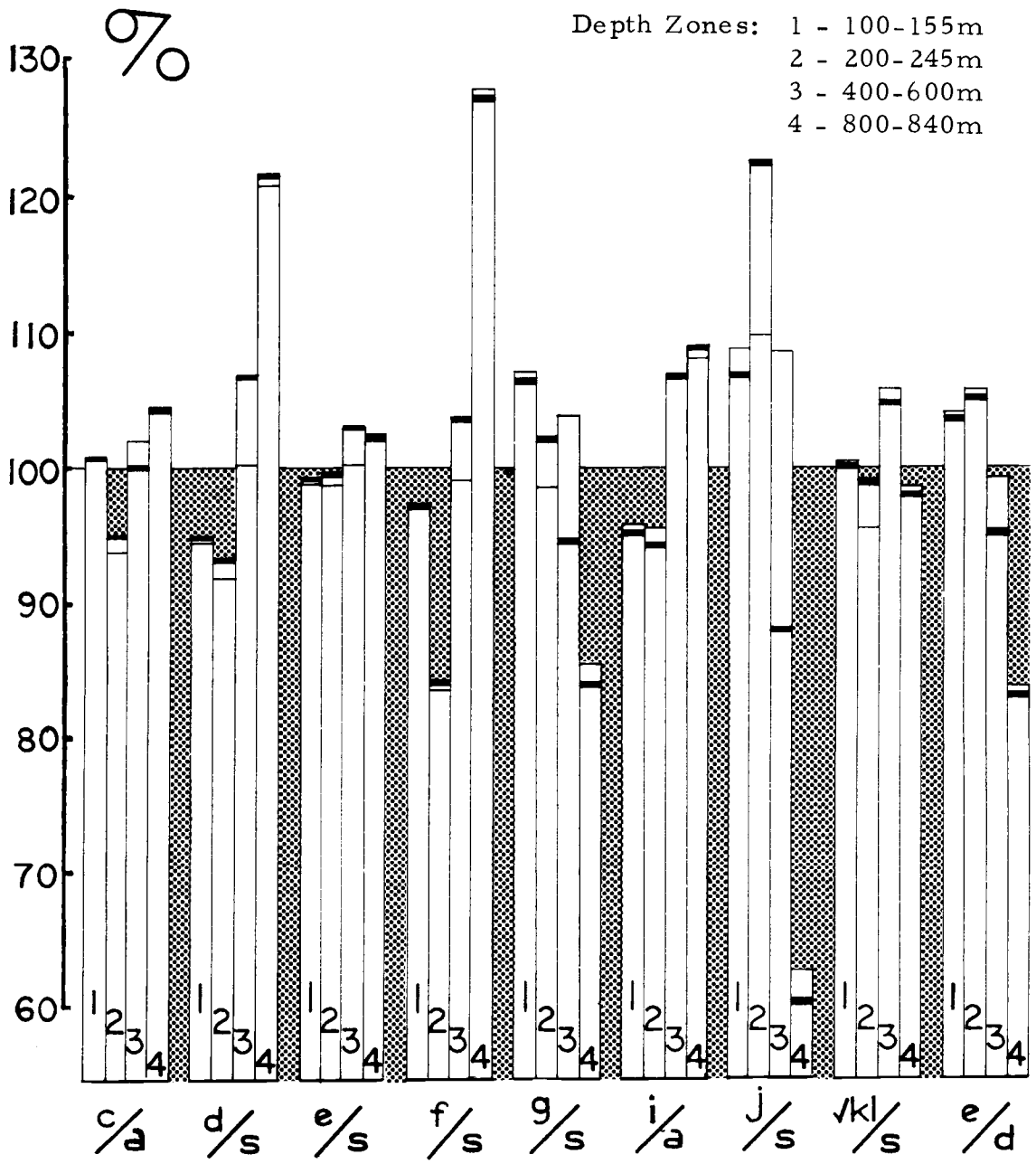

Figure 19. The means of corrected and uncorrected ratios for each depth zone expressed as a percentage of the mean of the uncorrected ratios of all specimens.

marked in specimens from the two deeper depth zones (400-600 m and 800-840 m).

(5) The peripetalous fasciole in interambulacrum 5 tended to be straighter in 200-245 m specimens than in specimens from other depths. Apical displacement of this part of the fasciole was greatest in specimens from the 800-840 m depth zone.

(6) The flexure of the antero-lateral petals was least in specimens from the 800-840 m depth zone.

(7) The respiratory tube feet were largest in specimens from the 800-840 m depth zone, smallest in specimens from the 200-245 m depth zone.

(8) Gonads of specimens from the shelf were considerably larger, throughout the year, than gonads of slope specimens.

(9) The alimentary canals of slope specimens were shorter, narrower, and less distended than those of shelf specimens of comparable size.

(10) The length, depth, width, spine density, and number of plates in the anterior ambulacrum were least in specimens from the slope.

(11) Variation among specimens collected even in the same trawl was considerable, but not of sufficient magnitude to mask the more consistent trends listed above. In eight of the nine ratio variates (periproct size excepted), the differences between the 200-245 m

and 800-840 m depth zones were significant at the 1% level. Differences between the 100-155 m and 200-245 m depth zones were significant at the 1% level in ratio of height to length (c/a), relative width of petal I (f/s), and relative separation of the posterior petals (j/s), only.

DISCUSSION

Several of the variates examined in this study permit one to separate the Oregon collection into two principal groups: those from about 400 m and less, and those from about 600 m and more. Specimens from the shallower depths bear a remarkable resemblance to descriptions of Brisaster (=Schizaster) latifrons published by Agassiz (1898, 1904), Clark (1917), and others. Likewise, specimens from the deeper depths bear a remarkable resemblance to published descriptions of B. townsendi. The division is far from decisive, however, as certain individuals, particularly those from intermediate depths, present affinities to both groups. Nevertheless, the motivations of early taxonomists in distinguishing more than one species are readily appreciated. McCauley (1967) showed that the names latifrons and townsendi are synonymous.

The two principal variants are hereafter referred to as the "shallow variant" and the "deep variant," and are represented by the two drawings at the bottom of Figure 20. These drawings are somewhat diagrammatic and exaggerate (intentionally) those features characterizing the variants which they represent.

The origin(s) of the differences between adult populations of shallow and deep variant might best be discussed by first distinguishing three pathways of differentiation: (1) differential selection

operating ontologically, i.e., particular genotypes are selected during the maturation of a single generation, (2) non-genetic adaptation by the individual to its surroundings. If partial or complete isolation of progeny occurs, a third pathway is possible: (3) differential selection operating phylogenetically, i.e., particular genotypes are selected cumulatively over many generations. Determining which of the three pathways is active in any single type of variation requires information on life history, geographic and bathymetric distribution, and ambient conditions, in addition to some knowledge of the functions of those structures that vary. My immediate aim is to bring to light as much of this information as is currently available, and subsequently, to attempt to identify the selective agencies involved.

Life History

The life history of B. latifrons is incompletely known. Pre-metamorphic stages have never been reported and there is some question as to whether the species really passes through a planktonic stage. Eggs are relatively large (300-350 μ in diameter) and yolky, indicative of a life cycle involving direct development (Mortensen, 1951).

The discovery by Runnstrom (1929) of a planktonic larva attributable to one of the Atlantic Brisaster species, B. fragilis,

is really the only evidence in support of the hypothesis that B. latifrons passes through a pelagic stage. Brisaster fragilis also has large yolky eggs (Mortensen, 1951).

The deeper limit of the urchin's bathymetric range (about 840 m off Oregon) would seem prohibitive to the success of a larva which must make an ascent to the surface and return before metamorphosis can commence. Apparently the problems involved are not insurmountable, as the regular echinoid Allocentrotus fragilis, known to have a pelagic, planktotrophic larva (Moore, 1959) has a bathymetric range exceeding that of B. latifrons (unpublished records of OSU collections).

With some hesitation, I accept Mortensen's (1951) conclusion that B. latifrons has pelagic larvae. The implications of the mobility afforded a species with planktonic stages are considerable. Geographical, hydrological, or temporal barriers may permit genetic isolation of populations in some instances, regardless of the nature of the larva, but evidence of such barriers off Oregon is lacking. Although the time and duration of spawning in B. latifrons is still not known with certainty, evidence from gonad index analysis collected in this study indicates that release of gametes occurs preferentially in the spring. If this is a valid interpretation of the observed seasonal gonad fluctuation, summer upwelling off Oregon coincides satisfactorily with the expected larval phase, and can only

contribute to intermixture of progeny from the various populations.

Geographic Distribution and Hybridization

Several specimens collected by the Albatross from areas north and south of Oregon, and deposited in the U. S. National Museum, have characters that fall outside the limits of the Oregon specimens. The distribution of the species is extensive, and there is no reason to expect genetic homogeneity throughout. According to Mortensen (1951) the species extends from the Gulf of Panama, along the west coast of North America, to Alaska. Mortensen suggested re-examination of those specimens collected in the northwest Pacific to determine whether they are true B. latifrons or B. owstoni. Russian taxonomists Baranova (1955, 1957) and Djakanov (1958) reported B. latifrons and B. townsendi from the Bering Sea, Sea of Okhotsk and south to Japan, but did not mention B. owstoni. Russian ecologists Savilov (1961) and Filatova and Neyman (1963) wrote of B. latifrons in the Sea of Okhotsk and Bering Sea, respectively, but in accordance with their compatriots above, made no B. owstoni identifications. McCauley (1967) examined collections of Asiatic Brisaster (from the Sea of Okhotsk, Pacific Ocean off Japan, and Western Bering Sea) and found them sufficiently different from American Brisaster to warrant their separation under the name B. owstoni. Nisiyama (1968), in his comprehensive paleontological work on the

echinoids of Japan, reported both fossil and extant B. owstoni but did not include B. latifrons (or B. townsendi) among those species currently inhabiting Japanese waters. There is obviously still some confusion here concerning the identification of the two Brisaster species of the North Pacific, latifrons and owstoni. It is conceivable that hybridization between these two species is responsible for some of the confusion.

Specimens collected off California lead Clark (1948) to believe that Brisaster latifrons hybridizes with Brissopsis pacifica in that area. As there are no spatangoids sympatric with B. latifrons off Oregon, there is little chance of similar phenomena occurring here.

Monstrosities

Out of 368 specimens of B. latifrons handled in this study, only about a half a dozen monstrosities were encountered. Koehler (1924, Pl. III. Figures 5, 6, 10, 11, 15) and Mortensen (1951, Pl. XXIV, Figures 9-13) both published photographs of B. latifrons monstrosities. Their cause is completely unknown. Brattström (1946, p. 18) found Brissopsis lyrifera monstrosities in large numbers in the Gullmar Fjord and considered a few possible explanations: "1) external injuries, 2) influences from the surroundings, 3) parasites, and 4) genetical conditions." Several individuals examined in the present study showed obvious signs of injury, but, as

pointed out by Koehler (1924) and Brattström (1946), it is unlikely the the more persistent types of deformities can be attributed to imperfect reparation of former wounds.

The discovery of a specimen of B. latifrons in the Oregon material with four, instead of three, genital pores brings to mind the study by Tornquist (1903) on the significance of the reduction in the number of genitals among certain Schizaster species since the Cretaceous, and suggests that an interesting case of atavism has been encountered here. The specimen also has an additional genital duct, though its associated gonad is very poorly developed.

Parasitism

Coelomic parasites of the sporozoan family Urosporidae occur in B. latifrons at a high incidence rate (Brownell and McCauley, in preparation), but no correlative morphological alterations of any consequence were noticed. Giard (1876) reported finding "small nodosities" on the test interior of Echinocardium cordatum where the cysts of closely related parasites made contact with the host, but such effects would seem to be of minor importance here.

Parallel Variation

It is apparent from the literature that the same types of variations observed in B. latifrons off Oregon are also found in

B. latifrons from other areas, and, in other species of Brisaster. Agassiz (1898) found two variants (one of which he named Schizaster latifrons, the other S. townsendi) in Albatross collections from the Gulf of Panama. Filatova and Neyman (1963) found two variants in the Bering sea, one of which predominated on the slope of the western part of the sea (identified as B. latifrons), and the other on the slope of the eastern part of the sea (identified as B. townsendi). Presumably the identifications were made on the basis of the same characters Agassiz and others used to distinguish the two variants and therefore indicate types of variation similar to those seen in Oregon Brisaster.

Examples of other species of Brisaster exhibiting these variations are also to be found in the literature. Agassiz and Clark (1907, p. 137) wrote of the variation they observed in specimens of "Schizaster ventricosus" (B. owstoni, according to Mortenson (1951), but possibly B. latifrons or both):

> A remarkably interesting series of this species was taken, ranging from 9 to 74 mm. in length. There is the greatest diversity, shown in the relative length of the anterior and posterior petals and in the angle made by the latter with the longitudinal axis of the body. While it is possible to divide the specimens into three groups, ((1) with short, widely diverging, posterior petals, (2) with long, stright, little diverging, posterior petals, and (3) with very long petals, the posterior pair straight and moderately diverging) it is impossible to draw hard and fast lines between such groups, and although the typical examples of each group are obviously different from each other, it seems best to regard them all as ventricosus.

Mortensen (1907, Pl. I, Figure 7) published a photograph of a B. fragilis variant with overdeveloped posterior petals. Although these variations seem to be identical to those seen in our local B. latifrons, it is not known whether the same factors are responsible.

A Hypothesis of Differentiation

The most obvious difference between the deep and shallow variant is in the size of petals I, II, IV, and V. Through most of the size range studied, the paired petals of the deep variant are proportionately larger than the same petals of the shallow variant. The relative growth rate of petal I (both length and width; see Figures 4, 8) is maximal in specimens from the two deeper depth zones, whereas the relative growth of petal II is very nearly identical in all four depth zones (Figure 7). Since populations of B. latifrons reach maximum size and maximum densities on the outer shelf and upper slope (i.e., between about 150 m and 400 m) off the Oregon coast (McCauley and Carey, 1967), it follows that that habitat provides conditions optimal for growth or nearly so. This optimal depth range is essentially the habitat of the shallow variant. The possibility that the morphology of the deep variant is the result of an environmental stress is worthy of consideration. I suspect (for reasons to be made apparent later) that one such stress is causing differential petal growth, which, in

turn, is responsible for several of the other features of the deep variant's test. Following are five statements, offered somewhat tentatively, as means whereby differential petal growth may be effecting the proportions of certain of these other test structures. The structures referred to are more easily visualized with the aid of Figure 20.

(1) Disproportionate lengthening of the lateral petals, either by additional plate production or by growth of existing plates, would tend to force the apical disc upward, and thereby increase the relative height of the test (note tendency of 800-840 m specimens to have slightly greater c/a values, Figure 3).

(2) Disproportionate lengthening of the posterior petals would tend to force the apical disc forward, and thereby increase the eccentricity of the apical system (note tendency of slope specimens to have slightly greater i/a values, Figure 12).

(3) Disproportionate widening of the posterior petals would tend to reduce the separation between them, that is, decrease the width of interambulacrum 5 near the apical system (note tendency of 800-840 m speciments to have substantially lower j/s values, Figure 13).

(4) Disproportionate lengthening of the posterior petals would tend to increase the distance the peripetalous fasciole must travel apically in order to reach plates 5a8 and 5b9 (the plates across

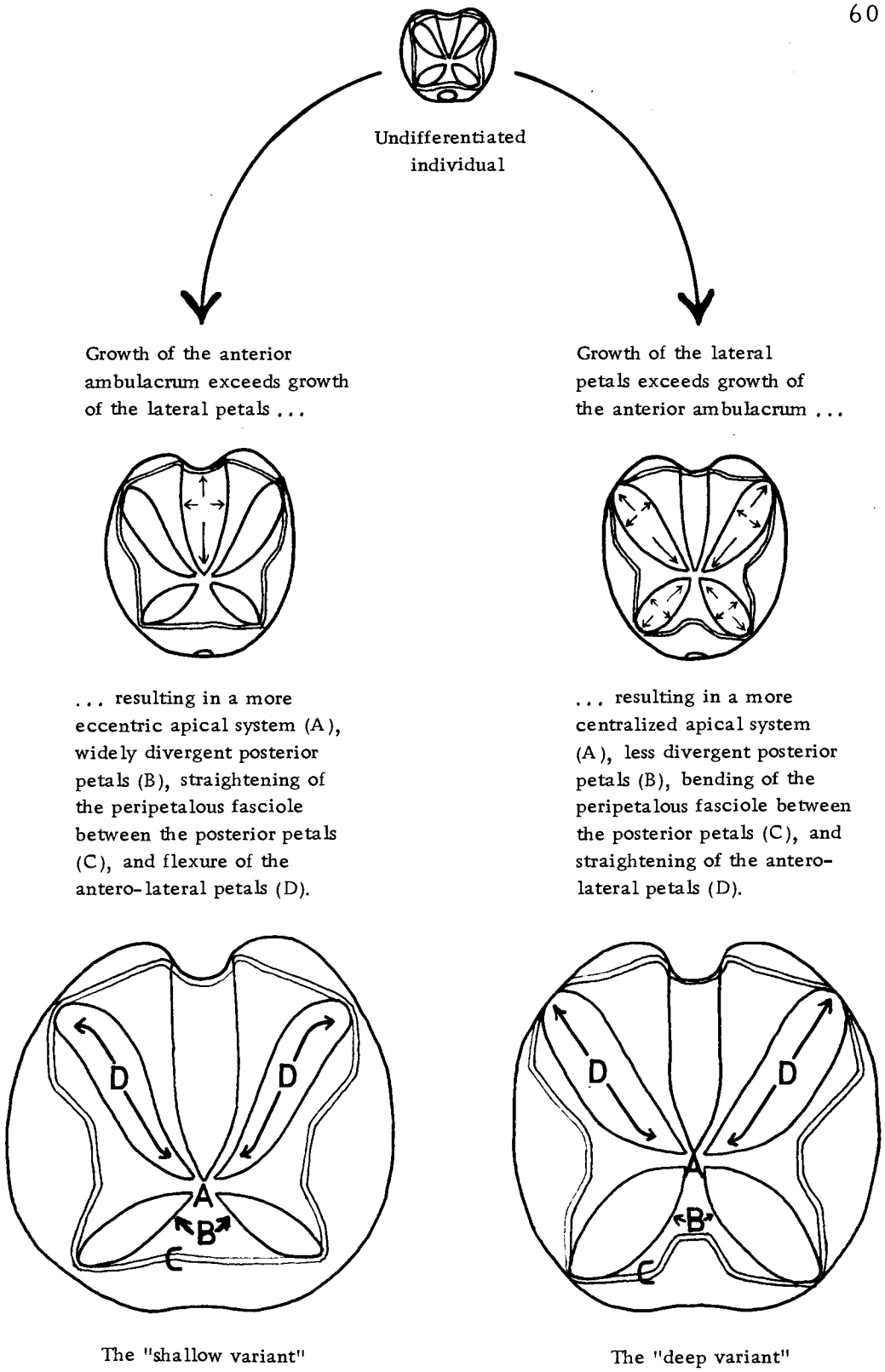

Figure 20. Hypothetical differentiation of the "shallow variant" and "deep variant."

which the fasciole normally runs). This would give the fasciole a truncated cone appearance in interambulacrum 5, typical of that observed in the deep variant (Figure 20).

(5) Disproportionate widening of the antero-lateral petals would seem to have a compressing effect on the more youthful (i.e., near the ocular) plates of the anterior ambulacrum. It is conceivable that the narrowness of the anterior ambulacrum in the deep variant is causally associated with this lateral compression. The same pressure may somehow be instrumental in reducing the number of ambulacrals budded off the ocular, as well as the number of spines each eventually supports (Figures 11, 18).

The above five points cover all the major morphological distinctions one can make between the two variants. I am quite convinced of the soundness of all but the last point. Differences in the anterior ambulacra of the two variants are substantial. It is hard to believe that they are all due to indirect effects of simple lateral pressure; more likely they are also of primary origin. Accelerated growth of the lateral petals is more likely accompanied by a simultaneous, but perhaps unrelated, inhibition of anterior ambulacrum development. At any rate, one may argue that the primary morphological features of the adult test of the deep variant are dependent on as few as two simple growth characteristics. . . one associated with the lateral petals, the other with the anterior ambulacrum.

Lesser variations have been encountered which do not correlate with depth of capture and cannot be attributed to differential petal growth. These make it clear that variability in B. latifrons is of several types, and probably of several sources.

Differences Between the Two Shallower Depth Zones

Separating the Oregon specimens into shallow and deep variants neglects differences between urchins from the 100-155 m and 200-245 m depth zones (e.g., see Figure 9). It will be remembered that it was the 200-245 m and 800-840 m and not the 100-155 m and 800-840 m depth zones that set the extremes in six of the nine ratio variates. Since the various environmental factors or agents that are most likely influencing test characteristics form a continuous gradient from 100 m to 840 m, there exist two possible explanations: (1) that a single such agent is responsible for optimal conditions at the 200-245 m depth or (2) that two (or more) such agents are effecting test development, the first by creating a contrast between the 100-155 m and 200-245 m specimens; the second, by creating a contrast between shelf and slope specimens.

It is conceivable that the differences between specimens of the two shallow depth zones are a result of the geographical separation of collection sites. Whereas most of the non-150 m stations were situated off Newport, Ore., the two stations that supplied the vast

majority of specimens for the 100-155 m depth zone were taken off Tillamook Head, Ore., about 150 km to the north. The differences are minor, but appear consistent enough to warrant further study.

Environmental Gradients

Up to this point, no selective agent has been suggested as being responsible for the differentiation of shallow and deep variant. Likely candidtates are those variables that exist in a gradient with depth. Four such agents (particle size of the sediment, water temperature, organic carbon content of the sediment, and dissolved oxygen concentration) are dealt with below. Other possibilities, notably pressure, may eventually be shown capable of influencing test morphology, but gross ignorance of the modes of influence precludes their discussion at present. Concentration gradients of most salts and dissolved gases are probably too weak to fall within the physiological experience of the heart-urchin and, likewise, are not considered here.

Particle Size of the Sediment

That B. latifrons inhabits the sediment is undeniable; its position relative to the sediment surface, however, has not been established with certainty.

Savilov (1961), in his paper on bottom invertebrates of the

Okhotsk Sea, included a figure of B. latifrons with everything but the apical tuft of spines covered by sediment. The apical spines of an urchin burrowing in this way would certainly betray its presence. Bottom photographs, taken in areas of high B. latifrons densities off Oregon reveal no such traces. Box core samples taken off Oregon indicate that the urchin inhabits the zone immediately beneath the sediment surface (Roush, personal communication). Whether it builds respiratory or sanitary tubes as is the case with certain other spatangoids (see Durham, 1966) is unknown.

The literature supplies several instances where sediment quality is thought to have influenced echinoid morphology. After investigating several species of British irregular echinoids, Nichols (1959a, p. 350) was led to make the statement:

> The evidence obtained shows that their special modes of burrowing, feeding, sanitation, and locomotion are closely correlated with the particle size of the substratum in which they live, and this adaptation is expressed in many features of their tests. . .

In a subsequent publication (1962) Nichols expounded on one of these features, namely, the sub-anal fasciole of Echinocardium cordatum, which is thought to be important in maintaining a water current down the soak-away burrow for elimination of respiratory and excretory wastes. He believed the shape of the sub-anal fasciole was a critical factor in a young Echinocardium's ability to survive in the substrate in which it finds itself following metamorphosis. Nichols (1962)

proposed that urchins with a fasciole of the wrong shape would be incapable of constructing a suitable sanitary tube and would perish before reaching full size. Only those individuals with a sub-anal fasciole of a particular shape would survive. The fasciole morphology of the adult population appeared to be controlled, in this case, by the particulate nature of the sediment.

B. latifrons also has a sub-anal fasciole, but it is often vestigal and its importance to survival has not been established. Since B. latifrons appears to be a shallow burrower anyway, the problems involved in eliminating by-products of respiration and digestion would not be as severe as would be expected in the deeper burrowing Echinocardium.

A study of the sand-dollar Echinarachnius parma by Lohavanijaya (1965) showed that in an area where the surf was heavy and the sand hard-packed, the width of the test exceeded the length. In an area of slower currents and a higher percentage of the finer sediments, the test length exceeded its width. Raup (1956) had previously reported that Dendraster excentricus from areas of heavy surf were more eccentric than those from sheltered bays. Kelly (1965), by means of multivariate analysis of three ratios, confirmed Raup's observation that there is a significant morphological difference between estuarine and open-ocean D. excentricus.

Published data on the sediment off the Oregon coast are limited. Summarized results of sediment analyses have been supplied by Carey (1965), McCauley and Carey (1967), and Griggs, Carey, and Kulm (1969). Information on sediment for this thesis was taken from those papers. Unless otherwise stated, analyses were not made on sediment from the station at which the urchins were taken and therefore provide only an approximation of sediment characteristics of the animals' habitat.

Particle size decreases with increasing depth off Oregon. At one 780-800 m station, the sediment was about 3% sand, 68% silt, and 30% clay; at a 100 m station, the sediment approached 100% sand (McCauley and Carey, 1967). A large collection (130 individuals) was made from the latter depth; they were clearly stunted. Out of a randomly selected subsample of 30 specimens, only two measured more than 40 mm in length. Even those as small as 34 mm in length, however, were sexually mature, as evidenced by the presence of full-sized ova. Specimens of comparable size from silty habitats do not ordinarily have gonads develop to this extent.

Particle size in this instance, may not necessarily be responsible for stunting. In general, particle size is more important in limiting an animal's range than in stunting its development (Hallum, 1965). McCauley and Carey (1967) reported low concentrations of

organic carbon (0.1% by weight) at the same station from which the stunted individuals were taken. This would seem to be a more plausible explanation for the stunting.

The question of how large a role sediment quality plays in effecting the differentiation of the shallow and deep variant must, at present, remain unanswered. The particle size gradient off Oregon is a strong one and does correlate well with test morphology. Sediment data on Albatross stations from which specimens are available are too general to be of value in attempting to extend the correlation into non-Oregon waters. The best course at present seems to be to simply avoid making a decision on the importance of particle size until information is acquired on the urchin's burrowing habits and the mechanics of a direct cause-and-effect relationship can be revealed.

Temperature

Publications abound in the field of thermal biology. A few deserve mention here, particularly those that involve echinoid morphology.

Body size is often linked to temperature. Mortensen (1907) reported Brisaster fragilis from colder waters north of Bergen along the Norwegian coast to be larger than specimens from warmer waters to the south. Moore (1937) reported Echinocardium cordatum from

warmer waters south of Plymouth to be larger than specimens from colder waters to the north. Brattström (1946) reported Brissopsis lyrifera from cold, deep water in the Gullmar Fjord to be larger than specimens from warmer, shallow water. As is the case with many field observations, one cannot be certain whether temperature is directly influencing growth, indirectly influencing growth, or whether the observed correlation is entirely coincidental.

Child (1950) reared larvae of Dendraster excentricus under two different temperatures: 12°C and 22-24°C. The 10° temperature difference here greatly exceeds our requirements, but the results are nevertheless noteworthy. He found that plutei from the higher temperature lots had more widely divergent oral and aboral arms and larger oral lobes. Child made no attempt to feed the larvae and therefore, eventual effects on post-metamorphic morphology are unknown.

A later study of the same sand-dollar by Raup (1958) dealt with collections from different habitats along the Pacific coast of North America. He discovered that specimens from the warm end of the range had lighter tests with thinner margins, were more hump-shaped, had a more pentagonal outline, more inflated petals, and fewer large spine tubercles. Raup suggested that D. excentricus is relatively constant in genetic make-up throughout its range, but that water temperature applies subtle influences over patterns of

growth as the animal matures.

A temperature profile based on unpublished Hydro Data Reports of the Dept. of Oceanography, OSU, for the year 1967 is presented in Figure 21. Temperature readings entered in the graph were taken, in each case, at the shallowest station yielding data for the depth in question. In other words, these readings were not taken on the bottom, but they do give the best available approximation of true bottom temperatures. All stations are situated on a transect extending due west of Newport, Ore.

The decrease in bottom temperature one encounters moving offshore amounts to only a few degrees through our range of interest: 800 m temperatures are about 4 1/2° less than 100 m temperatures, and about 3° less than 200 m temperatures. Seasonal fluctuation at the latter two depths amounts to about 1°.

To attribute the marked differences in morphology observed in B. latifrons between 200 m specimens and 800 m specimens to a temperature gradient of only 3° seems hasty at this time. Rearing individuals under controlled temperature conditions would seem a prerequisite for drawing any conclusions. Plans were originally made to conduct such experiments but were later aborted by my inability to get healthy heart-urchins to the lab.

If temperature is the primary controlling factor in B. latifrons morphology, one would expect specimens taken off Alaska from cold

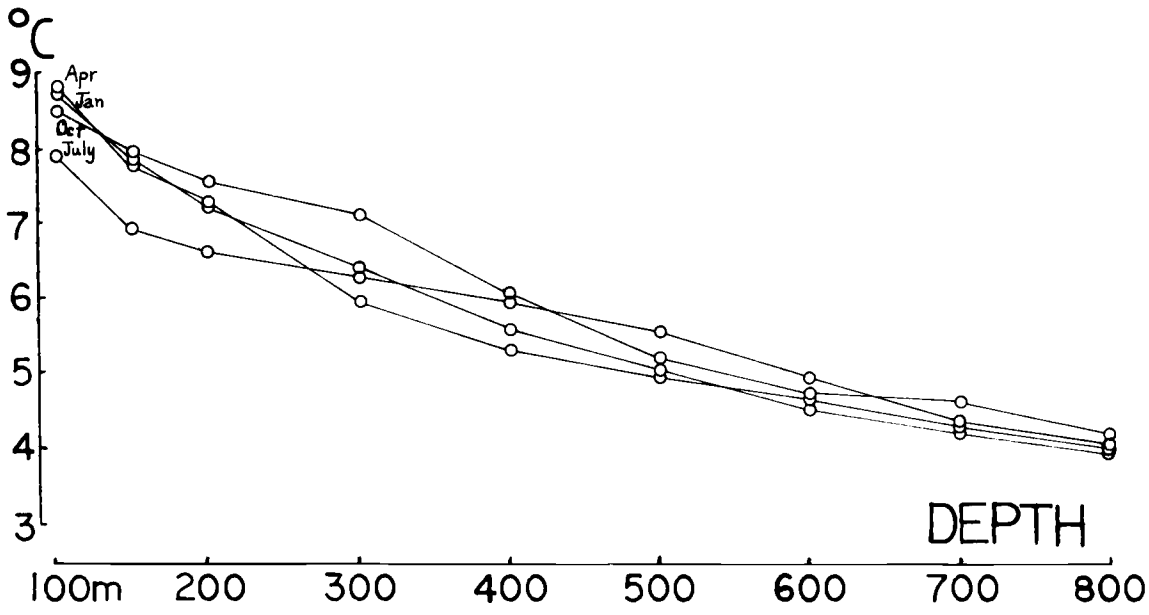

Figure 21. Graph of temperature versus depth off Newport, Ore. for the months of Jan., Apr., July, and Oct. From unpublished Hydro Data Reports, 1967, Dept. of Oceanography, OSU.

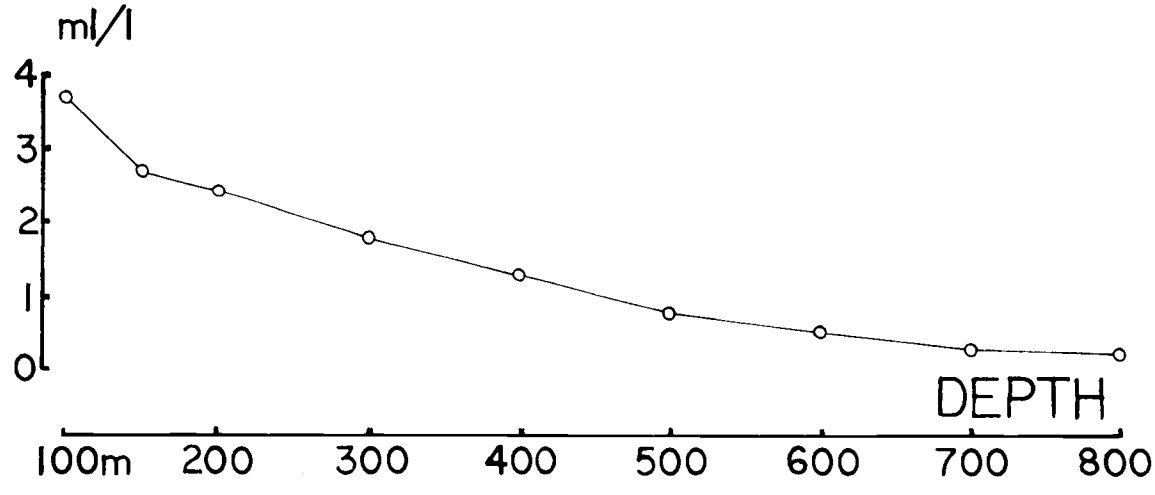

Figure 22. Graph of dissolved oxygen concentration versus depth off Newport, Ore. From unpublished Hydro Data Reports, 1967, Dept. of Oceanography, OSU.

but relatively shallow water to be similar to specimens taken off Oregon from deeper water of the same temperature. The same situation, only in reverse, would be expected among specimens taken off southern California. Albatross collections made in Alaskan and Californian waters were borrowed from the U. S. National Museum to test this hypothesis.

Three Albatross stations off Alaska yielded measurable specimens of "size" ($\sqrt[3]{\text{length x width x height}}$) greater than 30 mm, that is, comparable to local specimens. Bottom temperatures at the three stations fell within the temperature limits of our own 100-155 m, 400-600 m, and 800-840 m ranges. However, instead of exhibiting characteristics similar to those of Oregon specimens from corresponding temperatures, they revealed nearly an opposite trend. Specimens taken from the coldest water, (near Unalaska) had short, relatively narrow posterior petals, not at all like those from 800 m Oregon water. Specimens from warmer water, corresponding to our 100-155 m depth range, exhibited characters within the limits set by our local urchins from the same temperature but on the whole were more similar to Oregon specimens from the 400-600 m depth range.

Albatross collections from south of Oregon consist mostly of immature specimens. A broken test of a full-grown specimen taken at 1504 m off San Diego was found to compare more closely with

Oregon specimens from the 400-600m depth zone than with those from the 800-840 m depth zone; the bottom temperature, however, was identical to that at 800 m off Oregon.

Because the temperature difference between 200 m and 800 m is so slight and because the Albatross data present contradictions, one is strongly discouraged from suggesting that water temperature is responsible for the differentiation of the shallow and deep variant.

Organic Carbon Content of the Sediment

Before the relationship between food availability and test morphology are discussed, it may be wise to attempt an understanding of the animal's feeding habits under normal conditions. Much confusion exists in the literature concerning this matter.

The first observations of spatangoid feeding were made by Robertson (1871). He maintained that the penicillate tube feet of the anterior ambulacrum of Echinocardium cordatum were extended up the respiratory funnel to the sediment surface where they groped around for particles of food. Certain subsequent authors (Nichols, 1959b) doubted that these antics of the tube feet were part of a feeding mechanism, rather that hypoxious conditions in the aquarium were forcing the urchins to exhibit abnormal behavior. Chesher (1963), with Moira atropos, and later Buchanan (1966) with E. cordatum conclusively demonstrated with stained particles that the tube feet

of the frontal ambulacrum do, indeed, extend up the funnel and pick food from the sediment surface. Instead of bringing the particles around to the mouth, however, as Robertson suspected, the tube feet drop them into the anterior ambulacrum where they are bound in a mucous rope and swept orally by spines along its floor. Oral tube feet then transfer the particles of food to the mouth.

B. latifrons has highly modified tube feet and mucous-secreting spines but, to my knowledge, has never been observed feeding. The anterior ambulacrum is deep and seems well suited for the type of feeding described above for Moira and Echinocardium. On the basis of morphology alone, I expect that it has the capacity to feed in a very similar manner.

Savilov (1961) attached considerable importance to feeding behavior when he organized the fauna of the Okhotsk Sea into biocoenoses. B. latifrons is included among the "bottom swallowers" characterized by the following:

> They feed by means of unselective swallowing of a large volume of bottom rich in organic matter. The absence of special organs for selective capture of food and good development of the intestines are characteristic of these animals which dig into the bottom and are not usually very motile. (Savilov, 1961, p. 79)

Filatova and Neyman (1963, p. 8 of the JPRS translation), who defined a number of benthic biocenoses in the Bering Sea, also report that Brisaster ". . . scavenges the ground non-selectively . . ."

I conducted a simple experiment to test the bottom swallowing hypothesis: the contents of the gut of several specimens were removed and analyzed for percent organic carbon in a manner described by Carey (1965). The contents of the small intestine yielded 3.75% organic carbon by weight, the large intestine, 3.45%. The organic carbon content of sediment taken in the same area was approximately 1%; indicating at least a 3-fold increase in organic carbon as one goes from the sediment to the heart-urchin's gut.

While the results of this experiment do not conclusively disprove bottom swallowing, they do make it a slightly less tenable hypothesis: it is difficult to account for the 3-fold increase in organic carbon if feeding is entirely non-selective.

Eichelbaum (1910) examined the gut contents of 13 specimens he believed to be Brisaster fragilis. He reported that the gut was plumply filled with the bottom material which the urchin inhabits. He found foraminifera in such large quantities, however, that he designated them as the principal food type. Gut contents of B. latifrons that I examined consisted of very little identifiable material. Gross examination revealed little difference from the sediment itself. A few foraminiferan, radiolarian, and empty diatom tests; assorted calcareous spicules, and an occasional polychaete tube fragment were among the identified objects. No obvious concentration of any particular food type was observed.

It seems advisable at present to accept the proposition that the animal is capable of indulging in both types of feeding behavior. . . selective feeding and bottom swallowing. The alimentary tracts of Echinocardium cordatum from the channel coast of France were found to be plumply filled with sand low in organics (Lafon, 1953), despite the fact that the animal's ability to feed selectively has been established (Buchanan, 1966).

The mouth and adjacent areas of 28 specimens of B. latifrons were closely examined in this study. Small pedicallariae, born by several of the peristomial plates lining the dorsal lip of the orifice, were discovered in 19 of the specimens. They were of four types: tridentate (sessile or stalked with valves up to 0.7 mm long), biphyllous, triphyllous, and tetraphyllous (the latter three always stalked with much smaller valves). Because they are directed posteriorly into the lumen of the esophagus and probably cannot be extended outside the mouth, it is improbable that these pedicellaria could be of any use in selection of food types. Nevertheless, their presence (and in particular the presence of the bi- and tetraphyllous varieties, which were not found anywhere else on the urchin) may be of some interest to the anatomist.

The hypothesis to be tested presently is that the availability of food is responsible for the differences between the shallow and deep variants. Analysis of the sediment reveals that there is a marked

increase in organic carbon concentration as one moves offshore. McCauley and Carey (1967) reported concentrations of 0.93-1.27% by weight at a 200 m station, and a 2.53-2.77% at a 780-800 m station off Oregon. At present, this is our best measure of food availability; its relevance, obviously, will depend on the results of further research into the dietary habits of the urchin.

The fact that B. latifrons reaches a maximum size at 200 m, and reaches a maximum density at 150-400 m, i.e., where carbon content is not maximal, detracts from the worth of the above hypothesis. One would expect size and density maxima to coincide with high, not low, organic carbon concentrations if food shortage were, indeed, the basis of the stress involved in the differentiation of shallow and deep variant.

Although not necessarily associated with the availability of food, it was noticed in this study that specimens from about 400 m and less (essentially the shallow variant) had well-developed alimentary tracts, characteristically filled plumply with sediment. Specimens from 600 m and more (the deep variant) had very poorly developed tracts, often devoid of sediment. Not only were the diameters of the lumina of these deeper specimens much reduced, but the lengths of the various intestinal loops and ceca were less. These observations lead to the hypothesis that the pressure of a distended intestine against the inside of the urchin's test could, in time, have

an effect on the shape of the test. Mortensen (1907, p. 109) called attention to the tendency of Brisaster fragilis and especially Spatangus purpureus to yield a greater length if the right side of the test is chosen for measurement rather than the left side. He offered no explanation for the phenomenon. Brattström (1946) considered specimens exhibiting this trait monstrosities. I have encountered the same situation many times in specimens from 400 m and less, but only rarely in deeper specimens. The fact that a low bulge on the ambitus about midway along the left side of the test usually accompanies an overdeveloped right side lead me to search for an explanation. It happens that the junction of the small intestine and large intestine forms a loop immediately beneath the anterior extremity of the test on the right side; and that the large intestine forms a loop immediately beneath the test along the ambitus on the left. Both loops are situated exactly under those two areas of the test that bear the asymmetrical swellings and are almost certainly responsible for them. I would attribute the rarity of these test variations among deep-water specimens to the fact that their guts only infrequently are found distended with food.

The asymmetrical bulging seems to effect the length of nearby petals. Petal V, situated near the left ambital bulge, is typically longer than its counterpart (petal I) in those specimens exhibiting the anomaly. The contrast between petals II and IV (the former,

more often than not, exceeds the latter) is not as marked: the effect of the left ambital bulge on petal IV nearly offsets the effect of the right anterior bulge on petal II.

In addition to petal length, internal pressure may effect the ratio of width to length and the level of maximum width. Neither of these parameters were compared statistically in this study but qualitative observation pointed to a tendency for specimens from shallow water to have a greater relative width and a more posterior level of maximum width than deep water specimens. The bulk of the alimentary canal, the large intestine, is situated in somewhat of a semicircle in the posterior part of the urchin. One would expect internal pressure to be maximal in this region. The logical consequence would be a widening of the test of the shallow variant in the posterior region, a tendency supported by observation. Whether this hypothesis is the basis of the taxonomic character "Greatest width of test at or in back of middle" suggested by Clark (1917, p. 179) to distinguish B. latifrons and two other Brisaster species from B. townsendi is not known.

To suggest that pressure from internal organs is solely responsible for the several differences between the shallow and deep variant would be overstepping the facts. As just noted, a slight increase in petal length accompanies a nearby bulge. It is the shallow variant that bears the bulges, but it is the deep variant that bears the longest

petals. This contradiction in itself forces one to reject the hypothesis that internal pressure is the sought-after variable.

Dissolved Oxygen Concentration

Dissolved oxygen concentrations in the oceans range from zero to about 8.5 ml/l (0.75 mg-at/l) (Sverdrup et al., 1942). Concentrations in surface waters are high (primarily due to dissolution of atmospheric oxygen); concentrations in deeper waters are lower (primarily due to biological depletion). An oxygen minimum at intermediate depths is practically a universal feature in the world ocean (Richards, 1957). Figure 22 illustrates graphically the oxygen gradient encountered as one moves into deeper water off the Oregon coast through our range of interest. Data for the graph were taken from unpublished Hydro Data Reports for the year 1967, Dept. of Oceanography, OSU.

Again, the water samples yielding the data were not collected on the bottom, and therefore only approximate the oxygen tension to be measured there. Even if data on oxygen concentration at the sediment surface were available, however, it would not be strictly applicable to this study. The water from which B. latifrons derives its oxygen is necessarily influenced by the interstitial oxygen concentration of the sediment. The extent of the influence cannot be estimated without information on the existence or size of accessory

respiratory burrows the urchin might construct. Nevertheless, it can be assumed that the water available to the urchin has somewhat less dissolved oxygen than that shown in Figure 22 at the same depth. This may be particularly true near the deeper limits of B. latifrons' range (about 800 m) for two reasons: (1) the finer sediment results in poorer ventilation between particles, (2) the higher organic content invites a greater number of oxygen-depleting decomposers. At any rate, purely on the basis of hydro reports, the oxygen concentration at 800 m (0.26 ml/l) is about 1/9 the concentration at 200 m (2.42 ml/l) and about 1/14 the concentration at 100 m (3.70 ml/l). A strong gradient exists here which should not be overlooked as a potential factor in B. latifrons variation.

Modes of respiration in the spatangoids have been deduced from morphology alone. The gills found in most of the regular echinoids are lacking in the Irregularia; instead, they have specialized respiratory podia. In B. latifrons these podia are restricted to the lateral petaloid ambulacra (I, II, IV, and V). Ciliary currents moving down the ambulacra are believed to enhance respiratory exchange across the surface of the tube feet (Cuenot, 1948). Some spatangoids, particularly those that burrow deeply, maintain communication with the water column via an accessory burrow called the respiratory funnel (Durham, 1966). As mentioned earlier, it is not known whether B. latifrons builds such a burrow.

Oxygen consumption rates have been determined for a number of echinoderms (Farmanfarmaian, 1966; Lewis, 1968), but Brisaster is not among them. If the oxygen supply to an organism is lessened to a critical level, that organism may or may not have the ability to adjust. Those holothurians with respiratory trees increase their breathing rate under hypoxious conditions (Lutz, 1930). To my knowledge, no such outlets are available to spatangoids. Farmanfarmaian (1966, p. 255) wrote: "It is well established that asteroids do not regulate oxygen consumption. This may also be true of echinoids." In B. latifrons, adaptation to low oxygen concentrations might be accomplished in several ways: (1) produce a greater number of respiratory podia, (2) increase the size or efficiency of existing respiratory podia, or (3) reduce the demand for oxygen by suppressing digestion, reproduction, and other metabolic functions.

There is evidence to suggest that B. latifrons from depths of 600 m and greater have actually implemented the latter two of the above three possibilities. The respiratory podia, and possibly their accompanying ampullae, are best developed in specimens from the 800-840 m depth zone. This would seem to increase the effectiveness of the podia by enlarging the surface area across which gaseous exchange can take place. The development of the alimentary tract and gonads reaches a minimum in specimens from the 800-840 m depth zone. Other things equal, one would expect a reduction in the

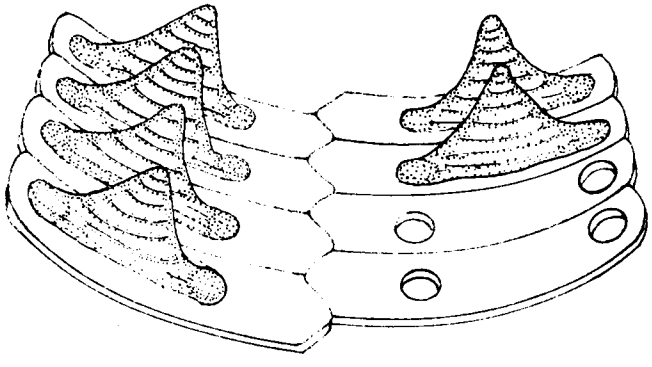

Figure 23. The central portion of one of the lateral petaloid ambulacra. Two of the respiratory podia have been removed from the right-hand column to show the position of the pores.

total oxygen requirements of the organism.

The first of the three possibilities is not subscribed to, in fact the opposite may be true. The deep variant usually has more respiratory podia in the posterior petals than the shallow variant of comparable size, but this difference is more than offset by a shortage of respiratory podia in the antero-lateral petals (see Table 11). A specimen from 200 m, then, may actually have more respiratory podia than a comparable 800 m specimen though the latter has longer petals. The individual plates comprising the petals of the 800 m specimens are simply longer and wider.

The plates of the lateral petals form two intercalating columns extending the length of the petal. Each plate is roughly rectangular (the long axis being perpendicular to the axis of the petal) and bears an upright, triangular podium (Figure 23). Each podium is anchored to its plate at two points, namely, the pore at each end of the plate. The greater the width of the column (or the petal), the greater is the length of the plates, the greater is the separation between the pores, and in turn, the greater is the base of the podium that spans the pores. Thus, if a lateral petal widens, its respiratory podia lengthen, thereby generating additional surface area.

If a lateral petal lengthens, the increase in length may be attributable to two components, both of which would seem to result in more efficient respiration: (1) the plates may increase in number,

(2) the plates may increase in width. The former increases the number of respiratory podia; the latter increases the distance between consecutive podia and thereby, enhances ventilation. The importance of keeping the podia free from one another is born out by the existence of long, narrow spines whose purpose apparently is to act as a "picket fence" to separate each podium from its neighbors. This function, of course, is conjectural, as it is based on the morphology of preserved specimens rather than on observations on living animals.

The purpose of the above is simply to point out the relationship between disproportionately large lateral petals and respiratory capacity. If dissolved oxygen concentration is, indeed, the environmental agent that is responsible for the contrast between the deep and shallow variants, one would expect to find differences in the respiratory apparatus to be particularly pronounced.

It is tempting to suggest that the lower oxygen tension at 800 m is responsible for disproportionate growth of these plates that bear the respiratory podia. An increase in the length and width of the lateral petals has been shown capable of effecting other morphological characters, such that a transition from shallow variant to deep variant on this basis becomes entirely realistic.

Differential growth of the lateral petals in the deep variant may or may not be simply a case of non-genetic adaptation. It is not yet

possible to indicate exactly which of the three pathways of differentiation listed on page 51 are acting here. One can, however, largely reject pathway (1), on the basis of the following reasoning: Assuming, for the moment, that intermixture of larvae is complete, metamorphosing urchins at each depth zone would run the complete gamut of genotypes. Individuals carrying genes for small, as well as large, petals would settle in both shallow and deep water. A selective agent such as oxygen concentration could, by creating a stress on the deep population, eliminate those individuals carrying genes for small petals, and thereby effectively control the petaloid characteristics of the adult population. No such stress would be placed on the shallow populations, however, and their members would be both of the small- and large-petaled variety. Since the shallow populations yielded small-petaled specimens only, the relative importance of pathway (1) must be minimal.

Pathways (2) and (3) are less easily dealt with. Despite the likelihood that the species has a pelagic larval stage, differential selection, acting over many generations (pathway 3), is a distinct possibility. This, of course, implies reproductive isolation, and involves somewhat of a reversion to the times when the names latifrons and townsendi were taxonomically distinct. McCauley (1967) presented sufficient evidence to justify suppressing the name townsendi, but did not eliminate the possibility that genetic

differences, arising from cumulative natural selection, are present, nonetheless. It will probably be necessary to conduct rearing experiments to determine whether the differences between the two variants are genetic or otherwise. A strong case for non-genetic adaptation (pathway 2) has been developed here, but whether its importance outweighs that of pathway (3) is simply conjectural.

The literature supplies very few examples of morphological alterations resulting from respiratory pressures. Nicol (1960) noted that Alcock (1902) reported finding the branchial chambers and gills of spider crabs and other decapods to be unusually large in an area of low oxygen concentration in the Indian Ocean. Gray (1957) measured the gills of 16 different species of brachyurans and found a reduction in gill area as he went from wholly aquatic species, through intertidal, to land species. The more active species had larger gill surfaces than inactive species. Gray's study concerns inter-specific differences in morphology, however, and in that respect is not truly applicable to the intra-specific variation observed in B. latifrons. A recent publication by Vernberg & Vernberg (1968) mentioned several respiratory modifications in intertidal crustaceans, including barnacles, but again, the variation under consideration was inter-specific.

The results of a biometrical analysis of Albatross specimens borrowed from the U. S. National Museum do not contradict the

oxygen hypothesis as they did the temperature hypothesis. Albatross Station 3316 at 565 m in the Bering Sea near Unalaska, yielded five specimens, three of which were of size $\geq$ 30. They have short lateral petals, much shorter than Oregon specimens from approximately the same depth. Dissolved oxygen determinations made at a station about 18 km to the northeast were published by Barnes and Thompson (1938, Table 15; Station C3). Oxygen data only to a depth of 400 m was reported, though a sounding revealed the depth at that station to exceed 1000 m. The concentration of dissolved oxygen was found to decrease (a small maximum was measured at 150 m) from the surface (0.586 mg-at/kg or about 6.7 ml/l) to 400 m (0.310 mg-at/kg or about 3.6 ml/l). Although the Albatross specimens came from slightly deeper water (565 m), it is apparent that oxygen concentrations in the area are considerably higher than those off Oregon in water of comparable depth: oxygen concentration at 400 m off Newport, Ore. averages only about 1.3 ml/l (unpublished Hydro Data Report, Dept. of Oceanography, OSU, 1967). I suspect that the high oxygen content of the water from which the urchins were taken allows them to respire adequately without developing disproportionately large lateral petals.

Other Albatross stations north of Oregon from which specimens are available are situated in the inland waters of the U. S. and Canada. Oxygen conditions there are more strongly influenced by

local currents and local phytoplankton blooms than are oxygen conditions in the open ocean. Lacking long-term data on dissolved oxygen concentration in the proximity of the Albatross stations, one is not equipped to search for a correlation between test morphology and oxygen concentration in these specimens. The same holds for collections made in Puget Sound. Biometrical analysis of specimens collected from hypoxious areas of certain fjords would be an excellent test of the hypothesis.

Albatross Station 3196 off San Luis Obispo at 366 m yielded individuals whose test features allied them to specimens collected in the 400-600 m depth zone off Oregon. Oxygen concentration measured at a nearby station (Station 77.55, CalCOFI Cruise 6607, Scripps Institution of Oceanography) was reported to be about 1.0 ml/l, a concentration which is typically measured at about 450 m off Oregon. This finding contributes to the correlation between oxygen and morphology.

Albatross Station 2923, in much deeper water (1504 m) off San Diego, yielded a single specimen whose features (short lateral petals, wide anterior ambulacrum) compare with those of the "shallow variant" taken off Oregon. Oxygen data from stations farther offshore reveal that the 1504 m depth lies below the oxygen minimum zone. Oxygen concentration at 1562 m at one such station was reported (Station 80.90, CalCOFI Cruise 5907, Scripps Instit. of Oceanog.)

to be 1.17 ml/l, a value which corresponds to concentrations measured off Oregon at about 400 m . . . . more evidence in support of the hypothesis that dissolved oxygen concentration and test morphology are related.

Because (1) there is a correlation between dissolved oxygen concentration and test morphology, both off the Oregon coast and elsewhere; (2) regulation of oxygen consumption has not been demonstrated in echinoids and growth of the petals bearing the respiratory apparatus would seem to be an effective method of increasing respiratory capacity; and (3) many of the other characteristics of the deep variant can be attributed to disproportionate growth of the lateral petals, I believe that oxygen concentration is the environmental variable primarily responsible for the differentiation of the shallow and deep variant. Although the several other factors discussed above existing in a gradient with depth (and, therefore, correlating, in this case, with test morphology) have been named by previous authors as agents of variability, they cannot, at this time, be linked in a cause-and-effect fashion to those structures that vary. Only the oxygen hypothesis has this advantage.

SUMMARY OF CONCLUSIONS

(1) Variation in Brisaster latifrons is a result of many factors, both genetic and non-genetic.

(2) Specimens taken in Oregon waters can be separated into two generalized variants corresponding roughly to published descriptions of B. latifrons and B. townsendi. The first, the "shallow variant," was taken at depths ranging from about 100 m to 400 m; the second, the "deep variant," was taken at depths ranging from about 600 m to 840 m. Intervening depths yielded intergrading specimens.

(3) The "deep variant" differs from the "shallow variant" by the following characteristics: (1) posterior petals longer and wider; (2) antero-lateral petals the same length or slightly longer, definitely wider, but consisting of fewer plates; (3) anterior ambulacrum narrower, shallower, bearing fewer spines, and consisting of fewer plates; (4) test height slightly greater; (5) apical system less eccentric; (6) gonads and gut less developed; (7) respiratory podia larger; (8) maximum attainable size less.

(4) Particle size has been suggested (Nichols, 1962) as a factor capable of influencing morphological characters of echinoids. A strong particle size gradient exists off Oregon. Its effect, if any, on test morphology is unknown.

(5) Water temperature, also, has been suggested (Raup, 1958)

as a factor capable of influencing echinoid morphology. The gradient existing off Oregon, however, amounts to only about 3^{o} between 200 m and 800 m. To attribute the marked morphological differences exhibited by specimens from these depths to so small a gradient seems hasty at this time.

(6) Feeding in Brisaster has been described (Savilov, 1961) as bottom-swallowing. On the basis of morphology, however, a more selective secondary feeding mechanism seems probable. Gut contents indicate little, if any, selectivity; nevertheless, organic carbon concentration of gut contents was about three times that of the sediment. Conclusions must be withheld until direct observations can be made.

(7) The trawl taken at a station with sandy sediment yielded stunted specimens. The low organic content of the sediment is tentatively held responsible for inhibiting growth in this case.

(8) Pressure from a distended gut may, in time, alter test morphology. Low bulges on the tests of some specimens, particularly those from 400 m and less, correlated with fullness of the intestines; the bulges are situated directly over intestinal loops.

(9) Dissolved oxygen concentration decreases markedly with increasing depth off Oregon through the range of interest here. It is proposed that low oxygen tension during the development of B. latifrons at depth is responsible for differential growth of the

plates that bear the respiratory podia. Many of the other characteristics of the "deep variant" can be linked to disproportionate enlargement of the lateral petals.

(10) Rearing specimens under controlled conditions may be necessary to fully understand the processes that govern differential inhibition or acceleration of growth: differential growth rates derived from longitudinal data being vastly superior to those from cross-sectional data. Suggestions for further work would best be made along these lines.

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