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Growth of a Sea Urchin, *Allocentrotus fragilis*, off the Oregon Coast[1]

JAMES L. SUMICH[2] AND JAMES E. MCCAULEY[3]

ABSTRACT: *Allocentrotus fragilis* (Jackson) was obtained from six stations at depths of 100 to 1,260 m on the continental shelf and upper slope off Newport, Oregon.

Ages and growth rates of *A. fragilis* were determined by two methods: (1) from size-frequency distributions of trawl collections from 200 m, and (2) from growth zones on skeletal test plates. Collections from other depths were not adequate for size-frequency analyses. Gonad indices of *A. fragilis* from 200 m were used to determine spawning periodicity and frequency. A semiannual frequency was suggested, with spawning occurring in early spring and early autumn. No individuals collected below 400 m were reproductively mature. A procedure was developed to make growth zones of the skeletal test plates visible. Dark growth zones are thought to correspond to semiannual periods of growth, one-half the number of dark growth zones indicating the urchin's age.

The growth curve of *A. fragilis* from 200 m, which was plotted from the mean test diameter of age groups defined by test plate growth zones, shows a good least-squares fit to von Bertalanffy's growth equation. Growth rates determined from plate growth zones appeared to be similar for *A. fragilis* from 100 to 600 m, but decreased for specimens from 800 to 1,260 m. The asymptotic size decreased with increasing depth below 200 m.

THE PINK SEA URCHIN *Allocentrotus fragilis* (Jackson) inhabits the continental shelf and upper slope of the west coast of North America from Baja California, to Vancouver Island, British Columbia, from a depth of 50 to 1,150 m (Mortensen, 1943). The physiology, reproduction, and ecology of this species have been studied by A. R. Moore (1959), Boolootian et al. (1959), and Giese (1961); and McCauley and Carey (1967) have discussed and summarized its distribution. *Allocentrotus fragilis* occurs in large numbers off Oregon where it is found on unconsolidated sediments, ranging from sand to clay silts (McCauley and Carey, 1967); and it is the dominant benthic organism, in terms of biomass, at 200 m off Newport, Oregon (Carey, 1972). Yet, no information on size specific growth and longevity of *A. fragilis* or other deepwater echinoids is available.

Ages and growth rates of sea urchins have been determined by one or a combination of the following methods: (1) tagging and observation of selected individuals in their natural habitat, (2) laboratory observation of urchins, (3) size-frequency distributions, or (4) analyses of cyclic growth indicators in spines and test plates.

Individual tagging, such as that used by Ebert (1965), is an effective way of following the growth of individual urchins, but is restricted to areas where urchins may be collected, tagged, and replaced for later recovery. Laboratory growth studies are normally restricted to shallow water urchins, because deepwater species such as *A. fragilis* often do not survive the rigors of collection or do not survive long in the laboratory (Boolootian et al., 1959). Giles (personal communication) kept a few *A. fragilis* from 200 m off Oregon in aquaria for about 5 months but made no conclusions about growth rates. Size-frequency distributions, used successfully by Fuji (1967) and Ebert (1968) to establish the ages and growth rates of two intertidal species of *Strongylocentrotus*,

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[2] Grossmont College, El Cajon, California 92020.

[3] Oregon State University, Corvallis, Oregon 97331.

require periodic large samples representative of a population.

A variety of patterns observed in the hard parts of various marine invertebrates has been related to periodic variations in the structure or pigmentation during growth. These are exemplified by growth lines of pelecypod shells (Clark, 1968; House and Farrow, 1968) and seasonal pigment bands in the shells of abalone (Olsen, 1968). Many echinoids also exhibit alternating light and dark bands in the plates of the test and in spines which are superficially similar to the annual growth rings found in woody plants.

Some echinoids, including *A. fragilis*, have spines which are too small for the ring-count method. The dark bands observed in the test plates of echinoids have received less study as age indicators than have spine rings, yet interpretation is theoretically much simpler. Breakage and loss of plates do not normally occur, whereas spine loss and damage is common (Ebert, 1967; Weber, 1969). The earliest formed plates are always associated with the urchin for its entire nonlarval life and, therefore, should represent the age of the urchin more accurately.

Deutler (1926) ground the plates of a variety of echinoids to make the dark bands visible, and H. B. Moore (1935), using a similar method with the genital plates of *Echinus esculentus* Linnaeus, found good agreement between the number of dark bands and age of the urchins as determined from size-frequency distributions. A darkly pigmented zone was added to each plate during the summer, and a lighter nonpigmented zone was added during the winter.

A much less tedious method of making dark bands visible, described by Jensen (1969), involves clearing the plates with an organic solvent. She found a pattern of test-plate-band formation for the North Atlantic urchin *Strongylocentrotus droebachiensis* (D. F. Müller) that suggested a maximum number of dark zones in the test plates representing the urchin's age in years.

For the present study, a modification of Jensen's method was used in conjunction with size-frequency distribution analyses to determine the age and growth rate of *A. fragilis*.

METHODS AND MATERIALS

Allocentrotus fragilis was collected by the Oregon State University Department of Oceanography as part of regular sampling programs. Samples from depths of 100, 200, 400, 600, 800, and 1,260 m were obtained along a line extending west from Newport, Oregon, near lat 44°39′ N, with otter and beam trawls. Population density at 200 m was estimated from an odometer-wheeled beam trawl collection.

The urchins, preserved in neutral formalin, were returned to the laboratory, scrubbed with a stiff brush to remove the spines, and measured from ambulacrum to the opposite interambulacrum. The two halves of an emptied test were rinsed, then placed in 25-percent household bleach (e.g., Clorox) for maceration, but were removed from the bleach solution before disarticulation of the test plates occurred. One interambulacral column and the adjacent ambulacral column of test plates extending from the peristome to the periproct were separated from the remainder of a test half. The plates were arranged in order, flat, on a 1-by-3-inch microscope slide with the inner side of the test plates up, and heated on a hot plate at 85° C for 3 hours to remove all moisture. After cooling, the plates were wetted with xylene, then saturated with Permount, and allowed to dry. Dark bands were counted under a 6 × dissecting microscope.

RESULTS

At the six stations sampled, *A. fragilis* was taken consistently only at the 200-m station (Table 1). The values are given only as a rough indication of *A. fragilis* abundance at each station, because trawling times were not always the same.

A beam trawl collection made on 15 March 1970 at the 200-m station yielded 687 *A. fragilis*. Approximately 3,200 m^2 of bottom area were sampled. Only otter trawl samples were obtained at the other stations. McCauley and Carey (1967) have shown, using a Benthos Time-Depth Recorder, that the otter trawl may be off the bottom as much as 75 percent of the time, making estimates of the area sampled extremely difficult and unreliable. Even so, data

Table 1

SUMMARY OF *Allocentrotus fragilis* COLLECTIONS AT LAT 44°39′ N SINCE APRIL 1963

STATION DEPTH	100 m	200 m	400 m	600 m	800 m	1,260 m
Number of Otter Trawls	10	38	4	6	26	6
Trawls with *A. fragilis*	1	38	3	3	4	1
Percent with *A. fragilis*	10	100	75	40	15	17
Maximum Number *A. fragilis*/Trawl	16	750	35	93	89	5

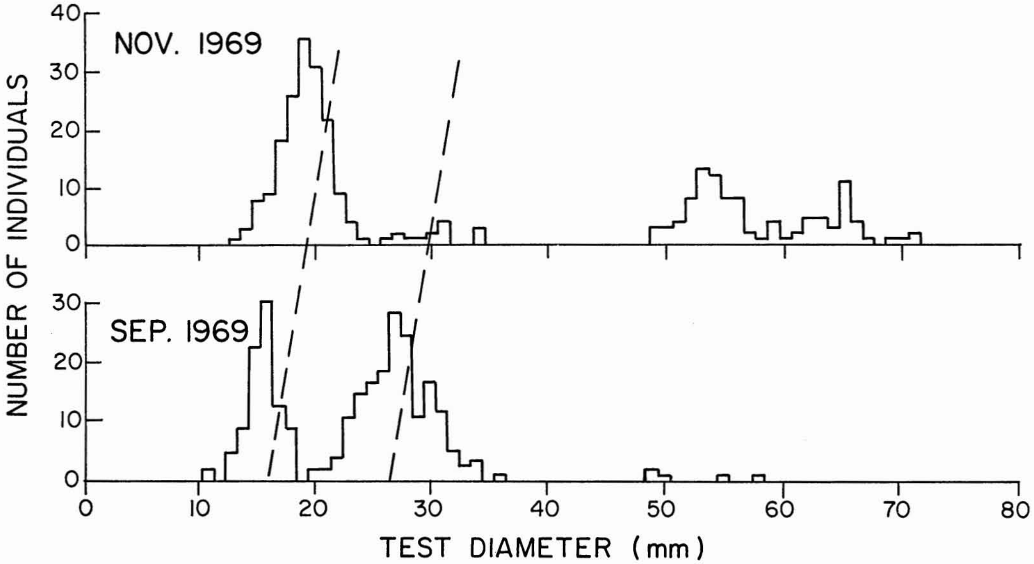

FIG. 1. Time series of *Allocentrotus fragilis* size-frequency distributions from 200 m. Dashed lines intersect the means of well-defined size classes which indicate assumed size increase with time.

provided in Table 1 show that *A. fragilis* were much more abundant at the 200-m station than at the other stations. Although trawling times were not consistent, shallow stations (100 and 200 m) tended to be trawled for shorter times, so that estimates of abundance at these stations are conservative.

The smallest *A. fragilis* test diameter, 8 mm, was assumed to be the minimum size catch capability of either the beam or the otter trawl nets, and test diameters smaller than the stretched size of the net liner (12 mm) were probably not representative of the sampled population.

Five *A. fragilis* from 1,260 m (lat 44°36′ N, long 125°02′ W) extend the bathymetric range 110 m deeper than 1,150 m (reported by Mortensen, 1943).

Size-Frequency Distribution Analysis

The usefulness and accuracy of size-frequency distributions as indicators of age depend on the following assumptions: (1) size-frequency peaks of successive age groups must be discernible; (2) growth rates within an age class are normally distributed; (3) the population sample should include representative numbers from all size classes present in the population; and (4) spawning must occur periodically with a spawning duration short in relation to the length of the reproductive cycle. Trawl collections of *A. fragilis* from stations other than 200 m were neither numerous nor periodic. Size-frequency analyses of these collections were not attempted due to small numbers of individuals collected

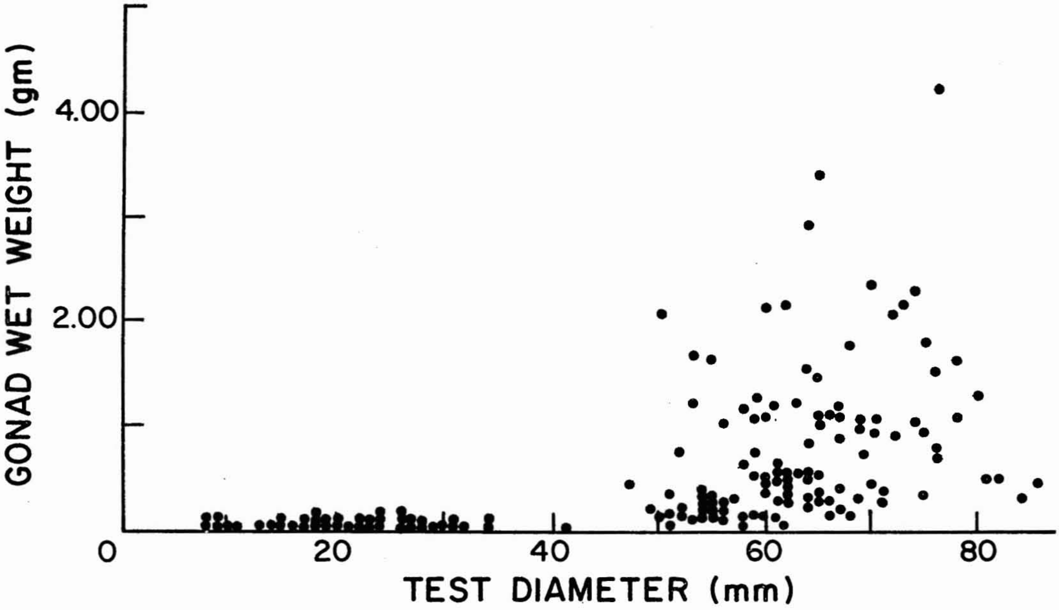

FIG. 2. Variation of gonad wet weight with test diameter of *Allocentrotus fragilis* from 200 m.

per trawl and to the lack of successive periodic collections at any one station.

The test diameters of *A. fragilis* from 11 trawl collections taken between October 1968 and March 1970 from the 200-m station were measured. The size-frequency distributions for the September and November, 1969, samples represent complete trawl collections and are shown in Fig. 1. The remaining trawl collections were either subsampled at sea or consisted only of large adult urchins exhibiting no discernible size classes.

The trawl collections taken in September and November, 1969, have two well-defined size classes of small urchins, each with means centered 10 to 11 mm apart. By assuming that each peak represented a separate age class and that the two November peaks were derived from the slightly smaller September peaks, we determined two different measures of *A. fragilis* growth rate. If the increase in the mean test diameter of each size class during the 2-month interval between the September and November collections was 3.2 mm for the smaller peak and 2.6 mm for the larger peak, this was equivalent to approximately 20 mm of annual test diameter increase for the small size class and 16 mm for the larger peak. This assumed annual size increase was approximately twice as large as that computed from the mean size difference between successive age classes (10 to 11 mm). The lack of agreement between the results of the two methods suggested that the growth rate calculated for the 2-month interval from September to November, 1969, was substantially greater than the average annual growth rate, that the size classes determined from size-frequency analysis corresponded to semiannual rather than annual recruitment classes, or that the trawls sampled separate populations.

Very little information exists about monthly or seasonal growth rate fluctuations of echinoids. Fuji (1967) obtained monthly measurements of the diameters of five-year classes of the intertidal *Strongylocentrotus intermedius* (A. Agassiz) and found that each year class exhibited a constant annual growth rate which differed from the other year classes. Similar observations of deepwater echinoids have not been made.

Reproductive Periodicity

Reproductive periodicity was studied only in specimens from the 200-m station, as the remaining stations had not been sampled successively.

Table 2

SUMMARY OF *Allocentrotus fragilis* GONAD WET WEIGHTS FROM STATIONS BELOW 200 METERS

DEPTH (m)	NUMBER OF SPECIMENS	GONAD WET WEIGHT (g) MEAN ± 1 SD	RANGE
400	14	0.22 ± 0.43	0.00–1.73
600	21	0.02 ± 0.05	0.00–0.22
800	21	0.02 ± 0.04	0.00–0.14
1,260	5	0.00 ± 0.00	0.00–0.01

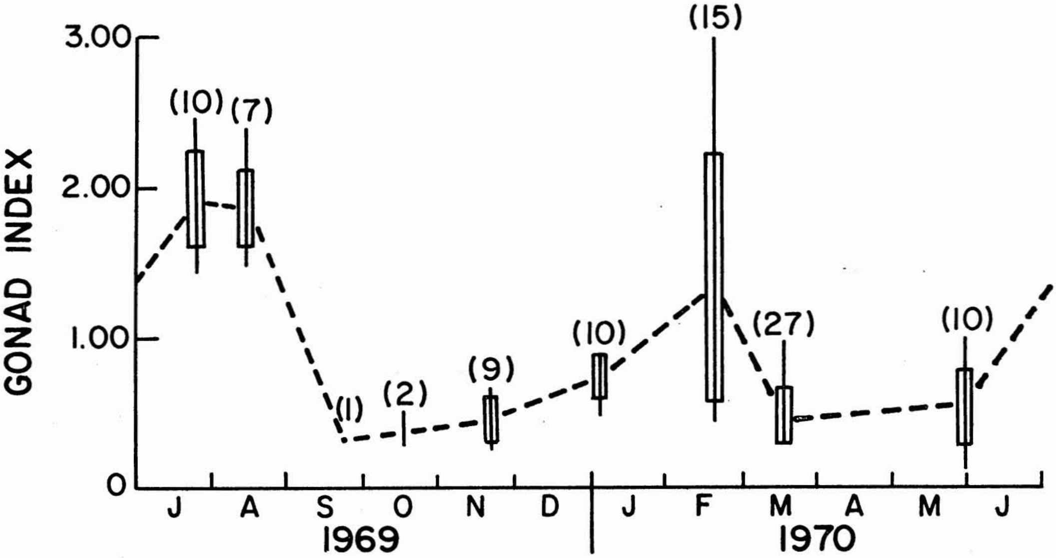

FIG. 3. Monthly gonad index variation of *Allocentrotus fragilis* greater than 49 mm in test diameter. Range of values is shown as a central vertical line. One standard deviation on each side of the mean is represented by a rectangle. The numbers of specimens are shown in parentheses.

The minimum size at sexual maturity was estimated by plotting gonad wet weight as a function of test diameter for 200-m station specimens (Fig. 2). The maximum gonadal weight was low for animals less than 45-mm test diameter, then increased rapidly for specimens larger than 50-mm diameter. The actual minimum size at sexual maturity may be less than 50 mm, but an unexplained paucity of specimens with test diameters between 35 and 50 mm restricted the study of gonadal development in this range.

Gonad indices, determined from the gonadal biomass, have been widely used as indicators of reproductive state and spawning period of echinoids (Boolootian et al., 1959; Giese, 1961; Boolootian, 1966; Fuji, 1967). The gonad index has generally been calculated as the ratio of gonad wet weight to the total wet weight of the animal (Boolootian, 1966). Accurate wet weights quite often could not be obtained from *A. fragilis* because of crushing and abrasion of the tests and spines during trawling and because the amount of fluid contained within the test or adhering to it could not be controlled. Therefore, test diameter rather than test volume or total wet weight was selected as a simple, but effective, indicator of size because the urchins used were approximately the same size. A gonad index was computed from the following formula:

$$\text{gonad index} = \frac{\text{gonad wet weight}}{\text{test diameter}} \times 100.$$

The gonad index values ranged from less than 0.1 for immature specimens to 3.3 for mature individuals.

Gonad wet weight determinations suggested that some urchins from the 400-m station were reproductively mature but all specimens from 600, 800, and 1,260 m had gonad indices of less than 0.3 and appeared immature (Table 2). Although data for the deep stations are limited, gonad indices suggest that *A. fragilis* does not achieve sexual maturity below 400 m.

Specimens from 200 m which were larger than the estimated minimum size at sexual maturity show marked semiannual peaks in gonadal weight, which strongly suggests two spawning seasons per year: one in late summer and one in later winter (Fig. 3). Two age classes are thus spawned each year. Earlier studies on the reproductive periodicity of *A. fragilis* at Monterey Bay, California, established a spawning period between January and March (Boolootian et al., 1959; Giese, 1961; Boolootian, 1966), but no reference was made to an autumn spawning period. There the spawning of *A. fragilis* is closely related to the onset of local upwelling, a condition common for benthic invertebrates which produce planktonic larvae. The spawning periods of *A. fragilis* off Oregon also appear to be closely associated with periods of high primary productivity of the surface waters (Anderson, 1964).

A. R. Moore (1959) found that at equivalent temperatures *A. fragilis* and *S. franciscanus* (A. Agassiz) larvae develop similarly up to at least the 5-day stage. After 5 days, his experiments were terminated. Details of the later larval development of *A. fragilis* are not known, but *S. franciscanus* larvae required 62 days to complete development from fertilization to metamorphosis (Johnson, 1930). Newly metamorphosed *S. franciscanus* are less than 1 mm in diameter. If the rates of late larval development of both species remain nearly equal, larval metamorphosis and settling of *A. fragilis* would be expected approximately 2 months after spawning. Off Oregon, settling would probably occur in April–May and October–November of each year.

Growth Zone Counts

Visible dark bands, or growth zones, in test plates of 5 to 30 specimens from each trawl collection were counted. The maximum number of growth zones in *A. fragilis* is not exhibited in any one plate of an interambulacral column. Plates near the peristome are the oldest. As the urchin grows, its existing plates increase in width and new plates are formed in the apical region. As more plates are formed they migrate from the apical region toward the ambitus, where they increase greatly in width but not in height. It is in the wide lateral areas of the plates that growth zones are best seen and counted. This growth process is shown in Fig. 4.

As the test diameter continues to increase, older plates migrate past the wide ambitus region toward the more narrow peristome. Lateral growth ceases as they pass the ambitus because the test area in which they are now located is no longer increasing in size. Cessation of lateral growth halts the formation of growth zones in these plates; but zones continue to be formed in the plates above the ambitus. Thus, the oldest plates near the peristome exhibit only earlier formed growth zones, not more recent zones. Younger plates, near the apical area, do not exhibit early growth zones but show only the more recent, some of which are not exhibited by older plates.

We counted growth zones by beginning with the center of the oldest plates near the peristome, counting growth zones laterally, moving up the corresponding growth zone to a younger plate, and counting laterally again. This process was repeated until all growth zones within an interambulacral series had been counted. (See Fig. 4.)

The maximum number of dark growth zones was determined for one interambulacral plate series of each urchin examined. The least number of dark growth zones found was one, in specimens 8 to 9 mm in diameter; the greatest number was 15 in a specimen 80 mm in diameter. Both specimens were collected from the 200-m station. The number of dark growth zones of the individuals was related to the distribution of test diameters. Some scatter and overlap occurred in specimens larger than 50 mm, but the size-frequency peaks less than 40 mm in diameter generally were composed of specimens with the same number of growth zones; specimens of successive age classes had consecutive numbers of dark growth zones.

The test diameters were plotted as a function of the maximum number of dark zones of the test plates of each specimen. A growth curve for

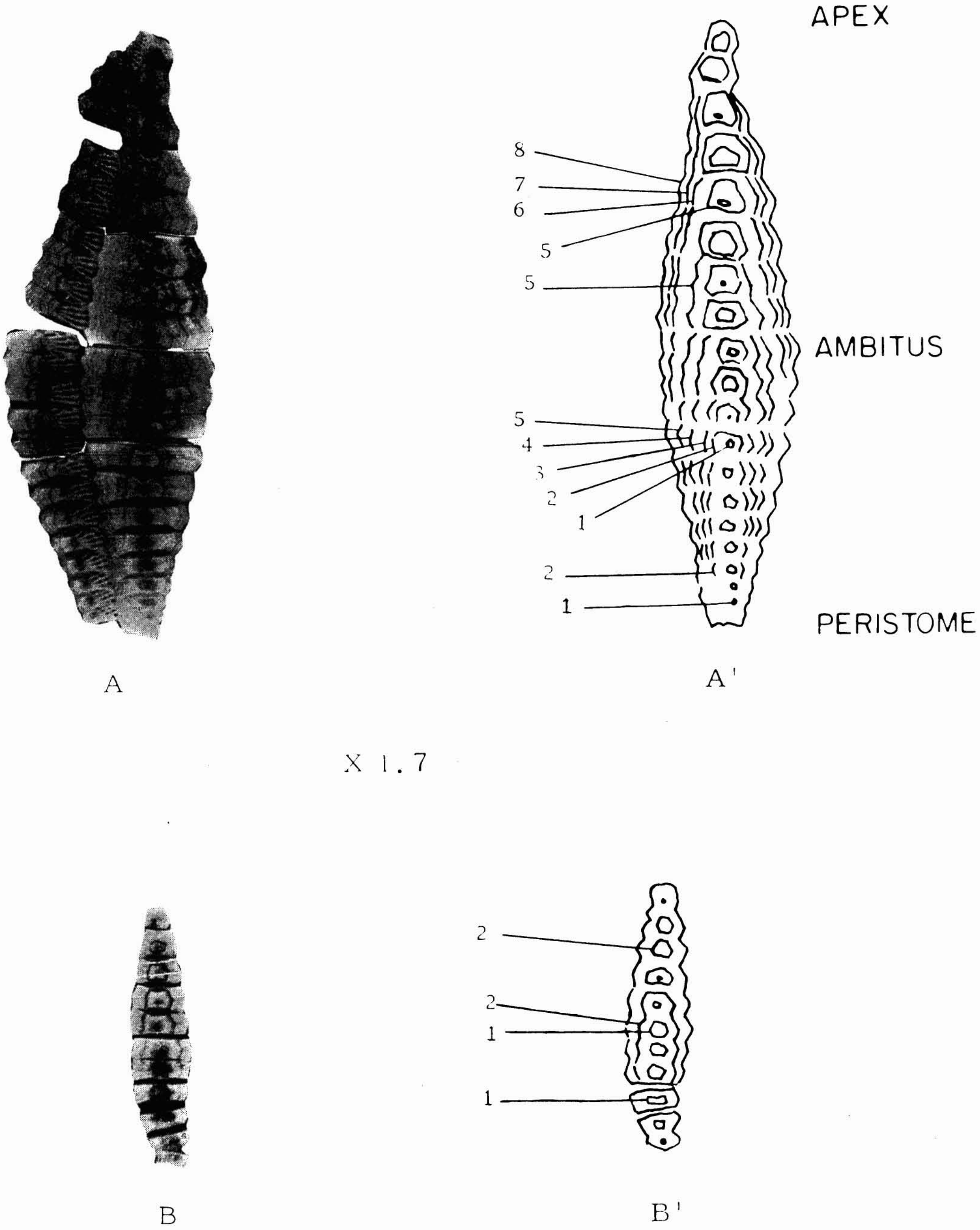

FIG. 4. Photographs and tracings of interambulacral columns of two *Allocentrotus fragilis* specimens from 200 m: *A*, from a specimen 53 mm in test diameter; B, from a specimen 17 mm in test diameter. The dark growth zones are numbered in *A'* and *B'* according to the order in which they were formed.

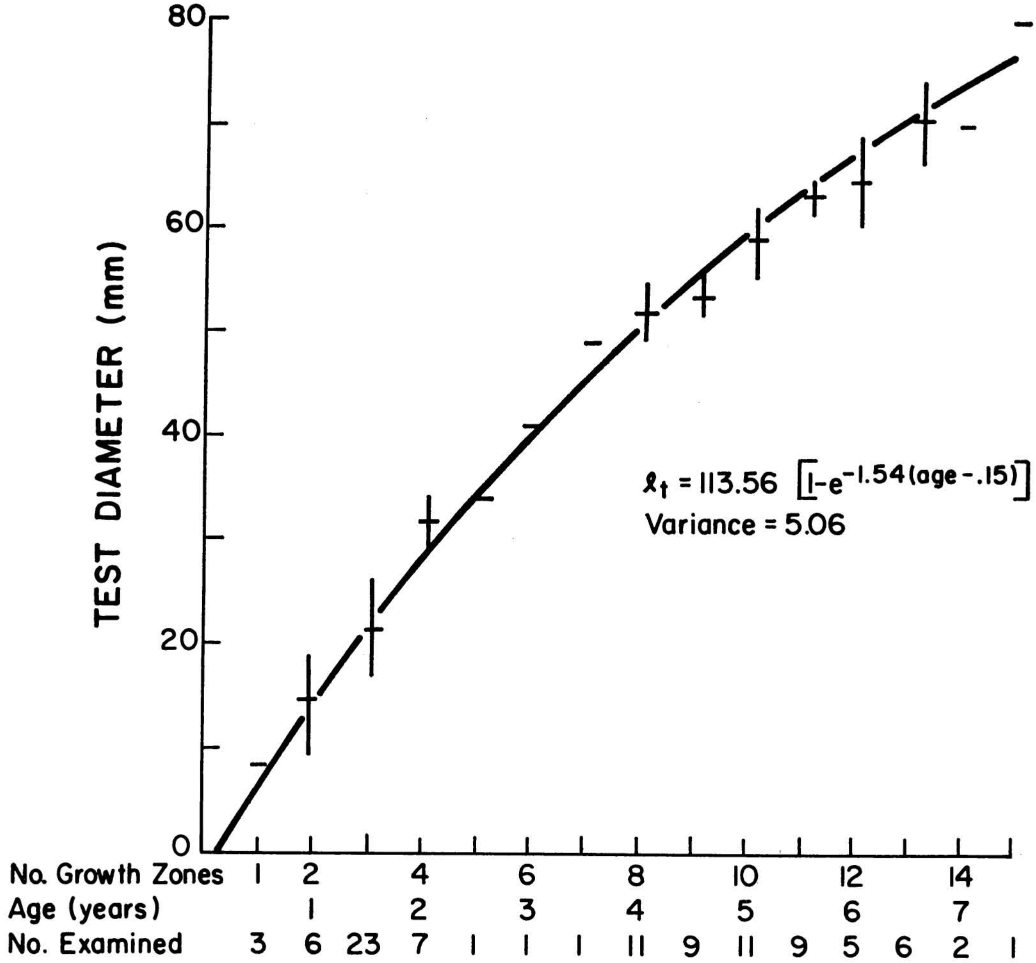

FIG. 5. Least-squares fit of von Bertalanffy growth curve for *Allocentrotus fragilis* from 200 m. Means ±1 standard deviation of each growth zone class are shown.

A. fragilis at 200 m was constructed using the test diameter means and standard deviations of each "growth zone class" (Fig. 5). The von Bertalanffy type of growth curve was fitted to the mean growth zone sizes using the method of least squares described by Tomlinson and Abramson (1961). Urchins from 200 m have approximate growth rates of 9 mm per growth zone period for 15-mm urchins, and 7 mm per growth zone period for 30-mm urchins.

These growth rates compare favorably with those determined by the mean size difference of successive age classes. This means that the frequency of spawning and the frequency of growth zone formation are the same. However, these growth rates do not agree with the growth rates estimated from the mean annual size increase of the age class.

Synopsis of Growth Rate Determinations

Agreement between the results of gonadal studies and of the different methods of growth rate determination can occur only if each age class and each new dark growth zone is added semiannually. H. B. Moore (1935) considered the growth zones of *Echinus esculentus* to be bands of food-derived pigment which were incorporated seasonally into growing skeletal material during the season of rapid intertidal plant

Table 3

FREQUENCY DISTRIBUTION OF TEST DIAMETERS OF *Allocentrotus fragilis* BELOW 200 METERS

TEST DIAMETER (mm)	400 m JUNE 1966	600 m APRIL 1963	600 m JUNE 1964	800 m AUGUST 1966	1,260 m JUNE 1966
16	—	—	—	—	—
17	—	—	—	1 II	—
18	—	—	—	—	—
19	—	—	—	1 II	1 III
20	—	—	—	1 III	—
21	—	—	—	1 III	—
22	—	1 III	—	1	—
23	—	—	—	1	—
24	—	—	1	—	—
25	—	2	—	—	—
26	—	1 IV	1 III	2 V	—
27	—	6	1	3 IV	1 V
28	—	4	2 III	2 IV	—
29	1 IV	11 IV	1	1	—
30	1 IV	8 IV	1	2	—
31	2	8	—	8 V	1 VI
32	—	6	2 IV	7 V	—
33	—	8	2 IV	4 VI	—
34	—	6	1	3 V	—
35	1 V	8 V	2	6 V	—
36	2 V	3	3	9 VI	—
37	1 V	4	3 V	6 IV	—
38	1	3 V	6 IV	9 VI	—
39	—	4 V	2	3 VI	2 VIII
40	1	2	1 V	3	—
41	1	3	1	3 VII	—
42	3	1 V	—	5	—
43	2	—	1 V	2	—
44	3	—	—	1	—
45	1 VI	1	—	2 VIII	—
46	2 VI	—	—	1	—
47	3	—	—	1 IX	—
48	—	2 VII	—	—	—
49	1	—	—	—	—
50	—	—	—	—	—
51	2	—	—	—	—
52	2 VII	—	—	—	—
53	3 VII	—	—	—	—
54	—	—	—	—	—
55	—	—	—	—	—
56	—	—	—	—	—
57	1 IX	—	—	—	—
58	—	—	—	—	—

NOTE: Arabic numerals represent numbers of animals for each size class. Roman numerals represent numbers of dark growth zones found in urchins of that size class.

growth. Growth zones in the plates of *A. fragilis* seem to reflect semiannual fluctuations of the amount of pigmented organic material available from surface productivity, which suggests that the two pigmented zones formed annually are the result of semiannual plankton blooms in surface water.

Examination of *A. fragilis* gut contents shows that this species is a particulate detrital feeder and could incorporate into its test seasonally fluctuating amounts of plant pigment produced during spring and fall phytoplankton blooms. However, no published information on the chemical composition of the pigmented bands

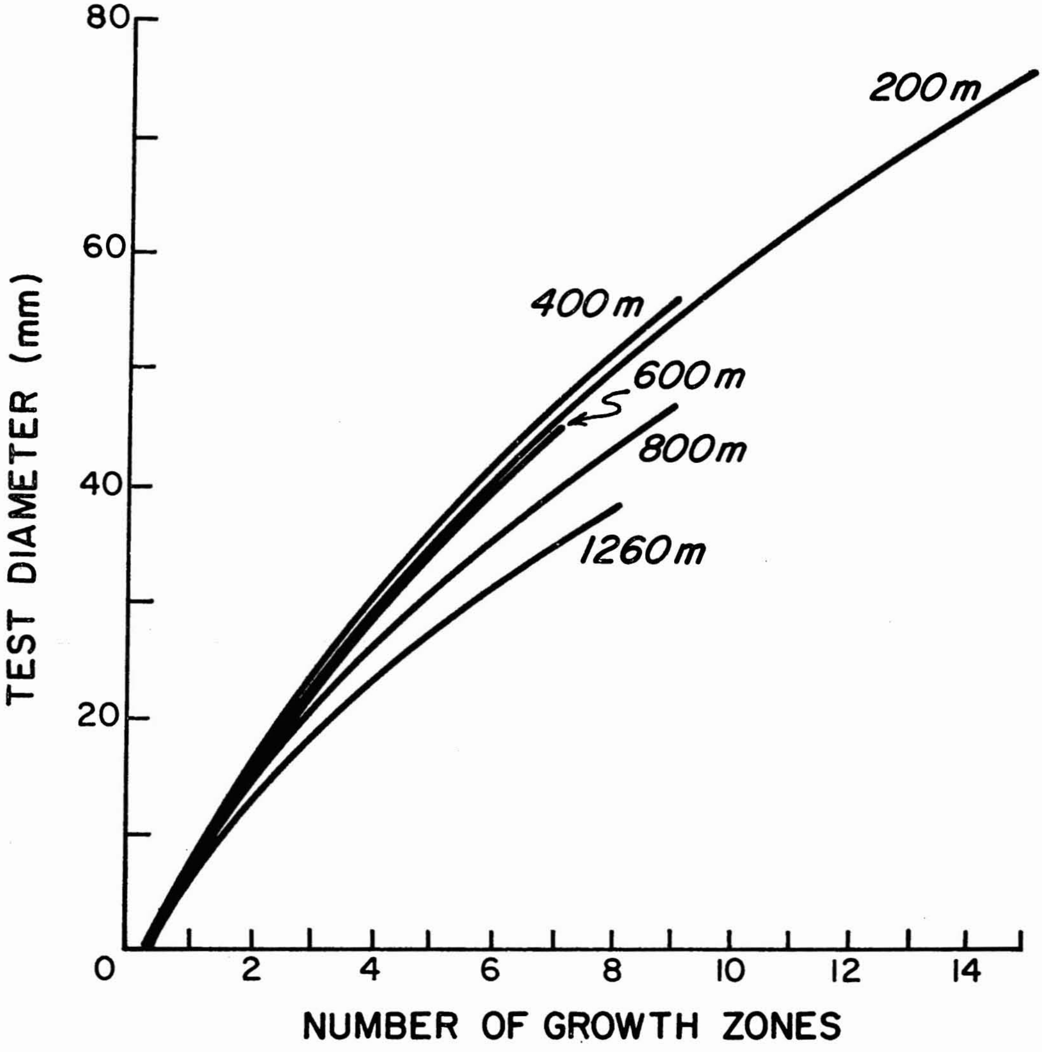

FIG. 6. Compilation of *Allocentrotus fragilis* growth curves from all stations. The 200-m growth curve is from Fig. 5. Other curves are fitted by eye to data presented in Table 3.

of any echinoid test plates is available to confirm this.

If two growth zones are formed each year, the data in Fig. 5 suggest growth rates of 20 mm per year for 20-mm urchins and 18 mm per year for 30-mm urchins from the 200-m station. These growth rates were essentially equal to those calculated from the shift of the mean size of each age class between September and November, 1969.

Although information on maximum ages for other strongylocentrotoid urchins is sparse and to a large extent based on circumstantial evidence, some comparisons may be made. Fuji (1967) followed the growth of *S. intermedius* for 5 years, until the urchins were near the maximum size for that locality. Swan (1961) found, using size-frequency studies and laboratory growth studies, that *S. droebachiensis* attained a test diameter of 52 to 54 mm in 4 years, but Jensen (1969) reported 11 annual growth zones in the test plates of a 51-mm *S. droebachiensis* specimen from Norway. *Strongylocentrotus purpuratus* are thought to live at least 10 years (Ebert, 1967).

The maximum *A. fragilis* age of 7.5 years, determined from growth zone counts of an 80-mm specimen, compares favorably with the reported maximum ages of other strongylocentrotoids. Individuals up to 88 mm in test diameter were collected in this study and larger specimens have been reported. Thus, this species may be expected to live at least 10 years.

Age and growth rates for *A. fragilis* from the remaining stations were computed from data presented in Table 3 in a manner similar to those at 200 m, but data were insufficient to apply the Tomlinson and Abramson (1961) least squares method of curve fitting. Growth curves for these stations were fitted by eye. These curves and the fitted curve of the 200-m station are shown in Fig. 6. The age range of *A. fragilis* from the 100-m station was small and no growth curve was plotted; however, its growth rate appears to be similar to that at 200 m. The growth curves for all stations were assumed to have the same *x*-intercept, representing the assumed duration of the larval stage.

Little apparent difference exists between the growth rates for *A. fragilis* from 100, 200, 400, and 600 m. This similarity suggests that food availability does not vary significantly among these stations. However, the growth rates for the urchins from 800 and 1,260 m are markedly less than the rates for the more shallow stations. Maximum age and maximum test size are also less at the deeper stations. It is tempting to propose such factors as low food availability or poor larval settlement as possible causes for the reduced growth rates, smaller maximum size and age, and reduced densities exhibited by *A. fragilis* at the deeper portions of its bathymetric range. However, the general lack of information regarding the feeding habits, substrate preferences, patterns of larval settlement, and responses to hydrologic conditions of *A. fragilis* and many other deepwater species of benthic animals makes such suggestions premature and emphasizes the need for further research in these areas.

LITERATURE CITED

ANDERSON, G. C. 1964. The seasonal and geographic distribution of primary productivity off the Washington and Oregon coasts. Limnol. Oceanogr. 9: 284–302.

BOOLOOTIAN, R. A. 1966. Reproductive physiology, p. 561–614. *In:* R. A. Boolootian [ed.] Physiology of Echinodermata. John Wiley and Sons, Interscience, New York. xviii + 822 p.

BOOLOOTIAN, R. A., A. C. GIESE, J. S. TUCKER, and A. FARMANFARMAIAN. 1959. A contribution to the biology of a deep sea echinoid, *Allocentrotus fragilis* (Jackson). Biol. Bull., Woods Hole 116: 362–372.

CAREY, A. G., JR. 1972. Ecological observations on the benthic invertebrates from the central Oregon continental shelf, p. 422–443. *In:* A. T. Pruter and D. L. Alverson [ed.] The Columbia River estuary and adjacent ocean waters: bioenvironmental studies. Univ. Wash. Press, Seattle. xiii + 868 p.

CLARK, G. R., II. 1968. Mollusk shell: daily growth lines. Science 161: 800–802.

DEUTLER, F. 1926. Über das Wachstum des Seeigelskeletts. Zool. Jb. 48: 119–200.

EBERT, T. A. 1965. A technique for the individual marking of sea urchins. Ecology 46: 193–194.

———. 1967. Negative growth and longevity in the purple urchin *Strongylocentrotus purpuratus* (Stimpson). Science 157: 557–558.

———. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. Ecology 49: 1075–1091.

FUJI, A. 1967. Ecological studies on the growth and food consumption of Japanese common littoral sea urchin, *Strongylocentrotus intermedius* (A. Agassiz). Mem. Fac. Fish., Hokkaido 15: 83–160.

GIESE, A. C. 1961. Further studies on *Allocentrotus fragilis*, a deep-sea echinoid. Biol. Bull., Woods Hole 121: 141–150.

HOUSE, M. R., and G. E. FARROW. 1968. Daily growth banding in the shell of the cockle, *Cardium edule*. Nature 219: 1384–1386.

JENSEN, M. 1969. Age determination of echinoids. Sarsia 37: 41–44.

JOHNSON, M. W. 1930. Notes on the larval development of *Strongylocentrotus franciscanus*. Publ. Puget Sd. Mar. (Biol.) Sta. 7: 401–411.

McCAULEY, J. E., and A. G. CAREY, JR. 1967. Echinoidea of Oregon. J. Fish. Res. Bd. Can. 24: 1385–1401.

MOORE, A. R. 1959. On the embryonic development of the sea urchin *Allocentrotus fragilis*. Biol. Bull., Woods Hole 117: 492–496.

MOORE, H. B. 1935. A comparison of the biology of *Echinus esculentus* in different habitats. Part II. J. Mar. Biol. Ass. U.K. 21: 109–128.

MORTENSEN, T. 1943. A monograph of the Echinoidea. Vol. 3, Pt. 3. Camarodonta II, Echinidae, Strongylocentrotidae, Parasaleniidae, and Echinometridae, p. 183–193, 254. C. A. Reitzel Co., Copenhagen.

OLSEN, D. 1968. Banding patterns of *Haliotis rufescens* as indicators of botanical and animal succession. Biol. Bull., Woods Hole 134: 139–147.

SWAN, E. F. 1961. Some observations on the growth rate of sea urchins in the genus *Strongylocentrotus*. Biol. Bull., Woods Hole 120: 420–427.

TOMLINSON, P. K., and N. J. ABRAMSON. 1961. Fitting a von Bertalanffy growth curve by least squares. Fish. Bull. Calif. Dep. Fish Game 116.

WEBER, J. N. 1969. Origin of concentric banding in the spines of the tropical echinoid *Heterocentrotus*. Pacif. Sci. 23: 452–466.