LIFE HISTORY PATTERNS OF THREE ESTUARINE BRITTLESTARS
(OPHIUROIDEA) AT CEDAR KEY, FLORIDA

by

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Chairman: Frank J. S. Maturo, Jr.
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The polyhaline estuary at Cedar Key, Florida, has a high diversity of echinoderms, most of which possess reproductive modifications that appear to adapt them to unpredictable environmental variability. To gain clearer insight into this problem, populations of three ophiuroids with different modes of development were studied. Collection of monthly population samples and analysis of growth, mortality, reproduction and respiration showed that the three populations exhibit different life history patterns, each providing them with high fitness in an unpredictably variable environment. The disappearance of the Ophiothrix angulata population at the end of the first year of study (July, 1973) was correlated with a poor spring recruitment due to low salinities and with high summer mortality of adults during periods of warm water temperatures. O. angulata has a short life and low tolerance of environmental fluctuations. It has a short-lived planktotrophic larva and spawns year-around. Individuals have only one

spawning season. It is a fugitive species selected for high dispersal and the ability to colonize and recolonize disturbed habitats after local extinction. Ophiophragmus filograneus is a short-lived species, probably has direct development, and breeds year-round. Individuals have but one spawning season. Its tolerance of environmental variability is broad and it appears to be selected for low dispersal and high survival of both adults and young through most environmental fluctuations. Ophioderma brevispinum is long-lived, has a short-lived vitellaria larva and broad environmental tolerance range as an adult. The spawning season is short, but individuals spawn each season for several years. O. brevispinum seems to be selected for high adult survival, with adaptations in the larval stage to help avoid environmental fluctuations while retaining some dispersal abilities. The life history patterns of these three ophiuroids provide empirical evidence which supports theoretical predictions for life history and reproductive strategies in disturbed or variable environments.

Chairman

INTRODUCTION

Echinoderms are usually considered to be relatively stenohaline organisms, although there are numerous examples of species which occur in low or variable salinity regimes (Binyon, 1966). The occurrence of at least 25 species of echinoderms in the euryhaline estuary at Cedar Key, Florida, suggested that this might be an interesting area in which to examine echinoderm adaptations to variable estuarine conditions. Since the youngest stages or larvae of many benthic populations are most sensitive to variable conditions (Kinne, 1964), reproductive and larval biology were studied first. Stancyk (1973) found that up to 75% of the echinoids and ophiuroids at Cedar Key had some sort of developmental modification which helped to reduce larval exposure to the capricious pelagic environment. These were of three basic types: short-lived planktotrophic development, in which feeding plutei remain in the plankton for a week to ten days; planktonic lecithotrophic development, in which non-feeding motile vitellariae metamorphose in three days; and direct development, in which a juvenile emerges directly from the egg, with no intermediate larval stage. Concerning older stages, Turner (1974) found distinct adaptations for avoiding variable surface conditions in juvenile Ophiophragmus filigraneus, a common brittlestar of the area. He stated (p. 276) that "O. filigraneus has probably developed physiological, morphological, and behavioral mechanisms at all stages of its life cycle for avoiding or reducing contact with extreme conditions in the water column." The

idea that organisms have such adaptations is in agreement with the views of numerous population biologists, such as Gadgil and Bossert (1970, p. 21), who wrote that "the tremendous variation in life history patterns of organisms is best explained as adaptive."

Since Cole (1954) published his classic paper on life history phenomena, a great deal has been written about life history patterns and their adaptive nature (e.g., Murdoch, 1966; Holgate, 1967; Murphy, 1968; Calow, 1973; Schaffer, 1974). Most of this work involved models or was based on scant empirical evidence, and all of it dealing with marine or unpredictably variable environments was theoretical. However, there have been some excellent qualitative reviews of the reproductive and larval strategies of marine invertebrates (Thorson, 1950, 1964, 1966; Mileikovsky, 1971), and these have helped to generate some intriguing theoretical papers concerning the life history patterns of marine benthic invertebrates (Strathmann, 1974; Vance, 1973, 1974). The purpose of the research reported here was to study the biology of three estuarine ophiuroids with different developmental patterns (Ophioderma brevispinum (Say), Ophiothrix angulata (Say), Ophiophragmus filigraneus (Lyman)) in order to elucidate their adaptations to an unpredictably variable environment, and to see the effects of these adaptations on their life history patterns. The information derived from this study may lend support to certain of the theoretical arguments in the literature, and help to shed light on life history strategies of benthic invertebrates in unpredictably variable environments.

DESCRIPTION OF SPECIES

Ophioderma brevispinum (Say) is a large (adult disk diameter about 15 mm) and motile green or brown brittlestar with a leathery disk covered by fine granules (Figure 1a). It has four bursal openings in each interbrachium (Figure 1b), a characteristic of the family Ophiodermatidae. The arms are sturdy, of medium length (4-5 times disk diameter), and have closely appressed short spines. It is a common species, occurring in littoral areas from Massachusetts to Florida, the Gulf of Mexico and the Caribbean (Ziesenhenné, 1955). Stancyk (1970) found that O. brevispinum was capable of feeding on detritus, as well as being an active scavenger-predator, which inhabits the substrate surface of the extensive grass flats of the Cedar Key area of western Florida. The adults have a high tolerance of salinity fluctuation, surviving prolonged exposures to 15 parts per thousand (o/oo) with no apparent ill effects.

The embryology of O. brevispinum was described by Grave (1899, 1916), who also made several observations on its ecology, parasitology and physiology. The larva is a lecithotrophic, short-lived planktonic form called a vitellaria which metamorphoses in 4-5 days. This type of development has since been described in only four other species (Mortenson, 1921, 1938; Fenaux, 1969; Stancyk, 1973) and its adaptiveness to an unstable environment has been discussed by Stancyk (1973).

Figure 1a. Aboral view of Ophioderma brevispinum (Say, 1825).

Figure 1b. Oral view of same.

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Ophiothrix angulata (Say) is a member of the widespread and diverse family Ophiotrichidae. At Cedar Key it is most abundantly found clinging to sponges in high-current areas, although it also occurs less commonly on tunicates and in crevices of mollusk shells of pilings. A typical adult has a disk diameter of about 9 mm, possesses large radial shields and trifid spines aborally (Figure 2a), and lacks oral papillae on the jaws (Figure 2b). The arms have long, thorny, glassy spines and the tube feet are long and covered with papillae. These are used in the process of feeding, which consists of secretion of strands of mucus between the spines to capture suspended detritus particles and subsequent wiping of the spines and forming of a bolus to be passed to the mouth (Fontaine, 1965; Stancyk, 1970). The color of O. angulata is so variable that Clark (1933) named nine varieties, of which only one is common at Cedar Key. This variety is generally light blue, gray-green, or violet, with an orange arm-band every fourth segment. While a completely orange form is found occasionally, the more "typical" variety, which has a distinct, white aboral arm stripe, is never taken at Cedar Key. Ophiothrix angulata is widespread, from Cape Hatteras and Bermuda to Brazil, and from littoral regions to 200 fathoms.

Ophiothrix angulata is thought to have a short-lived planktotrophic larva. Mortenson (1921) raised the larvae to an early pluteus stage in 4 1/2 days before they died, and they were of the typical ophiotrichid pluteus form. However, they had reached the same developmental stage that the boreal Ophiothrix fragilis reaches in 18 days

Figure 2a. Aboral view of Ophiothrix angulata (Say, 1825).

Figure 2b. Oral view of same.

(MacBride, 1907). Were this trend to continue, they would metamorphose in much less than the month required by Ophiothrix fragilis, and the possible significance of this abbreviated development was discussed by Stancyk (1973). No one has succeeded in raising the larvae to metamorphosis.

Ophiophragmus filigraneus (Lyman) is a member of the family Amphiuridae. It has extremely long arms (up to 150 mm) and a small disk (up to 9 mm). There is a low fence of papillae, characteristic of the genus, on the edge of the aboral side of the otherwise smoothly scaled disk (Figure 3a). The oral side of the disk is covered with low spines or papillae (Figure 3b), helping to distinguish this species from Ophiophragmus wurdemani, with which it is sympatric at Cedar Key. The aboral side is light gray-brown and the oral side is cream-colored. The type locality of O. filigraneus is Cedar Key and it is limited in distribution to Florida, occurring from Alligator Harbor on the west coast to Cape Kennedy on the east coast (Thomas, 1962; Stancyk, 1970).

Ophiophragmus filigraneus buries its disk in silty sand and extends one to three arms to the surface through mucus-lined tubes. These arms pick up detritus, which is passed down to the mouth. Like most amphiurids, O. filigraneus autotomizes easily, and will readily throw off the disk (consisting of gonads, stomach and disk cover) or parts of the arms upon disturbance. Most adult animals show some regeneration of the arms, and many individuals with newly regenerated disks are found in any collection. While regeneration has not been extensively studied in this species, J. L. Simon (personal communication) indicates that it might be quite rapid, with individuals regenerating at least a rudimentary disk cover within two weeks.

Figure 3a. Aboral view of Ophiophragmus filigraneus (Lyman, 1875).

Figure 3b. Oral view of same.

Thomas (1961) found populations of Ophiophragmus filograneus in Coot and Whitewater Bays, Florida, where the bottom salinity was recorded at 7.7 o/oo. This is the lowest recorded salinity within the geographic range of any echinoderm (Binyon, 1966). It is probable that the ability of this ophiuroid to withstand such low salinities is not purely physiological. Stancyk (1970) found that adult O. filograneus probably could not withstand prolonged exposure to salinities lower than about 15 o/oo, and Turner (1974) described differential postmetamorphic arm growth which would allow young brittlestars to burrow into the more stable substrate and still reach the surface to feed with the longer arms.

The embryological development of O. filograneus has not been described, but Stancyk (1973) argued that it is probably modified from the planktotrophic type, and may be direct demersal development, such as that described by Hendler (1973) for Amphioplus abditus.

DESCRIPTION OF THE AREA AND STATIONS

The area of Cedar Key, Levy County, Florida, consists of a group of mangrove islands, sand hills, and shell mounds located in the Gulf of Mexico (29° 07' N, 83° 04' W; Figure 4). It is situated about 11 miles southeast of the mouth of the Suwanee River and 14 miles west of the mouth of the Wacassassa River, and is thus subject to large amounts of freshwater runoff. The whole area can be characterized as a broad, vertically homogenous estuary. The islands are surrounded by extensive shallow, soft-bottomed flats whose dominant vegetation consists of three species of marine angiosperms: Halodule wrightii (Ascherson); "turtle grass", Thalassia testudinum Koenig and Sims; and "manatee grass," Syringodium filiforme Kutzing (Phillips, 1960, 1967). The extent of these banks is shown by the six-foot depth contours in Figure 4.

Environmental conditions at Cedar Key are extremely variable, with a relatively predictable seasonal pulse and frequent unpredictable changes, particularly of salinity. The acidity fluctuates (pH 7.3-7.9) and is below the normal range of oceanic pH. Highly acid water enters the area from the two rivers, and seepage from the Ocala Limestone aquifer may also account in part for pH variation (Ingmanson and Ross, 1969). Figure 5 shows monthly means and ranges of surface water temperature and salinity from January 1971 to December 1973 (Source: U. S. Coast and Geodetic Survey, 1970-1974). The minimum and maximum temperatures occurring during this study were 9.4°C in January 1973 and 32.8° in July 1973. This range is fairly representative for deeper waters at

Figure 4. Map of the Cedar Keys, Levy County, Florida. Circled numbers indicate the stations where ophiurcids were regularly collected. (After U.S. Coast and Geodetic Survey Chart 1259).

Figure 5. Graph of monthly salinity and temperature means and ranges, Cedar Key, Florida, January 1971 to December 1973. (Source: U. S. Coast and Geodetic Survey).

Cedar Key, but in the present investigation it was found that the water temperature may rise as high as 34°C and fall to 8°C in shallower areas. The graph demonstrates that temperature varies in a regular and predictable manner, with a major temperature drop between October and November of each year and a significant rise once again between March and May. Monthly variation is least in the summer and greatest in the winter. While predictable, temperature may still strongly affect organisms in the area, particularly when a very low or high temperature coincides with a low spring tide which leaves the grass flats exposed.

Salinity is much less predictable. Although the normal salinity range (18 to 30 o/oo) is always below that of full seawater, there may be additional sudden changes in salinity at any time of year, as in February 1972, when it decreased to 11.8 o/oo. The effect of this drop on certain organisms in the area was discussed by Stancyk (1973). The difference in salinity between 1972 and 1973, particularly in the spring months, deserves attention. Figure 6 shows in detail the salinity changes for April, May and June of these two years (derived from Figure 5). The mean monthly salinity for 1972 never dropped below 20 o/oo, and the April-May-June low was 19.1 o/oo (which actually occurred on July 1, 1972). The mean salinity in April and May of 1973 was 16.6 o/oo and minima of less than 14 o/oo were recorded in both months. Such a prolonged and drastic drop in salinity during the time of year when water temperatures are rising and salinity is normally much higher could have considerable impact on the more sedentary inhabitants of the area.

Three stations were selected in order to obtain reasonable numbers of the ophiuroids under study. Station 1, located in Daughtery Bayou (Goose Cove) is on the southeast side of Cedar Key (Figure 4). There

Figure 6. Comparison of salinity measurements of Cedar Key, Florida, April - June, 1972 and 1973. Open circles, 1972; closed circles, 1973.

is no grass in this area, and the substrate is composed of silty sand (median grain size: 0.3-0.7 mm) with a thin overlying layer of detritus and mud. The bottom is uneven due to heavy feeding by sting-rays. It is only exposed at extremely low tides, but is particularly susceptible to desiccation during these times due to lack of plant cover. Station 1 has the highest densities of Ophiophragmus filograneus found at Cedar Key, but other amphiuroids are common, particularly Micropholis gracillima, Ophiophragmus wurdemanni, Amphioplus sepultus (see Hendler, 1973), Amphioplus thrombodes, and Hemipholis elongata.

Station 2 (Figure 4) is a shallow (maximum depth: three meters) tidal creek on the north side of Seahorse Key. The banks of this creek consist of oyster bars, and the bottom is well-washed sand and shell. Most of the oyster bars are exposed by any low tide, but the deeper portions are exposed only once or twice a year, and on these parts occur dense sponge colonies, made up of Hymeniacidon heliophila, Halichondria sp., and Lissodendoryx isodictyalis. These colonies and the shell rubble beneath them usually contain large numbers of Ophiothrix angulata. The water in the creek sometimes reaches extremely high temperatures (34°C on August 6, 1972), and there is a very strong current whenever the tide changes. Most of the invertebrates in this area are members of the sponge or oyster community.

Station 3 (Figure 4) is located on the dense Thalassia flat on the south side of Seahorse Key, where a large population of Ophioderma brevispinum occurs. Although this station is exposed at extreme low tides, the thick grass cover prevents severe desiccation. Because of exposure to the open Gulf, wave action and salinity are slightly higher

here than any other station. Ophiophragmus filograneus, Amphioplus sepultus and Amphioplus thrombodes occur at this station, but are less dense than at station 1.

MATERIALS AND METHODS

The studies reported herein were carried out between February 1972 and June 1974. Monthly collections were made at each station from June 1972 to July 1973, except for station 2, which was also sampled in May 1972. Attempts were made to obtain a representative sample of at least 100 individuals of each population, although this was not always possible for Ophiophragmus filograneus. Collection techniques differed at each station, depending upon the species sought. Station 1 was sampled at low tides, and shovelsful of substrate were sieved through a 3.2 mm mesh sieve. The surface area of substrate taken per shovelful averaged 0.05 m^2 , so it was possible to determine the density of ophiuroids in the area by counting the number of shovelsful of substrate sieved. At station 2, two 0.1 m^2 areas of sponge and shell were collected and carefully sorted for Ophiothrix angulata. Station 3 was also sampled at low tides, but the density of the grass and the cryptic nature of Ophioderma brevispinum juveniles made it impossible to sort samples in the field. Therefore, two areas of 1.0 m^2 each were dug up and placed in tubs, sieved in a preliminary manner in the field to remove most of the sediment, and the remaining sediment and grass returned to the laboratory for hand-sorting. Additional collections of Ophioderma were made with a scallop dredge. Small individuals made up the same percentage of the population in well-sorted dredge samples as in the more carefully obtained meter samples. However, dredging could

not supply estimates of density, and was used only as a supplementary procedure.

Recruitment, growth and mortality were determined by size-frequency diagrams constructed from measurements of the oral frame diameter (OD) of all individuals in the monthly samples. Oral diameter (Figure 7) was used as the standard measure because the usual standard, disk diameter, is too variable in these species. Ophiophragmus filigraneus and Ophiothrix angulata are both capable of contracting the soft disk, and Ophiophragmus autotomizes and regenerates the disk cover quite easily. Many animals were collected without the disk cover, or with a newly regenerated disk cover which belied the actual size of the animal. To make the results of this study comparable with other studies, disk diameters and oral diameters of a series of each species were measured and equivalence values determined. The results are presented in Table 1. Unless otherwise specified, all measurements in this study will be oral diameter.

Growth and mortality for each population were also estimated by using values obtained from the size-frequency distributions in a computer program devised by Ebert (1973). Unless populations contain discrete size classes or are amenable to marking techniques, it is difficult to determine these parameters with certainty. The purpose of the program was to derive secondary growth and mortality estimates and to supplement findings determined from the monthly samples, to see if the interpretations of the size-frequency histograms were plausible. The program was corrected and modified by William Ingram for use on the IBM 370/165 computer of the Northeast Regional Data Center at the University of Florida.

The method uses the following data to estimate a mortality

Figure 7. Oral side of an amphiurid ophiuroid showing the oral frame (OD) and disk (DD) diameter measurements. (from Singletary, 1971)

Table 1. Regression of oral diameter (OD) on disk diameter (DD)
for three species of ophiuroids.

Species	Number of individuals	Regression equation	Correlation coefficient	Standard Error of slope
<u>Ophiophragmus filograneus</u>	114	$DD = 2.90(OD) - .297$	0.855	0.167
<u>Ophioderma brevispinum</u>	105	$DD = 2.30(OD) - .003$	0.935	0.808
<u>Ophiothrix angulata</u>	103	$DD = 2.39(OD) - .628$	0.954	0.434

constant and a Brody-Bertalanffy growth constant: average size of individuals at recruitment (S_{t1}), average size of the population at some later time, preferably as close to a year from the time of recruitment as possible (S_{t2}), an estimate of maximum size (S_{∞}), size of individuals at recruitment (S_R), and size of individuals of a known age (S_N). An approximation of mortality is obtained by placing the derived mortality constant, Z , in the following equation:

$$N_t = N_0 e^{-Zt},$$

where N_t is the number of individuals in an age class at time t , N_0 is the number of individuals in the age class at time 0, and e is the natural log constant, 2.718. Growth is estimated by placing the derived Brody-Bertalanffy growth constant, K , in the following equation:

$$S_t = S_{\infty}(1 - e^{-Kt}).$$

The derivation of the formulae for determining the constants is discussed by Ebert (1973).

To find growth and mortality constants from only two measurements of the population, the program must make several assumptions. The most basic are 1) mortality rate is constant (all ages included in the population have the same mortality rate); and 2) the population undergoes Brody-Bertalanffy growth, which implies that there is no lag phase or period of exponential growth of a linear dimension. Other assumptions are: 3) the species has a stable population with a stationary age distribution over the period sampled; 4) recruitment is confined to one month a year; 5) rates of growth and mortality are constant during a year; 6) estimated mean individual size is the parametric value of mean size; and 7) individuals approach their asymptotic size so the largest individual is a reasonable estimate of maximum size.

At Cedar Key, many of these assumptions do not hold strictly true. They are most important if one has only two measurements of mean individual size in a population. Supplementary data can be used to modify the assumptions and still derive good estimates of the necessary input for the method. Thus, if mortality rate was variable, the prediction of longevity would be distorted. This error would be undetectable unless one knew when mortality was higher, and could adjust the estimate accordingly. Similarly, variation in growth rate with age or season could also reduce the accuracy of the method. Seasonal variation in growth rate can be circumvented by choosing the times of measurement as close to a year apart as possible, so that they encompass periods of both fast and slow growth. The effect of these potential errors on the present study will be discussed later. Populations of organisms which live one or two years are not stationary and stable unless they have constant recruitment, and then they do not fit the assumption of one recruitment period per year. In such cases, population parameters are predictable if a single age class can be discerned and followed throughout the year, and the mean individual size of that age class only used as input into the method. As will be seen, such a modification was necessary for both Ophiothrix and Ophiophragmus.

Gonad development, based on a gonad index, was examined in 10 males and 10 females from each monthly sample. These individuals varied between OD 3.34-5.53 mm for Ophioderma brevispinum, 1.78-3.12 mm for Ophiophragmus filigraneus and 1.42-3.48 mm for Ophiothrix angulata. The gonads of Ophioderma and Ophiophragmus are multiple, with 200-400 in mature Ophioderma and 100-200 in Ophiophragmus. There are just two large gonads per interradius in Ophiothrix angulata. The gonads were

dissected away from the disk and arms, which were subsequently decalcified in acetic acid (2.5 M) for 24 hours. Disks, arms, and gonads were then placed in 5 x 10 cm glassine envelopes, dried overnight at 80°C and weighed to 0.1 mg on a Mettler H33 analytical balance. Because of the small weights of these dried tissues, blank envelopes were also weighed to eliminate error due to water absorption by the envelopes. A gonad index value was calculated by determining the percentage of total tissue dry weight made up by the gonads.

Since it was difficult to tell by inspection or gonad index when Ophiophragmus filograneus spawned, five females were kept each month for sectioning and histological analysis. Ovaries from these females were preserved in Bouin's solution and transferred to alcohol after several days. They were then embedded in Paraplast, sectioned at 7-10 microns and stained with Delafield's hematoxylin and eosin. For each female the diameter of the longest axis of 20 oocytes sectioned through the nucleolus was measured. The first 20 suitably sectioned oocytes were measured without discrimination as to size in order to obtain an unbiased sampling of the oocyte sizes present in the ovary. Occasional oocytes dissected from live material are 0.2 mm in diameter, but most of the large oocytes measured had a diameter of about 0.18 mm. The largest oocyte diameters in the sectioned material averaged about 0.165-0.170 mm. This 7-10% difference in size is probably due to shrinkage in the preserved material.

Egg numbers for Ophioderma and Ophiophragmus were determined as described in Stancyk (1973) by counting subsamples from interradii. A different method was used for Ophiothrix, which has large numbers of small eggs. Since the average egg size of Ophiothrix is .09 mm, the volume of an egg can be determined by the formula $V = 4/3\pi r^3$ to be $5.24 \times 10^{-7} \text{ mm}^3$. A

sample of ten female Ophiothrix ranging in size from OD 2.02-3.48 mm were collected and their gonads were removed and blotted. The volume of the gonads for each female was determined by the amount of water they displaced. This volume was divided by the volume of a single egg to give an estimate of the number of eggs per female. Since the gonads also contain smaller oocytes and empty places, the figures derived by this method are probably high. This is less important in Ophiothrix than the other species, since an error of 20,000 eggs is only about 20% of the total egg number.

To compare metabolic rates between species and at different temperatures, rates of oxygen consumption were measured in a Gilson Differential Respirometer between March and June, 1973. Individuals of each species were acclimated for two weeks at temperatures between 15 and 30°C. Drained wet weight of the animals was measured and oxygen consumption determined as ml O₂/gram wet weight-hr. Eight individuals were run at one time, and were placed in 50 ml flasks containing 25 ml of millepore-filtered seawater, with a piece of gauze saturated with 10% KOH in a sidearm of the flask to absorb CO₂. After the animals were placed in the flasks, they were allowed to equilibrate for one hour before readings were begun. Readings were taken every two hours for eight hours, but only the last six hours were used in determining the oxygen consumption. Since all three species normally avoid light, the experiments were run in the dark. Different series of animals were acclimated to different temperatures and were used only at those temperatures. All temperatures in this paper refer to water temperature.

RESULTS

Densities, Monthly Collections

Density (individuals/m²) of each species at each collection time is shown in Table 2. At station 2, Ophiothrix angulata is abundant, with densities ranging from 1740/m² in May 1973 to 365/m² in July 1972, and with only one individual in the July 1973 collection. This fluctuation in density at one station follows a pattern, and Ophiothrix is significantly less dense ($p = 0.05$) from July to November than at the other times of the year. Ophioderma brevispinum is less dense than Ophiothrix, with numbers ranging from 49/m² in June 1973 to 17/m² in October 1972, but its density also varies in a regular manner. However, while Ophiothrix grows rarer in the summer months, Ophioderma is less abundant in the winter. The density at station 3 drops from a mean of 41.8/m² in the spring and summer to a lower value of 30.8/m² in the colder months of September to February. The difference between these means is significant at a 95% confidence level. The density of Ophiophragmus filograneus at station 1 fluctuates from 8.33/m² in September 1972 to 31.6/m² in December 1972, but the fluctuation is irregular and there is no significant difference between concentrations during the sampling period.

The stations sampled were chosen because they were found to have the greatest densities of the species under study, but each species occurred elsewhere. High numbers of Ophiothrix angulata were found only in the

Table 2. Densities of ophiuroids during monthly collections at Cedar Key

Date	Density (individuals/m ²)		
	<u>Ophiothrix</u> <u>angulata</u>	<u>Ophiophragmus</u> <u>filograneus</u>	<u>Ophioderma</u> <u>brevispinum</u>
1972			
May	----	41.0	----
June	1030	45.5	19.45
July	365	43.7	21.4
August	445	39.0	16.0
September	780	26.5	8.33
October	440	17.0	14.3
November	710	29.5	----
December	1680	37.5	31.6
1973			
January	1430	35.0	16.8
February	1240	39.0	19.5
March	1360	41.0	18.9
April	800	----	23.0
May	1740	34.5	22.4
June	570	49.0	23.0
July	<u>1</u>	<u>41.0</u>	<u>31.0</u>
Mean and standard error	970 $\pm$ 130	37. $\pm$ 2.0	20.4 $\pm$ 1.7

tidal creek at station 2 and a few sponge beds on deeper shell bottoms. Ophiothrix is therefore extremely dense in a patchily distributed habitat, but can be found in densities of less than $1/m^2$ elsewhere, clinging to floating objects or solitary tunicates. Ophioderma brevispinum is very widespread, but its greatest densities occur on the grass flats where station 3 was located. Ophiophragmus filograneus is most abundant in bare sandy bottoms such as station 1, but can be found in densities up to $10/m^2$ in the softer substrates on the grass flats.

Figure 8 is a size-frequency histogram for collections of Ophiothrix angulata at station 2, from June 1972 to June 1973. A collection in July 1973 yielded only one individual. In 1972, there were two times of relatively high recruitment. The first occurred in April or May, and the large new size class can be seen in June at OD 0.75-1.5 mm, making up 69% of the total population. The second major peak occurs in August, at size 0.5-0.75 mm, and makes up 36% of the population. There is additional low recruitment during the rest of the year, at least until April, 1973. However, there was no repeated heavy settlement in the spring of 1973, and by July the population had disappeared.

The curved lines in Figure 8 are approximate growth lines of different settling classes, estimated by eye. Most of the growth of a newly settled group took place within one year. It is probable that few members of any one group survive for more than one year, although some of the larger animals (as in June, 1972) may be two years old. The total growth of a settling class was about 2.5 mm OD/year, or 0.21 mm/month. However, the graph shows that most of this growth took place only in the warmer months, and slowed or stopped from December to March, when mean water temperature was below about 20°C. Growth rates before and after this time were approximately the same, as discerned by the equality of the

slopes of the lines. There may be some slowing in somatic growth in the larger animals, as can be seen in the slopes of the top two lines from March-June, 1973. If growth were constant, maximum size of 3.85 mm would be reached in about 1.5 years.

Figure 9 is the size-frequency graph for collections of Ophiophragmus filograneus from station 1, June 1972 to July 1973. Recruitment at any time seemed low, about 3.4% of the population. It appeared to take place several times a year, with individuals of OD less than 1 mm being found in September, February, and July. The presence of individuals between 1.0 and 1.5 mm at nearly all times of year indicates a much more constant recruitment than just the three months stated. However, the small sample sizes in monthly collections makes it difficult to estimate the size or number of settling classes, especially when the animals are small. Approximate growth, indicated by lines, shows that most individuals lived less than one year. Growth rate estimates are about 0.12 mm OD/month, with little reduction in growth rate during the winter. Assuming this rate is constant, an age of about 2 years for growth to maximum size of 3.41 mm can be calculated. The fact that the percentage of the population made up by a settling class increases with size indicates that there is probably a sampling error which caused an underestimate of the number of small individuals in the population. In addition, the small sample sizes make it difficult to distinguish older classes, so growth determinations are approximations of real growth.

The size-frequency histogram of Ophioderma brevispinum collected from May 1972 to June 1973 at station 3 is shown in Figure 10. Two distinct younger classes can be distinguished, and the lines follow their growth through the year. The younger group appeared at OD 1.07 mm in July 1972, and reached an average of 2.75 mm by the next July, for

Figure 9. Size - frequency histograms for monthly collections of *Ophiophragmus filigraneus*, July 1972 to July 1973.

Figure 10. Size - frequency histograms for monthly collections of *Ophioderma brevispinum*, May, 1972 to July 1973.

a growth rate of 0.14 mm/month. The second small size class was visible in May 1972 at OD 2.0 mm, and had grown into the main population at 3.2 mm by October, for a calculated growth rate of 0.2 mm/month over the summer and fall. Recruitment was fairly low, or about 6-8% of the total population. In this population, as in Ophiothrix angulata, growth stopped from October through March, when the water temperature was below 25°C. Note that from October 1972 on, except for January (1 individual), there were no individuals of large size (OD greater than 5.5. mm) in the population; in fact, in December there were none over 5.0 mm. In later months, they reappeared, but not in as great numbers as before winter.

Estimates of Survivorship, Growth and Mortality

After modification of the basic program of Ebert (1973) and evaluation of the necessary assumptions, values of the parameters necessary to estimate survivorship, growth and mortality were selected from the population histograms in Figures 8-10. The values chosen for each species and the resultant growth (K) and mortality (Z) constants are shown in Table 3. Since Ophiothrix angulata and Ophiophragmus filigraneus both have relatively constant recruitment, a settling class was chosen for these species which could be followed throughout the year, and any individuals not in that class were not included in the average individual size calculations. The two estimates of average individual size in the populations were made as far apart as possible, so that growth figures encompass both fast and slow growth periods.

Calculated survivorship values of the ophiuroids in this study are listed in Table 4. According to the method used, a settling class of

Table 3. Data values and calculated growth and mortality constants for estuarine ophiuroids. St_1 = mean size near time of recruitment (t_1); St_2 = mean size at a second time of year (t_2); S_{∞} = maximum size; S_R = size of recruitment; K = mortality constant; Z = growth constant; $S(N)$ = size of individual of a known age ($D(N)$).

Species	St_1 (mm)	Month	t_1	St_2	Month	t_2	S_{∞}	S_R	K	Z	$S(N)$	$D(N)$
<u>Ophiothrix</u> <u>angulata</u>	0.75	Aug. 1972	0.0	2.74	June 1973	0.83	3.85	0.75	1.56	18.35	3.0	1.0
<u>Ophiophragmus</u> <u>fillograneus</u>	0.99	Sept. 1972	0.0	2.35	June 1973	0.68	3.41	0.99	1.21	3.15	2.70	1.0
<u>Ophioderma</u> <u>brevispinum</u>	3.94	Aug. 1972	0.17	4.35	May 1972	0.85	6.60	1.07	0.25	0.195	2.84	1.0

Table 4. Survivorship values of estuarine ophiuroids, determined from computer-generated estimates.

Age (years)	Species		
	<u>Ophiothrix</u> <u>angulata</u>	<u>Ophiophragmus</u> <u>filograneus</u>	<u>Ophioderma</u> <u>brevispinum</u>
0	1.000	1.000	1.000
1	0.000	0.043	0.823
2		0.002	0.677
3		0.000	0.557
4			0.458
5			0.376
6			0.310
7			0.255
8			0.210
9			0.173
10			0.142
15			0.054
20			0.020
25			0.007

Ophiothrix does not have any individuals survive for more than one year, and the mortality constant, Z , is high, 18.35 (Table 3). Ophiophragmus is also short-lived, and only 4% of a settling class survive until the next year, 0.2% until the third year. The mortality constant for Ophiophragmus is 3.15. Ophioderma has a mortality constant of 0.195 and is fairly long-lived, with 14% of a settling class still alive after 10 years, and 1% surviving until 23 years of age.

Growth curves for each species are plotted in Figures 11 to 13. Figure 11 shows that Ophiothrix, with a growth constant of 1.56, reaches a size of OD 3.0 mm in its first year; the largest individual found, 3.85 mm, could not have been more than 4 years old. The program thus predicts that Ophiothrix is a short-lived, fast-growing species, with few individuals surviving for more than a year. Ophiophragmus also appears to be fast-growing (Figure 12) with a growth constant of 1.21, and reaching an oral diameter of 2.7 mm in its first year. The largest individual captured (3.41 mm) could be as old as 5 years. Ophioderma is slower-growing (Figure 13), with a growth constant of 0.25, and takes about 9 years to reach a size of 6.0 mm. The method predicts that the largest individuals found may be as old as 25-28 years.

Reproduction

Fecundity, egg size, size and age at first reproduction, developmental type and sex ratio for each species are given in Table 5. Many of these data are derived from Stancyk (1973). Age at first reproduction was determined by finding the smallest individuals with large oocytes in the monthly samples and fitting them to the computer-generated growth curves for each species. Size at first reproduction in Ophiothrix angulata was difficult to determine, because any individual which could be sexed

Figure 11. Estimated growth curve for *Ophiothrix angulata*.

Figure 12. Estimated growth curve for *Ophiophragmus filograneus*.

Figure 13. Estimated growth curve for *Ophioderma brevispinum*.

Table 5. Reproductive parameters for ophiuroids from Cedar Key. Starred data indicate values from Stancyk (1973). Values in parentheses indicate the number of individuals examined.

Species	Egg Number	Egg Diameter (mm)	OO(mm) at reproduction	Estimated age at first reproduction	Development type	Sex ratio Male:Female
<u>Ophiothrix angulata</u>	19,084 - 91,603(10)	.09-.1* (10)	2.5-3.85	.7 yrs.	Short-lived Planktotroph?*	1:1.14 (1888)
<u>Ophiophragmus filograneus</u>	1,070 - 6,050*(10)	.18 (10)	2.5-3.41	.7 yrs.	Direct?*	1:01:1 (889)
<u>Ophioderma brevispinum</u>	785 - 1,385*(10)	.30* (10)	3.9-6.6	2.4-3.2 yrs.	Vitellaria	1:06:1 (1287)

contained many large oocytes. However, the gonad volume of individuals between OD 2.0 and 2.5 mm was the same, and began to increase in individuals larger than 2.5 mm. This size was therefore chosen as the earliest size of oocyte proliferation prior to spawning.

The table shows that Ophiothrix, which has planktotrophic development, has by far the highest egg number and the smallest eggs. The other two species, which have modified development, have larger and fewer eggs. The two species with the largest egg numbers (Ophiothrix and Ophiophragmus) begin to reproduce within their first year of life, while Ophioderma does not begin to reproduce until 2-3 years old. None of the sex ratios are significantly different from 1:1, so it appears that males and females are equal in all three species. A gonad index (% total decalcified dry weight made up by gonads) was used to determine when spawning took place. Figures 14 to 16 show the gonad index change over 1 year in each species. In Ophiothrix angulata (Figure 14) gonad index varied little over the year. There were peaks in September and November, 1972, and in April-May, 1973. These are associated with increases in the standard deviation about the mean and therefore increases in the range of variability of the monthly samples. It appears that some fraction of the population was nearing spawning condition at these times. This is interpreted as a demonstration that spawning is asynchronous, and some fraction of the population is in spawning condition at any time of year; the peaks merely represent the maturation of a large settling class. Note in Figure 8 that recruitment occurred throughout the year, with peaks in June and August.

Figure 14. Mean and standard deviation of gonad indices of Ophiothrix angulata, July 1972 to June 1973. Gonad index = % of total dry weight made up by gonads.

The opposite case appeared in Ophioderma brevispinum (Figure 15). The gonads made up less than 25% of the total dry tissue weight until April, when they rapidly increased to about 32%. By June, they decreased to about 18%, and they stayed at about 15-25% the rest of the year, with a minor peak in November. It appears that Ophioderma spawns synchronously in May, with the possibility of some low-level spawning during the summer and fall. Note that the recruitment shown in Figure 9 is fairly discrete, and indicates that settlement takes place over a short time, once a year.

There is no significant difference between the gonad indices for any month in the Ophiophragmus filigraneus samples (Figure 16). The means varied from 15 to 27%, but at several times of year there were some individuals in the sample with gonad percentages over 40%, particularly in the spring and summer. This lack of difference suggests that some fraction of the population is nearing spawning condition at any time of year. To clarify this picture somewhat, sectioned ovaries from five females per month were examined. The proportion of oocytes of varying diameters making up the ovary contents are shown in Figure 17. Large oocytes (0.17-0.2 mm) were present at nearly all times of the year. However, there was a significant change in their proportion between October and November 1972, February and March 1973, and May and July 1973. The polymodal distribution of oocyte diameters at all times of year indicates that there was constant growth of oocytes throughout the year. The decrease in large oocyte percentage at the three times of year discussed above suggests spawning of three different settling classes which made up a larger part of the population, but spawning was probably continuous at a lower level. The frequency of recruitment of small size classes (Figure 10) also indicates constant spawning. Note

Figure 15. Mean and standard deviation of gonad indices of Ophioderma brevispinum, July 1972 to June 1973. Gonad index = % of total dry weight made up by gonads.

Figure 16. Mean and standard deviation of gonad indices of Ophiophragmus filograneus, July 1972 to June 1973.
Gonad index = % of total dry weight made up by gonads.

Figure 17. Polygons showing frequency of primary oocyte diameters in the ovaries of Ophiophragmus filograneus, September 1972 to July 1973. Circles indicate mean diameter for each month.

that while spawning took place year-round in Ophiothrix and Ophiophragmus, there was a major peak in all three species in spring and early summer.

Respiration

Oxygen consumption of the three species used in this study was examined at various temperatures, from 15° to 30°C. In all species, total O₂ consumption increased logarithmically with the size of the animal. Figure 18 shows the relation of oxygen consumption to temperature for the three species used in this study. As might be expected, O₂ consumption increased with increasing temperature, and between 15° and 25°C there was no difference among the means of the three species. At 30°C, the respiration rate of Ophiothrix was twice as high as the other two species. Even with the small sample sizes used (N=8) the difference was significant at the 99.999% confidence level. There was no difference between Ophioderma and Ophiophragmus at 30°C. It appears that Ophiothrix is much more temperature-sensitive than the other two species, particularly at temperatures above 25°C. Note in Table 2 that the densities of Ophiothrix at station 2 decreased drastically in July, and did not increase to a higher level until November.

Figure 18. Oxygen consumption of three estuarine ophiuroids at different temperatures. Results are expressed as means surrounded by 95% confidence intervals.

DISCUSSION AND CONCLUSIONS

Population Dynamics

It is not unusual to find high densities of ophiuroids; Vevers (1952) found 340 Ophiothrix fragilis /m² off Great Britain, and amphiurids have been reported as high as 1,516/m² off southern California (Barnard and Ziesenhenne, 1961). This study shows that density changes over the year in both Ophioderma brevispinum and Ophiothrix angulata, and that in both species, the larger (older) individuals disappear (see Figures 8 and 10). The absence of large Ophioderma in the winter has two possible explanations. Local fishermen feel that some Ophioderma leave the grass flats for deeper waters in the winter because they find large numbers of them in their crab traps. However, most of the trapping is done in the winter, and dredge hauls have indicated that Ophioderma occurs in deeper water year-round. That they would concentrate around a bait source is not surprising, and Allee (1927) recorded that they would grasp and hold a baited hook. The other explanation is that the large individuals are members of the oldest year class, post-reproductives, who die with the coming of cold. In Figure 10 they comprise between 3 and 5% of the population. This corresponds rather closely with the figures derived from the estimate of survivorship.

Ophiothrix angulata has its lowest density in the summer, and most individuals larger than the size class recruited in April (OD 1.6 mm) are absent by the end of September (Figure 8). In light of this disappearance of older individuals, it is worthwhile to consider the data

on oxygen consumption in some detail. The mean respiration rate for each species between 22° and 25°C does not differ greatly from those of ophiuroids reported in the literature, all of which fall between 0.03 and 0.102 ml O₂/g wet weight/h, with a mean of 0.058 + 0.019 ml O₂/g wet weight/h (Nicol, 1960; Buchanan, 1964; Farmanfarmaian, 1966; Pentreath, 1971; Singletary, 1971; Hendler, 1973). However, Ophiothrix has a greatly increased metabolic rate at higher environmental temperatures, while the other two species show a less rapid rise. Temperatures at 30°C are not uncommon at Cedar Key; in fact, the mean temperature in July for the last three years (1971-1974) has been at or above 30°C (Figure 5) and values of 34°C have been recorded at station 2 several times since 1969. Thus, the Ophiothrix population may be subject to some temperature stress each summer. Older individuals might die more easily because they have lost their energy reserves to reproduction in June, and are thus unable to cope with increased metabolic costs associated with high temperatures. Smaller individuals have the necessary reserves, or can resorb unspawned gametes (Booolootian, 1966). The summer die-off is probably a regular phenomenon, as it occurred in both 1972 and 1973 (Figure 8).

The rates of population growth and survivorship derived from the method of Ebert (1973) appear to approximate the actual growth (Figures 8-10). Variation between the two is chiefly due to poor fit of the assumptions of the method to the real populations. In benthic invertebrate populations, mortality is probably not constant in all age groups. Thorson (1950, 1966) discussed the biological and Kinne (1964) the physical aspects of high mortality in young stages of benthic invertebrates. However, this high mortality would occur before the animals reach a large enough size to appear in my samples. High

mortality of older individuals would cause the program to predict a longer time to reach maximum size than is actually necessary. Thus, the program predicts a little over two years for both Ophiophragmus and Ophiothrix to attain maximum size, while Figures 8 and 9 indicate that this growth may occur in 0.8 to 1.5 years.

There is no adjustment in the model for a decrease in somatic growth rate with the onset of sexual maturity and gonad growth. Hendler (1973) demonstrated that in Amphioplus abditus there was an inverse relation between gonad growth and annual somatic growth, somatic growth being correlated with temperatures above 12°C and gonad growth with lower temperatures. He also showed that gonad development can be fairly rapid. In a semelparous species (one which spawns only one time) with a 1-1.5 year life span, growth to a large size could occur during the warmer parts of the year. Storage of nutrients or gonad growth could take place when temperatures were low, particularly if the species fed year-around, regardless of temperature. Stancyk (1970) found no cessation of feeding below 25°C by any ophiuroids at Cedar Key, although somatic growth stopped between 20 and 25°C. The major spawning peaks in the spring and early summer in both Ophiothrix and Ophiophragmus, following periods of reduced somatic growth in winter, indicate that large parts of the populations of these two short-lived species followed this pattern. Somatic growth to a given size, followed by rapid gonad growth and continued reduced somatic growth may be a general pattern in semelparous species. Buchanan (1967) found a similar pattern over three years in Amphiura filiformis, and Singletary (1971) found rapid gonad development in Micropholis gracillima. In any case, the variation in growth will reduce the closeness of fit of the growth

estimates to actual growth rates in the short-lived species.

Ophioderma brevispinum, like many other long-lived forms (Fell, 1966; Swan, 1966), has two to three years of somatic growth before reaching maturity. Somatic growth then continues at a more gradual rate, stopping each winter when temperatures decrease. Gonad growth occurs gradually over the winter, and most of the population spawns in the spring. This pattern was described for Gorgonocephalus caryi by Patent (1969), and for Amphiura chiajei and Ophioderma longicauda by Fenaux (1970, 1972). Because variation in growth is spread over a long period of time, the predictive method fits the actual population growth of Ophioderma better than the other two species.

The variation in growth increment is low between the three species (0.12 to 0.2 mm/month OD) although the patterns of annual growth vary greatly, which could suggest that roughly the same percentage of incoming energy is partitioned to somatic growth by all three species. This does not necessarily imply that they are all putting the same amount into maintenance and reproduction. In fact, the data on respiration suggest that Ophiothrix may have to expend more energy during part of the year than the other species.

Means of obtaining life history values from actual marking in populations of soft-bodied or fragile benthic invertebrates have not been devised, so the method used here is quite useful in refining and verifying field results. Given the modifications of the assumptions discussed previously, the final program appears to approximate the known parameters of the three ophiuroid populations, and therefore its values for parameters otherwise unobtainable (survivorship, mortality) are good first estimates of the actual population values. The method is most helpful in determining the dynamics of the slow-growing Ophioderma.

since age classes could only be followed for about 10% of their life span.

The results show that the ophiuroids studied have two basic life history patterns (excluding reproductive mode). One species (Ophioderma brevispinum) takes two or three years to reach maturity, then spawns repeatedly for up to 25 years (iteroparity). This resembles the more common case in ophiuroids: slow growth, iteroparity, and a long life of 10-15 years (Fell, 1966; Swan, 1966; Buchanan, 1964). Fenaux (personal communication) has found that Ophioderma longicauda in the Mediterranean may live up to 30 years, which compares favorably with my findings for Ophioderma brevispinum.

† The other two species (Ophiophragmus filigraneus, Ophiothrix angulata) grow to maturity in a year or less, spawn all reproductive products in one season, and die. Such rapid maturation is unusual in ophiuroids. Buchanan (1964, 1967) found that Amphiura filiformis reaches maturity in three years and dies. Fell (1966) noted that Ophiura texturata takes two years and Taylor (1958, from Singletary, 1971) found that Ophiothrix fragilis and Ophiopholis aculeata reach maturity in about 1 1/2 years. Singletary (1971) found three species of amphiurids in Biscayne Bay which matured in less than a year. In fact, Micropholis gracillima, which also occurs at Cedar Key, reached sexual maturity two months after settling. Buchanan (1964) attributes the fast growth of Amphiura filiformis to its high-energy suspension-feeding habit. However, it may be that these species with rapid maturation are also susceptible to periods of high mortality, as are Ophiothrix and Ophiophragmus.

Several theoretical papers on life history pattern and the environment have been published (Murphy, 1968; Gadgil and Bossert, 1970; Calow, 1973; Schaffer, 1974). All reach the same basic conclusion: if adult mortality

is high or variable, there will be selection for semelparity with a short life; if there is high mortality in pre-reproductives or increased positive feedback on reproductive processes with age (increased fertility or survival, decreased reproductive costs), there will be selection for iteroparity and long life. The ophiuroids examined in this study fit both patterns. Ophiothrix angulata adults are killed during periods of high temperature. Also, the evidence presented indicates that pre-reproductives do not survive periods of low salinity, since spawning occurred in spring 1972, but there was no recruitment. Ophiothrix clearly has a semelparous strategy.

Ophioderma brevispinum has iteroparous development and a long life, and the adults are well-adapted to physical variations in the environment (Stancyk, 1970). They appear to have low mortality from predation. I know of no organisms who eat Ophioderma brevispinum except for two sea stars, Luidia clathrata and L. alternata, which do not occur in the same grassflat habitat (Stancyk, 1974).

Ophiophragmus filigraneus is also well-adapted to environmental fluctuation (Stancyk, 1970; Turner, 1974; Thomas, 1961), and in light of its somewhat lower fecundity, might also be expected to have a long iteroparous life. However, heavy mortality in adults due to predation is possible in this species, although the predators are unidentified. In any given collection of Ophiophragmus, between 20 and 30% of the adults showed evidence of disk regeneration, and 100% of the animals had some of the arms partially regenerated. In the laboratory, hermit crabs of several species and young blue crabs, Callinectes sapidus, rapidly devoured the exposed arms of buried Ophiophragmus. If such predation causes high adult mortality, the semelparous development of this species

might be explained. Even if this is not true, Schaffer (1974) found in certain cases that increases in fertility or postbreeding growth and survival could result in either an iteroparous or semelparous equilibrium life history, and the mode could not be predicted. It is possible that Ophiophragmus fits such a pattern.

Reproduction

The relationship between egg number, egg size and developmental type has been discussed by numerous authors (Thorson, 1950; Mileikovsky, 1971; Schoener, 1972; Stancyk, 1973). Hendler (1973) summarized the known information for ophiuroids. In general, species with brooded or ovoviviparous development have few eggs of large size; species with modified development (direct demersal, vitellaria) have moderate numbers of eggs of medium size; and species with planktotrophic development have many small eggs. Out of 39 ophiuroid species for which egg numbers are known, for example, only five do not fit and the development of three of these is unknown. The species studied here do fit the expected pattern: Ophioderma brevispinum and Ophiophragmus are well within the range for abbreviated development; in fact, O. filograneus approaches the egg size and number of Amphioplus abditus, which has direct demersal development (Hendler, 1973). Ophiothrix has egg numbers at the lower range of those produced by most planktotrophic species. Perhaps production of a planktotrophic larva which will metamorphose in a short time causes a reduction in the numbers of eggs that can be produced, because there is a higher energy cost involved in building each egg.

The abbreviated development of all three species is interesting in light of a theoretical model proposed by Vance (1973), which predicts that only the extremes of the possible range of egg size and type of nutrition,

planktotrophy and lecithotrophy, would be evolutionarily stable.

Abbreviated development is an energetically expensive way to maintain restricted dispersal. However, when temporal variation in the adult environment was included, Vance (1974) found that disturbance favored an intermediate strategy with large eggs, a long benthic prefeeding development and a short planktotrophic stage. Functionally, that type of development is analogous to the vitellaria or short-lived planktotroph found in the Cedar Key ophiuroids. Vance's conclusions were based on the results of simulations which employed arbitrary parameter values, so it is noteworthy that they predict a strategy close to that followed by these ophiuroids.

Dispersal has the chief advantage of allowing rapid colonization and exploitation of disturbed habitats (Vance, 1974). Strathmann (1974) stated that factors favoring dispersal include variations in success of settling of larvae entering an area, in mortality in the benthic stage, in gamete production, in spawning losses, and in survival of early stages released in an area. In Vance's (1974) model dispersal becomes important in the evolution of reproductive mode only if benthic development is a more efficient means of juvenile production; that is, complete benthic development would be selected if it were not necessary to have dispersal for colonization (and recolonization) of disturbed environments. This may be the case in Ophiophragmus. Chia (1971) tentatively demonstrated that direct development may be energetically cheaper than planktotrophy, and at times of environmental fluctuation in an area like Cedar Key, benthic development certainly results in greater juvenile production than planktotrophy. Finally, Vance (1974) indicated that dispersal confers a greater advantage on planktotrophy when the energy available for reproduction is low. The possibility exists that Ophiotrix has planktotrophy because it

is most sensitive to environmental variation and must spend more energy for maintenance, leaving less for reproduction.

Thorson (1950, 1966) and Mileikovsky (1971) attempted to correlate the occurrence of abbreviated development in benthic invertebrates with the environment. Hendler (1973, p. 161) reviewed the situation in ophiuroids:

Clearly, the assemblage of abbreviated developers is not systematically cohesive. Similarity in size of eggs, larvae, and post-larvae as well as the related similarity in the number and mass of gametes produced and the rate of development indicate that they are ecologically and physiologically convergent. Apparently the abbreviated developers have been selected from different stocks and combine some of the advantages and disadvantages of viviparous and planktotrophic development to suit a specific larval "niche".

In Cedar Key, Stancyk (1973) argued that this larval niche helps reduce mortality in an unpredictably variable environment: the susceptible young stage has a better chance of getting out of the variable pelagic conditions and into the more stable substrate before a lethal environmental perturbation can take place. Carriker (1967) expressed the idea that abbreviated development provides an advantage by reducing dispersal so that young stages can settle in an environment of proven suitability to adults, often their own parents. Reduced or local dispersal of this sort would certainly not be an advantage to a species like Ophiothrix, where the population (and a single individual's genotype) would be eliminated if summer temperatures were high and the local salinity was low. Hendler (1973) demonstrated that the directly-developing eggs of Amphioplus abditus fared poorly in low salinities, but were normally kept out of such stress by being demersal and remaining in the higher salinity bottom layer. That environmental variability can affect recruitment was clearly demonstrated by Ophiothrix anguata in the spring of 1973. Gonad index

data indicate that many individuals spawned in the spring (as in the spring of 1972), but recruitment was very low (Figure 8) because the low salinity in March and April (Figures 5 and 6) undoubtedly killed most of the larvae.

Finally, the relationship between longevity, spawning periodicity and environmental variability must be examined. Few ophiuroids have very long breeding seasons (Booolootian, 1966). However, Guille (1964) found that Ophiothrix quinquemaculata breeds year round, with peaks in the spring and fall. Fell (1946) stated that the viviparous Axiognathus (Amphipholis) squamatus probably breeds all year round, and Singletery (1971) found this to be the case for Micropholis gracillima in Biscayne Bay. J. S. Pearse (personal communication) noted that Ophiocoma scolopendrina from the Red Sea also breeds year-round. The advantage of a long spawning period in a variable environment is clear: if some individuals are spawning at any time of year, the possibility is increased that some larvae will encounter a beneficial environment and settle successfully. Thus it is not surprising to find Ophiothrix angulata and Ophiophragmus filigraneus with continual spawning. However, having a long breeding season is not advantageous to the individual and its genes, carried in its offspring, unless it can spawn more than once itself. Not only will multiple spawning increase the chances for some of an individual's offspring to encounter a suitable pelagic environment, but Strathmann (1974) predicted that species with short-lived larvae, particularly pelagic nonfeeding larvae would have a higher incidence of multiple spawnings if there is selection for spread of larvae. It is logical, therefore, that Ophioderma not only spawns over several years, but may spawn heavily once, then at a reduced rate for a longer period each year

(Grave, 1916). Mortenson (1921) stated that Ophiothrix angulata releases all of its oocytes at once; however, the few O. angulata that spawned in my laboratory did not release all of their oocytes, and sections of gonads showed oocytes of several diameters, which indicates multiple spawning in a species that only lives 1 to 1 1/2 years. Ophiophragmus filograneus gonad sections (Figure 17) also reveal several sizes of oocytes. Note that the short-lived species had the longest spawning seasons. This may be an adaptation to avoid intermittent variability, or it may simply be a result of continual recruitment, so that some individuals are reaching maturity at all times of year.

In conclusion, this study provides empirical evidence which supports both recent models concerning the relationship of life history strategies and the environment, and recent theoretical work on reproductive strategies. The ophiuroids examined exhibit different life history strategies, each providing them with high fitness in an unpredictably variable environment.

1 Ophiothrix angulata is a widespread species similar to the fugitive species described by Hutchinson (1951). It is short-lived, with high fecundity, has a short-lived planktotrophic larva (allowing relatively high dispersal), and is relatively intolerant of environmental fluctuations in both adult and larval stages. The strategy of this species is to colonize and recolonize disturbed areas after local extinction.

Ophioderma brevispinum is long-lived, with low fecundity and moderate dispersal via a vitellaria larva. It is tolerant of environmental fluctuations as an adult, and the larvae are able to avoid most fluctuations by metamorphosing quickly. The strategy of this species is to survive in a given area through all environmental stresses. By having a vitellaria larva, Ophioderma maintains high larval survival while

retaining limited dispersal ability, and is thus moderately widespread.

Ophiophragmus filograneus is short-lived, with moderate fecundity. It probably has little or no dispersal, assuming that it undergoes direct demersal development. Its distributional range is small. There is not enough known about adult mortality to accurately define the strategy, but it appears that there has been selection for high survival in both adults and young, so that the population can maintain itself in the face of almost any environmental stress, and therefore need not retain dispersal mechanisms.

It is tempting to suggest that some of these species are r-selected and others K-selected; however, Gadgil and Solbrig (1972) point out that the definition of r and K selection is relative, and depends on differences in allocation of resources, not on birth rate. Categorization of these species into r and K selection is not necessary, as MacArthur (1973) pointed out that this division, while fairly natural, is not the only alternative. It would be better to say that the life history patterns seen here are the result of selection to maximize fitness in a variable environment, and the patterns vary with species because each has a different genetic background upon which selection acts.

SUMMARY

1. The life history strategies of three ophiuroids with different modes of reproduction, all inhabiting the unpredictably variable polyhaline estuary at Cedar Key, Florida, were studied by means of monthly collections and laboratory experiments from May 1972 to June 1974. Ophioderma brevispinum has a vitellaria larva, Ophiothrix angulata has a short-lived planktotrophic pluteus, and Ophiophragmus filograneus probably has direct demersal development.
2. The population density of Ophioderma brevispinum drops during the colder months (September to February), and that of Ophiothrix angulata drops in the summer when mean temperatures are above 30°C. Analysis of monthly collections shows that the older (larger) individuals in both cases disappear from the study area, either because of death due to temperature stresses (both species) or migration to deeper water (O. brevispinum).
3. Monthly collections indicate that spring recruitment of young Ophiothrix angulata was high in 1972 and low in 1973, when unusually low salinities occurred. The other species were unaffected by this salinity reduction.
4. Size-frequency analyses show that Ophiothrix angulata and Ophiophragmus filograneus are fast-growing, with constant recruitment under favorable conditions. Ophioderma brevispinum is slower-growing, and has a peak of recruitment in the spring and early summer.

5. Estimates of growth, mortality and survivorship confirm that Ophiothrix angulata and Ophiophragmus filograneus live about 1 - 1 1/2 years and mature in less than one year. Ophioderma brevispinum lives 20-25 years and matures in 2-3 years.
6. Study of gonad indices of all three species and sectioned ovaries of Ophiophragmus filograneus show that some members of the Ophiothrix angulata and Ophiophragmus populations spawn at all times of year, with a peak in the spring. Ophioderma brevispinum spawning peaks in the spring, with continued low-level spawning into the summer. All three species probably have multiple spawning by individuals.
7. Respiration measurements at temperatures between 15-30°C indicate that Ophiothrix angulata is more temperature-sensitive than the others at higher environmental temperatures (30°C). This may explain the mortality of older individuals in the summer.
8. Ophiothrix angulata, with semelparity, a short life and a relatively narrow environmental tolerance range in both young and adult stages, appears to be a fugitive species, selected for high dispersal and the ability to colonize and recolonize disturbed habitats after extinction.
9. Ophiophragmus filograneus is semelparous and short-lived with a broad tolerance of the range of environmental conditions. It appears to be selected for high survival of both adult and young stages through most environmental fluctuations, and has a reduced dispersal ability.
10. Ophioderma brevispinum is long-lived and iteroparous, and seems to be selected for survival of environmental variability as an adult, with adaptations in the larval stage to help avoid environmental fluctuations while retaining some degree of dispersal.

11. The life history strategies of these three ophiuroids provide empirical evidence which supports theoretical predications of life history and reproductive strategies in disturbed or variable environments.

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BIOGRAPHICAL SKETCH

Stephen Edward Stancyk was born on April 8, 1946, in Denver, Colorado. In 1954, he moved to Lakewood, Colorado, and was graduated from Lakewood High School in 1964. He entered the University of Colorado at Boulder in 1964, and was graduated with a Bachelor of Arts, majoring in biology, in June 1968. In September 1958, he began studies toward the Master of Science degree in zoology at the University of Florida, and was awarded that degree in December 1970. He has since been working toward the degree of Doctor of Philosophy, also at the University of Florida. From January 1969, through August 1973, he worked as a graduate assistant in the Department of Zoology, and from September 1973 to June 1974, as a half-time instructor in the Division of Biological Sciences.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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