

Salinity Tolerance of the Brackish-Water Echinoderm *Ophiophragmus filigraneus* (Ophiuroidea)

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ABSTRACT: *Ophiophragmus filigraneus* is an infaunal brittlestar inhabiting shallow brackish waters of Florida (USA). Its tolerance to salinity changes was studied in the laboratory using burrowing time as an activity criterion. Complete acclimation of burrowing time occurred within 21 d of continuous acute exposure to salinities of 17–38 ‰. All test animals died within 2 d at 42 ‰ and within 19 d at 10 ‰. Gradual reduction to 8 ‰ from ambient salinity (25 ‰) during 43 d exposure gave results similar to those of the first experiment. A third experiment gave evidence of acclimatization in a well-established population in the Indian River lagoon, where salinity dropped to 9 ‰ in August 1978. Salinity tolerance of *O. filigraneus* allows it to live in the organically rich sediments of Florida bays and lagoons, to which it is restricted, unlike the more stenohaline *O. wurdemanni* from nearby, marine, sandy habitats. This is the first documented case of an endemic brackish-water echinoderm.

INTRODUCTION

Although much evidence has been accumulated in the past few decades to document the presence of brackish-water populations of at least 22 species of echinoderms (Binyon, 1966), no echinoderm has been found which is endemic to brackish waters (Kinne, 1971; Remane and Schlieper, 1971, pp. 114, 116). The absence of brackish-water species is probably related to the poor ability of echinoderms to osmo- and ion-regulate (Binyon, 1972; Prosser, 1973a, b), the lack of an excretory organ (Binyon, 1972), and the biochemical, physiological, reproductive, and morphological effects of reduced salinities on laboratory and field populations (Kowalski, 1955; Kinne, 1971; Remane and Schlieper, 1971).

The echinoderm which has been found in the lowest salinity in the field is the infaunal, deposit-feeding brittlestar *Ophiophragmus filigraneus*, found by Thomas (1961) at 7.7 ‰ in Coot and Whitewater bays, Florida, USA. Based on Thomas' (1961) observation, circumstantial evidence on postmetamorphic growth (Turner, 1974) and reproduction (Stancyk, 1973), and a preliminary knowledge of its distribution, we regarded *O. filigraneus* to be a good candidate for an endemic

brackish-water species. Except for a preliminary unpublished study by Stancyk (1970), however, nothing was known about its range of salinity tolerance in the laboratory. Reports of its distribution were scattered, and correlations with salinity of its habitat were few. The purposes of the present paper are to provide experimental evidence for the euryhalinity of *O. filigraneus* and to document the restriction of this brittlestar to the brackish bays and lagoons of Florida.

MATERIAL AND METHODS

Individuals of *Ophiophragmus filigraneus* (Lyman) were collected by shovel and sieve from seagrass (*Halodule wrightii*) beds in the Indian River lagoon at Melbourne, Florida, USA (28° 03.7' N; 80° 35.5' W) in April, June, and September 1978. *O. filigraneus* were held in the laboratory 1–6 d before experimentation to overcome stress potentially imposed by handling and temperature change. Brittlestars were selected for uniformity of size, and those with broken arms or regenerating discs were not used. Clean beach sand from Indian River, Florida was sieved, and particles of 0.25–1.00 mm diameter were used to provide a standardized substratum for all experiments. Choice of particle sizes was based on the determination by Mur-

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doch (1976) of optimal substrata for burrowing by *O. filograneus*.

Brittlestars were held in 20.3-cm diameter glass bowls with 1–2 cm of beach sand covered with water to a depth of 3–4 cm. Except during burrowing trials, they were kept in the habitation bowls under reduced light intensity. Water was aerated continuously and changed every other day. The number of individuals per bowl did not exceed six (185 m^{-2} ; density in the field was 290 m^{-2}). Test salinities were prepared with combinations of ocean water, lagoon water, deionized water, and artificial sea salts. Field and test salinities were measured with an American Optical Corporation refractometer (Model 10419). Test bowls for burrowing trials contained 2–5 cm of beach sand and water to a depth of 1–2 cm. The burrowing response was used to evaluate the functional well-being of control and experimental animals. Burrowing was timed from the start of sand movement by podia to the disappearance of the disc into the sand. The criterion for death was the lack of podial response to touch.

Three experiments were run to test the effect of salinity on burrowing time. In the first experiment, eight groups of brittlestars were subjected to acute exposure to salinities of 42, 38, 33, 27, 21 (ambient), 17, 13, or 10 ‰ for up to 21 d. Burrowing times of the 6 individuals in each group were measured at ambient salinity prior to exposure and daily thereafter at the test salinity. Individuals that did not burrow within 7 min were assigned a time of 420 s. Mean time and standard deviation were calculated for each group in which all brittlestars burrowed within 420 s on a given day; otherwise, the median burrowing time was calculated.

In the second experiment, 10 individuals were exposed to stepwise reduction of salinity (25, 21, 17, 13, 10, and 8 ‰), and 10 were held at ambient salinity (25 ‰). Burrowing times were measured every 2 d. Salinity in the experimental bowls was reduced after the burrowing trial every sixth day, except for the 9-d exposure to 10 ‰ . Brittlestars that did not burrow within 25 min were assigned a time of 1500 s. Mean and median times were calculated as described above.

A third experiment was made after a natural reduction in salinity of the Indian River lagoon occurred between late July and late September 1978. (Abiotic factors other than salinity were not monitored in the field.) The purpose of this experiment was to test for acclimatization of burrowing time. The acclimatization experiment was conducted similarly to the first. The control group was held at ambient salinity (17 ‰), and each of three experimental groups was exposed to 14, 11, or 8 ‰ .

Ambient water temperatures at the start of the three experiments were 24, 35, and $29 \text{ }^\circ\text{C}$, respectively.

Laboratory temperatures were measured at least every other day during the experiments; means and standard deviations were $23 \text{ }^\circ\text{C} \pm 2 \text{ }^\circ\text{C}$, $25 \text{ }^\circ\text{C} \pm 2 \text{ }^\circ\text{C}$, and $24 \text{ }^\circ\text{C} \pm 1 \text{ }^\circ\text{C}$, respectively. Ambient, summer, water temperatures in the lagoon range as much as $6 \text{ }^\circ\text{C}$ diurnally (Thomas, 1974).

RESULTS

Ophiophragmus filograneus tolerates acute exposure to a wide range of salinities. Initial burrowing times did not differ statistically ($F = 1.37$; $P > 0.05$) among the eight groups, and burrowing times were similar among groups exposed to salinities of $17\text{--}38 \text{ ‰}$ after 21 d (Fig. 1b–f). At 42 ‰ , no brittlestars burrowed within 420 s after 1 d, and all were dead by the end of the second day (Fig. 1a). Individuals exposed to 38 ‰ did not burrow for the first 2 d, but they showed gradual acclimation during the subsequent 19 d (Fig. 1b). All brittlestars at 38 ‰ , however, autotomized their discs after several days' exposure, and one individual died by Day 9. At $17\text{--}33 \text{ ‰}$ (Fig. 1c–f), burrowing times were somewhat longer and more variable in individuals exposed to salinities above and below

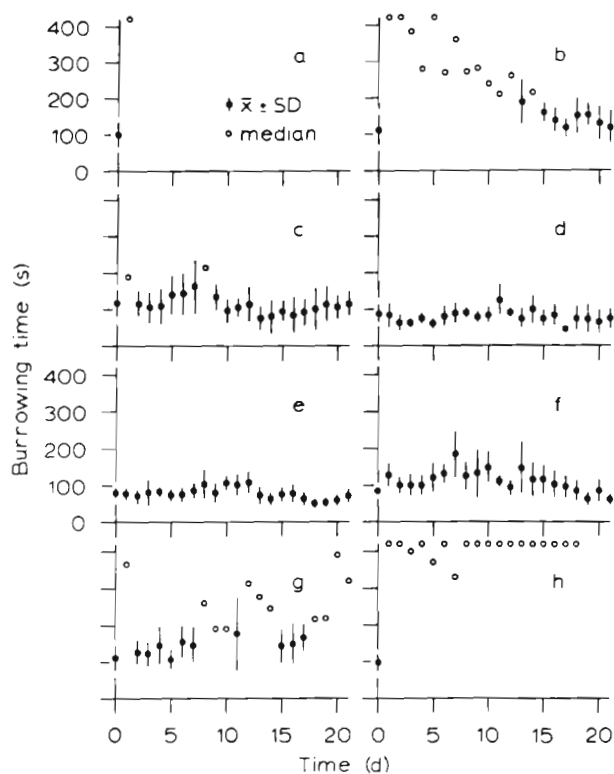


Fig. 1 *Ophiophragmus filograneus*. Tolerance to prolonged acute exposure to elevated and reduced salinities. a: 42 ‰ ; b: 38 ‰ ; c: 33 ‰ ; d: 27 ‰ ; e: 21 ‰ (ambient); f: 17 ‰ ; g: 13 ‰ ; h: 10 ‰ .

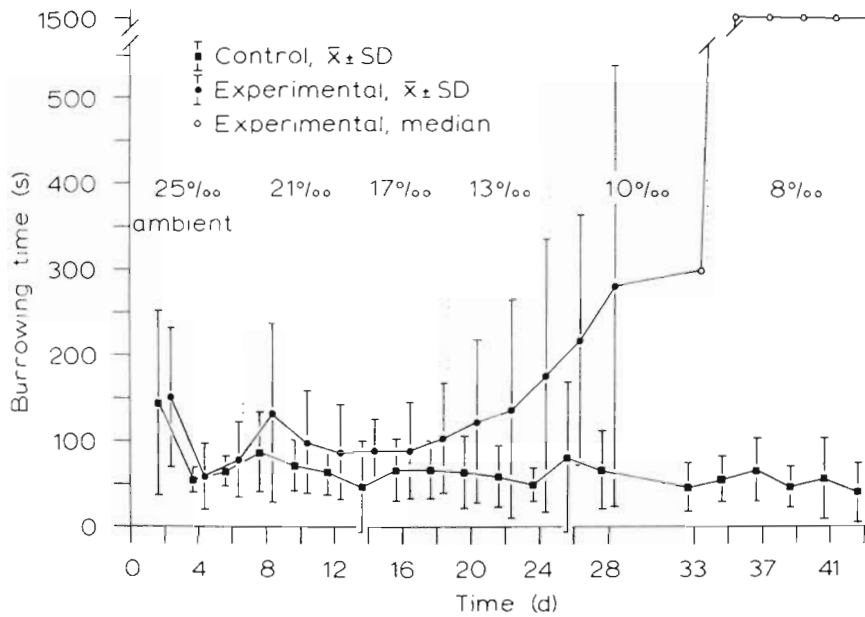


Fig. 2. *Ophiophragmus filigraneus*. Tolerance to gradual exposure to reduced salinities

ambient salinity (21 ‰). One individual in the group exposed to 33 ‰ did not burrow on Days 1 and 8. In contrast to the acclimation which occurred at 38 ‰, burrowing times and the number of non-burrowing individuals at 13 ‰ increased during the experiment (Fig. 1g). Few brittlestars in the 10 ‰ group burrowed within 420 s; all individuals autotomized their discs by Day 14 and died by Day 19.

Gradual exposure to reduced salinities gave results similar to those of acute exposure. During the 6-d control period, burrowing times of control and experimental groups were similar (Fig. 2). Burrowing times of the control group remained short during the remaining 37 d. At 21 and 17 ‰, burrowing times of the experimental group were slightly longer and more variable than those of the control group. During exposure to 13 and 10 ‰, burrowing times increased rapidly and were highly variable. One brittlestar did not burrow on Day 33 at 10 ‰, and few (0–4) burrowed within 1500 s at 8 ‰. Four individuals died on Day 41, and three on Day 43 when the experiment was terminated. Brittlestars did not undergo autotomy of arms and discs until exposure to a salinity of 8 ‰.

Salinity in the field was above 20 ‰ between April and late July 1978, after which the salinity decreased to 9 ‰ by late August. Salinity increased to 17 ‰ in early September, at which point it remained until the third experiment was begun in late September. Salinity of the interstitial water also was 17 ‰ in September. In the acclimatization experiment (Fig. 3), mean burrowing times of the control group (17 ‰) were similar to those of the control group (21 ‰) of the

first experiment. Individual burrowing times were, however, more variable, and one individual did not burrow on Days 19–21. Burrowing times were slightly longer at 14 ‰ than at 17 ‰, and one brittlestar did not burrow on several days. Burrowing times usually exceeded 200 s in the group held at 11 ‰; one individual did not burrow on many days, and one or two others did not burrow on Days 1–8. During exposure to salinities of 14 and 11 ‰ (Fig. 3b, c), burrowing times and the number of non-burrowing animals did not increase as they did at 13 ‰ in the first experiment (Fig. 1g) and at 13 and 10 ‰ in the second experiment (Fig. 2). No brittlestars burrowed after exposure to 8 ‰

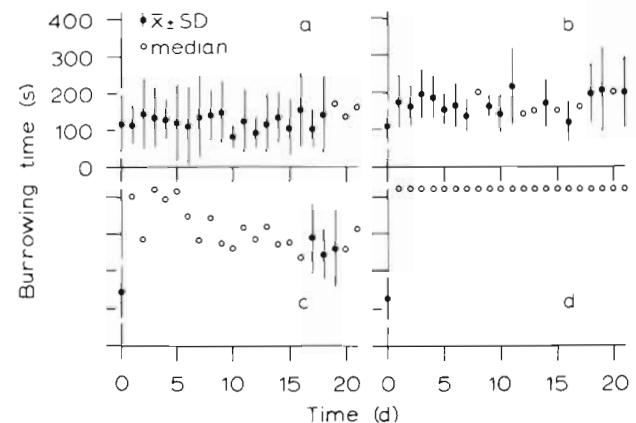


Fig. 3. *Ophiophragmus filigraneus*. Tolerance to prolonged acute exposure to reduced salinities following natural reduction to 9 ‰ in the field. a: 17 ‰ (ambient); b: 14 ‰; c: 11 ‰; d: 8 ‰

salinity (Fig. 3d); all individuals lived to Day 13, but only one test animal was alive after Day 16. Autotomy occurred only in brittlestars held at 8 ‰.

DISCUSSION AND CONCLUSIONS

Activity rates of the whole organism have been used as criteria of well being for individuals subjected to experimental and natural physiological stress. The rationale for using activity rates is that the whole organism functions within narrower environmental limits than do its component organs, cells, and enzymes (e. g. Prosser, 1973c); and only within these limits can ecologically important and highly coordinated processes such as defense, feeding, and orientation occur (Lawrence, 1975). The most widely used criterion for echinoderms has been the ability of an inverted animal to right itself (asteroids: Loosanoff, 1945; Kowalski, 1955; Ellington and Lawrence, 1974; echinoids: Giese and Farmanfarmanian, 1963; Lawrence, 1973, 1975; ophiuroids: Orr, 1955; Stancyk and Shaffer, 1977). Although righting time is an ecologically relevant criterion for epifaunal echinoderms, burrowing time is more appropriate for infaunal amphiuroid brittlestars. The burrowing response involves the rapid lateral movement of podia, horizontal coiling and mound construction by the arms, pulling of the disc into the substratum by the arms, and reciprocating rotation of the disc (Woodley, 1975; Murdoch, 1976; R. L. Turner and C. E. Meyer, personal observation). Moreover, the podia are used for feeding and burrow maintenance, and the arms for generation of respiratory currents (Woodley, 1975); these activities require a level of sensory and motor coordination similar to that necessary for burrowing. Burrowing time does not seem to have been used previously as a criterion of well being in echinoderms under physiological stress.

Burrowing times of *Ophiophragmus filograneus* from an ambient salinity of 21 ‰ were similar after 21 d acute exposure to salinities of 17–38 ‰. Coma and death occurred at 13 and 42 ‰. Although acclimation of the burrowing response occurred between 17 and 38 ‰, the lower tolerance limit could not be changed by gradual exposure to reduced salinity in the laboratory. Acclimatization did, however, occur in the field population following prolonged reduction of salinity to as low as 9 ‰. *O. filograneus* from an ambient salinity of 17 ‰ were under stress; but they were able to burrow after 21 d acute exposure to 11 ‰, and none at 8 ‰ died before Day 14. In a preliminary study, Stancyk (1970) measured recovery of the ability of *O. filograneus* and *Ophioderma brevispinum* to right at ambient salinity (30 ‰) after variable exposure times

in experimental salinities. *O. filograneus* held at 12 ‰ regained the ability to right within 41 h without being returned to ambient salinity. One individual recovered within 10 h at ambient salinity after 6 h exposure to 7.6 ‰; but five others did not recover from longer exposures. *O. brevispinum* was less tolerant of low salinity, but 10 individuals held at 15 ‰ for 283 h recovered in ambient salinity.

Only three other ophiuroid species have been studied, and they are less tolerant of reduced salinities under laboratory conditions (Binyon, 1966; Stancyk and Shaffer, 1977). Apparently, the upper tolerance limit has not been determined previously for an ophiuroid; *Ophiophragmus filograneus* recovered from exposure to the highest salinity (39 ‰) used by Stancyk (1970). Laboratory studies of other echinoderms show that most species are less tolerant than *O. filograneus* to prolonged reduction of salinity (Binyon, 1966, 1972; Lawrence, 1975). Some species do tolerate brief (Loosanoff, 1945) or cyclic (Stickle and Ahokas, 1974; Shumway, 1977) exposure. Acclimation of activity rates at reduced salinities has been found in some echinoderms (Binyon, 1972; Ellington and Lawrence, 1974). Acclimatization does not seem to have been studied, but Stancyk and Shaffer (1977) described a possible case of genetic adaptation to environmental salinities in estuarine populations of *Ophiothrix angulata*.

Populations of several echinoderms, especially ophiuroids, occur in brackish waters. Information on ambient salinities in which echinoderms are found was reviewed by Binyon (1966, 1972), Kinne (1971), and Remane and Schlieper (1971). Members of well-studied, brackish-water echinoderm populations differ in several ways from members of marine populations. Kowalski (1955), for example, found *Asterias rubens* from the Baltic Sea to have a longer righting time, smaller body size, different organic and inorganic composition, later maturation, and lower reproductive capacity than individuals from the North Sea. Some estuarine populations are sterile and are maintained only by recruitment (Kinne, 1971). When the effects of reduced salinities on echinoderms in the laboratory and field are considered, it is understandable that no truly brackish-water echinoderm has been reported (e. g. Remane and Schlieper, 1971).

Ophiophragmus filograneus is, however, endemic to the brackish-water bays and lagoons of Florida in association with the seagrass *Halodule (Diplanthera) wrightii*. The geographic distribution of *O. filograneus* (Fig. 4) is based on published and unpublished reports, museum field records, loans of preserved specimens, personal communications, and the authors' own field records. The distribution of its congener *O. wurdemani* in Florida (Fig. 4) is presented for comparison.

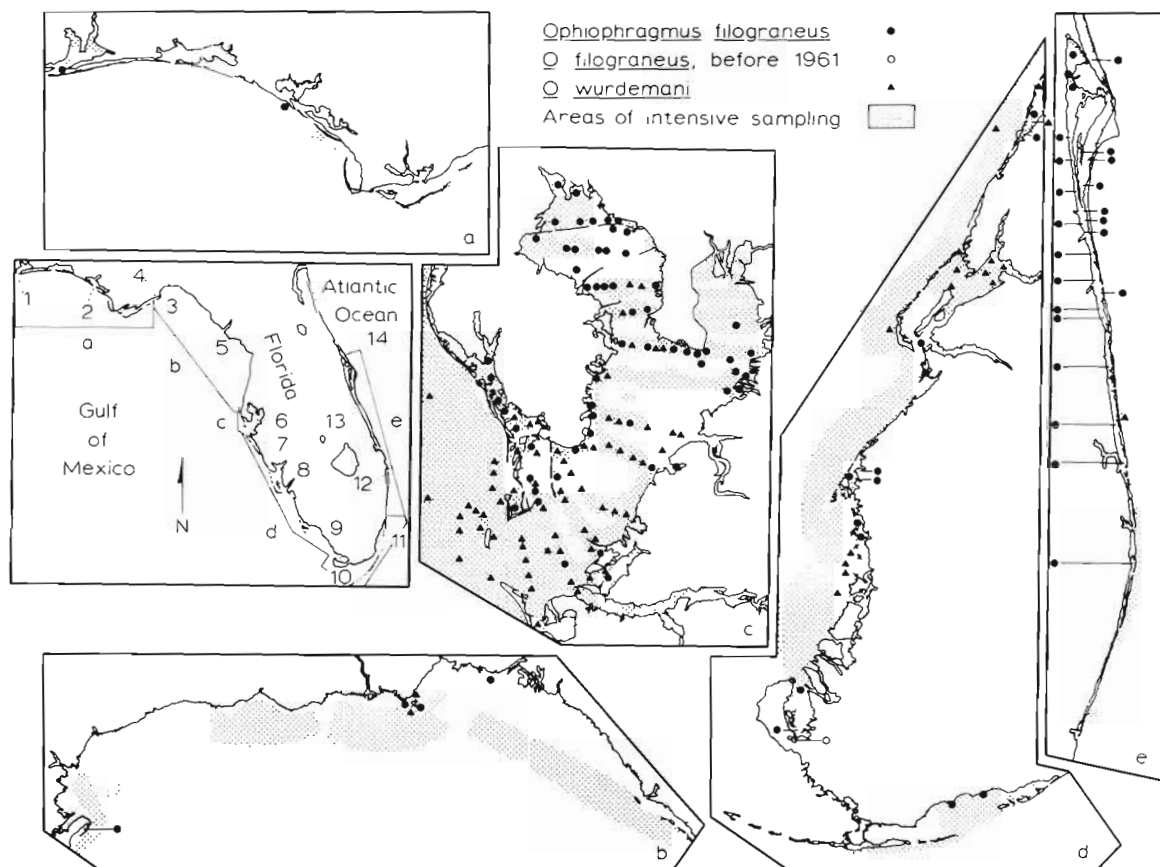


Fig. 4. *Ophiophragmus filigraneus* and *O. wurdemani*. Distribution in Florida, USA: a: western Florida; b: northeastern Gulf of Mexico; c: Tampa Bay region; d: southwestern Florida; e: east-central Florida. 1: Pensacola Bay estuarine system; 2: St. Andrew's Bay; 3: Apalachee Bay-St. George's Sound; 4: Alligator Harbor; 5: Cedar Keys region; 6: Tampa Bay estuarine system; 7: Sarasota Bay; 8: Charlotte Harbor; 9: Whitewater and Coot bays; 10: Florida Bay; 11: Biscayne Bay; 12: Lake Worth; 13: Indian River lagoon; 14: Mosquito Lagoon. Stippling: areas sampled intensively by dredge, grab, corer, shovel, or other methods which might retrieve infaunal brittlestars. Trawl samples not included. Sources of data given in the text.

Ophiophragmus filigraneus occurs in several estuaries of western Florida (Fig. 4a, b). Cooley (1978) found it in 1962–1963 at the mouth of the Pensacola Bay estuarine system ($S < 31\text{‰}$); but none was found by Olinger et al. (1975) in 1973–1974 in the rest of the estuary, where most seagrass beds gradually died between 1949 and 1974. Thomas (1965) found *O. filigraneus* in Alligator Harbor ($S = 28\text{--}32\text{‰}$; R. W. Menzel, personal communication). Menzel (1971) reported *O. filigraneus* from the estuarine Apalachee Bay-St. George's Sound region but gave no station data. *O. filigraneus* occurs in the Cedar Keys region (Stancyk, 1970) and at the mouth of Crystal River (Evink and Green, 1974); these areas are estuarine despite their apparent exposure (Stancyk and Shaffer, 1977). No *Ophiophragmus* spp. were found at 171 stations sampled by Godcharles and Jaap (1973) in the northeastern Gulf of Mexico ($S > 29\text{‰}$). The origin of one *O. filigraneus* found on an exposed beach near St. Andrew's Bay by Saloman and Naughton (1977) is in

doubt because the individual was collected 2 d after Hurricane Eloise (1975) passed through the area (C. H. Saloman, personal communication). *O. filigraneus* and *O. wurdemani* are sympatric in the Apalachee Bay-St. George's Sound (Menzel, 1971) and Cedar Keys (Stancyk, 1970, personal communication) regions.

Extensive faunal and hydrographic surveys of the Tampa Bay region (Fig. 4c) show that *O. filigraneus* is confined to brackish waters of all five sub-areas of the estuary (Godcharles, 1971; Bloom et al., 1972; Godcharles and Jaap, 1973; Turner, 1974; Hall and Saloman, 1975; Mahadevan et al., 1977; J. D. Murdoch and J. L. Simon, personal communications). Means and ranges of salinity for the five sub-areas are listed by Simon (1975). *O. wurdemani* does not penetrate as far into Tampa Bay, generally inhabits deeper, more saline waters, and occurs offshore (Godcharles, 1971; Godcharles and Jaap, 1973; Hall and Saloman, 1975).

Along the southwest coast of Florida (Fig. 4d), *Ophiophragmus filigraneus* occurs in the following

estuaries: Sarasota Bay (Thomas, 1965; Tiffany, 1974), $S = 24-40\text{‰}$ (J. B. Morrill, personal communication); San Carlos and Estero bays near Ft. Meyers (Thomas, 1962, 1965); near Marco Island, $S = 19-39\text{‰}$ (Weinstein et al., 1977); Fahka Union Bay, $S = 11-29\text{‰}$, and Fahkahatchee Bay, $S = 27-32\text{‰}$ of the Ten Thousand Islands region (Evink, 1975). Its apparent absence from Charlotte Harbor (Godcharles and Jaap, 1973) has been substantiated by our examination of more recently collected ophiuroid material on loan from Environmental Quality Laboratory, Inc. The absence of *O. filigraneus* is unexpected because of the estuarine conditions (Dragovich et al., 1966; Taylor, 1975) and the presence of *Halodule wrightii* (Godcharles and Jaap, 1973) in Charlotte Harbor. *O. wurdemani* is sympatric with *O. filigraneus* in Sarasota Bay (Tiffany, 1974), and it also occurs in Charlotte Harbor and in the Gulf of Mexico (Thomas, 1962; Godcharles and Jaap, 1973).

At the southern tip of Florida (Fig. 4d), *Ophiophragmus filigraneus* once occurred in large numbers in Coot and Whitewater bays (Tabb and Manning, 1961; Thomas, 1961; Tabb et al., 1962), where mean salinities (and ranges) were 25‰ ($6-41\text{‰}$) and 19‰ ($4-40\text{‰}$), respectively (Tabb et al., 1962). The population apparently died before 1961 (Thomas, 1961) along with *Halodule wrightii* (Tabb et al., 1962). Both the brittlestar and the seagrass were found in Whitewater Bay by Davis and Hilsenbeck (1974) in 1973-1974. *O. filigraneus* has not been collected in nearby Florida Bay, which has a mean annual salinity of 35‰ (Tabb et al., 1962).

In Biscayne Bay (Fig. 4d), low salinities occur only along the continental shoreline, where *Halodule wrightii* is found (Roessler and Beardsley, 1975) and where groundwater seeps upward through the sediment (L. P. Thomas, personal communication). *Ophiophragmus filigraneus* is found near shore (Pearson, 1937; Thomas, 1962) but not in Biscayne Bay proper (McNulty, 1961; McNulty et al., 1962; O'Gower and Wacasey, 1967; L. P. Thomas, personal communication). *O. filigraneus* occurs in Lake Worth (Thomas, 1962) (Fig. 4e), and it is common throughout the Indian River lagoon (Thomas, 1962; Thomas, 1974; Wiederhold, 1976; Grizzle, 1979; D. A. Bruzek, K. D. Levy, J. D. Rice, and R. P. Trocine, personal communications; Harbor Branch Foundation, field records; R. L. Turner, personal observation) in association with extensive beds of *H. wrightii* (Thompson, 1978). The lagoon is brackish (Wiederhold, 1976; Zweck and Adragna, 1976; Grizzle, 1979), although some areas are seasonally hypersaline (Young et al., 1976). The northernmost occurrence of *O. filigraneus* to our knowledge is in southern Mosquito Lagoon (D. A. Bruzek, personal communication), although *H.*

wrightii extends through northeastern Florida (Phillips, 1960; Hanlon and Voss, 1975). Several *O. wurdemani* were collected in the Atlantic Ocean off Hutchinson Island (Florida Department of Natural Resources, field records) (Fig. 4e), but no *Ophiophragmus* spp. were found at 94 offshore stations sampled by Godcharles and Jaap (1973) (Fig. 4d, e).

The brackish bays and lagoons of Florida are rimmed with mangroves and are vegetated with seagrasses. Both community types produce large quantities of detritus and provide a year-round supply for detrital food chains (Lugo and Snedaker, 1974; Thayer et al., 1975). *Ophiophragmus filigraneus* forms dense, reproductive populations in the seagrass beds (Tabb et al., 1962; Thomas, 1965; Stancyk, 1974; Turner, 1974, personal observation; Thomas, 1974) and probably feeds on autochthonous detritus as well as the imported detritus from mangals. It is a deposit feeder, whereas *O. wurdemani* is a suspension feeder which lives in grass-free, clean or muddy sands (Thomas, 1961, 1965; Stancyk, 1970). Although the range of salinity tolerance of *O. filigraneus* should not restrict it to brackish waters, food requirements might. Euryhalinity, in addition to behavioral, morphological, and developmental adaptations (Stancyk, 1973; Turner, 1974), probably has allowed *O. filigraneus* to inhabit successfully a nutritionally rich biotope where few other echinoderms are found.

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