

Florida Scientist

QUARTERLY JOURNAL OF THE FLORIDA ACADEMY OF SCIENCES

WALTER K. TAYLOR, *Editor*

HENRY O. WHITTIER, *Editor*

Volume 46

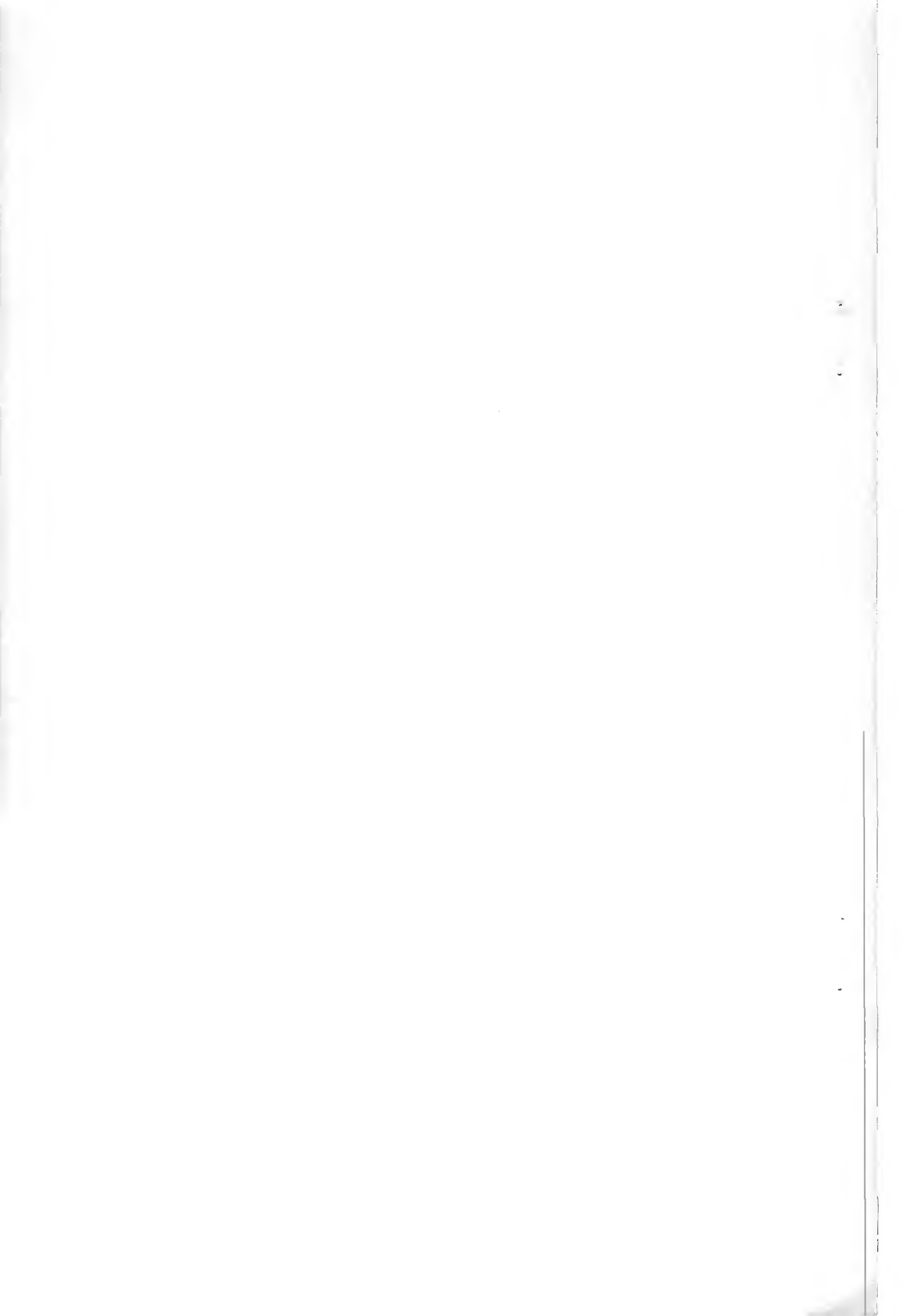
Summer, Fall, 1983

Number 3/4

OBSERVATIONS ON THE ECOLOGY AND
REPRODUCTION OF THE SIPUNCULAN
PHASCOLION CRYPTUS IN THE
INDIAN RIVER LAGOON

MARY E. RICE, JULIANNE PIRAINO, AND HUGH F. REICHARDT

Reprinted from
Florida Scientist
Vol. 46, Nos. 3/4, Summer, Fall, 1983



OBSERVATIONS ON THE ECOLOGY AND
REPRODUCTION OF THE SIPUNCULAN
PHASCOLION CRYPTUS IN THE
INDIAN RIVER LAGOON

MARY E. RICE, JULIANNE PIRAINO, AND HUGH F. REICHARDT

Smithsonian Marine Station at Link Port, Fort Pierce, Florida 33450

ABSTRACT: A study of the most abundant sipunculan found in the Indian River Lagoon, *Phascolion cryptus* Hendrix, 1975, was conducted on a monthly basis from June 1976 through May 1977. These animals, which inhabit discarded gastropod shells in shallow water, were found in densities of 667 to 3,856/m² at a station 9.25 km north of the Fort Pierce Inlet, Florida. Adult *Phascolion* were common in shells of 5 species of gastropods. Most frequently they inhabited *Cerithium muscarum* shells which comprised an average of 85% of those available for inhabitation. Population numbers were not limited by shell availability. Reproductive activity was estimated by the developmental state of coelomic gametes and spawning in the laboratory. Animals were reproductive throughout the year with a trend for higher reproductive activity from November through May. Juveniles, commonly occupying shells of *Bittium varium*, comprised 37 to 58% of the population during winter, spring and summer, decreasing to an average of 15.5% in the fall.

THE sipunculan *Phascolion cryptus* Hendrix, 1975, is a common inhabitant of the Indian River estuary on the central, east-coast of Florida. It is a small species (3 cm in extended length) living in discarded gastropod shells in a manner similar to that of hermit crabs (Fig. 1). When the sipunculan feeds or moves about, the anterior end or "introvert", is extended through the aperture of the shell, while the rest of the body remains inside. Usually



FIG. 1. *Phascolion cryptus* adult in a shell of *Cerithium muscarum*. Introvert bearing a crown of tentacles is extended from the aperture of the shell.

- McKAY, C.R., AND D.J. HARTZBAND. 1970. Propylene phenoxetylol: narcotic agent for unsorted benthic invertebrates. *Trans. Amer. Microsc. Soc.* 89: 53-54.
- NELSON, W.G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J. Exp. Mar. Biol. Ecol.* 38: 225-245.
- _____. 1981a. Experimental studies of decapod and fish predation on seagrass macrobenthos. *Mar. Ecol. Prog. Ser.* 5: 141-149.
- _____. 1981b. The role of predation by decapod crustaceans in seagrass ecosystems. *Marine Biology Symposium, Kiel 1980. Kieler Meeresforsch., Sonderh.* 5: 529-536.
- _____, K.D. CAIRNS, AND R.W. VIRNSTEIN. 1982. Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River lagoon, Florida. *Bull. Mar. Sci.* 32: 121-129.
- O'GOWER, A.K., AND J.W. WAGASEY. 1967. Animal communities associated with *Thalassia. Diplanthaera*, and sand beds in Biscayne Bay. I. Analysis of communities in relation to water movements. *Bull. Mar. Sci.* 17: 175-210.
- ORTH, R.J. 1977. The importance of sediment stability in seagrass communities. Pp. 281-300. *In: Coull, R.C. (ed.). Ecology of Marine Benthos.* Univ. South Carolina Press, Columbia.
- _____, AND K.L. HECK, JR. 1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—fishes. *Estuaries.* 3: 278-288.
- REISE, K. 1977. Predator exclusion experiments in an intertidal mud flat. *Helgoländer Wiss. Meeresunters.* 30: 263-271.
- _____. 1978. Experiments on epibenthic predation in the Wadden Sea. *Helgoländer Wiss. Meeresunters.* 31: 55-101.
- ROBERTSON, A.I. 1983. Trophic interactions between the fish and macrobenthos of an eelgrass community in Westernport Bay, Victoria. *Aquaculture (in press).*
- SANTOS, S.L., AND J.L. SIMON. 1974. Distribution and abundance of the polychaetous annelids in a south Florida estuary. *Bull. Mar. Sci.* 24: 669-689.
- SOKAL, R.R., AND F.J. ROHLF. 1969. *Biometry.* W. H. Freeman and Co., San Francisco. 776 pp.
- STONER, A.W. 1979. Species specific predation on amphipod Crustacea by pinfish (*Lagodon rhomboides*): Mediation by macrophyte standing crop. *Mar. Biol.* 55: 201-207.
- _____. 1980. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): Variation and functional responses. *Fish. Bull.* 78: 337-352.
- TABB, D.C. 1961. A contribution to the biology of the spotted seatrout, *Cynoscion nebulosus* (Cuvier) of east-central Florida. *Fla. State Bd. Conserv. Mar. Lab. Tech. Ser.* 35: 1-22.
- THOMPSON, M.J. 1976. Photomapping and species composition of the seagrass beds in Florida's Indian River estuary. *Tech. Rept. No. 10.* Harbor Branch Found., Inc., Ft. Pierce, Florida.
- _____. 1978. Species composition and distribution of seagrass beds in the Indian River lagoon, Florida. *Florida Sci.* 41: 90-96.
- VIRNSTEIN, R.W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58: 1199-1217.
- _____. 1978. Predator caging experiments in soft sediments: Caution advised. Pp. 261-273. *In: M.L. Wiley (ed.). Estuarine Interactions.* Academic Press, New York.
- _____. 1979. Predation on estuarine infauna: Response patterns of component species. *Estuaries.* 2: 69-86.
- WOODIN, S.A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. *Ecol. Monogr.* 44: 171-187.
- YOUNG, D.K., M.A. BUZAS, AND M.W. YOUNG. 1976. Species densities of macrobenthos associated with seagrass: a field experimental study of predation. *J. Mar. Res.* 34: 577-592.
- _____, AND M.W. YOUNG. 1977. Community structure of the macrobenthos associated with seagrass of the Indian River estuary, Florida. Pp. 359-382. *In: Coull, B.C. (ed.). Ecology of Marine Benthos.* Univ. South Carolina Press, Columbia.
- _____. 1978. Regulation of species densities of seagrass-associated macrobenthos: Evidence from field experiments in the Indian River estuary, Florida. *J. Mar. Res.* 36: 569-593.
- _____. 1982. A comparative study of macrobenthic invertebrates in bare sand and seagrass (*Thalassia testudinum*) in Carrie Bow Cay lagoon. *Smithsonian Inst. Contrib. Mar. Sci.* 12: 115-126.

buried within the upper 5 cm of the sediment, the sipunculan may stretch its introvert to the surface of the sediment or above. Thus extended, the crown of tenacles terminating the introvert may function for feeding on suspended particulate materials and for the exchange of respiratory gases through the tentacular wall.

Phascolion cryptus occurs in large numbers along the length of the Indian River in sandy bottom areas, frequently with a cover of seagrasses. In a study of community structure of the macrobenthos associated with seagrass beds in the Indian River, Young and Young (1977) ranked this species third in order of abundance at a station near Haulover Canal, and fourth at both the centrally-located station near Link Port, and the more southerly station near the St. Lucie Inlet. Of the percentage of total individuals in the top-ranked 10 species at these 3 stations, *Phascolion cryptus* comprised 11, 9, and 6%, respectively from north to south.

We investigated selected features of the ecology and reproduction of *Phascolion cryptus* for 1 yr at the Link Port station. In monthly collections we noted densities, occurrence in habitats of bare sand or seagrasses, and the utilization of shells of different sizes and of different gastropod species. In the laboratory we observed the behavior of the animal in relation to its occupied shell. As an indication of reproductive activity, we recorded at monthly intervals in field-collected specimens the sizes of coelomic oocytes, states of differentiation of coelomic sperm, and spawnings of laboratory-maintained animals.

MATERIALS AND METHODS—This study was conducted from June 1976 to May 1977 in the Indian River Lagoon north of the Link Port canal, 9 km north of the Fort Pierce Inlet, Florida at latitude 27°32.1'N, longitude 80°20.9'W. The collecting area was characterized by sandy patches amidst grass beds dominated by *Halodule wrightii* (shoal grass). Water depths at the time of collection ranged from 2 to 59 cm. Temperatures ranged from 12.5 to 38°C and salinities from 16 to 35‰.

For measurements of density, a sampling grid was established covering an area of 12 × 24 m where 3 or 4 replicates were collected at monthly intervals for 1 yr. At the initial collection, a rope 24 m in length was stretched in an east-west direction between 2 fixed points and samples were taken at 6 m intervals from the easternmost point towards the shoreline on the west. Samples in succeeding months were taken at points 1 m due north of the previous month's collections. Samples were collected with a stainless steel sampling device which isolated sections of the bottom 5 cm in depth and 15 × 15 cm in surface area (Fig. 2). Upon collection, the samples were transferred to 1 mm mesh bags and material less than 1 mm in size was sieved out at the collecting site. Samples were sieved through 2.8, 2.0 and 1.0 mm wire mesh sieves in the laboratory, and gastropod shells trapped by each sieve were collected and counted. The number of uninhabited and *Phascolion*-inhabited shells retained by each sieve was recorded for use in density and shell occupancy determinations.

Animals were collected just outside the density sampling grid for measurements of reproductive activity. Gastropod shells were cracked in a vise to extract the *Phascolion cryptus*. Coelomic contents of adults (i.e., animals over 20 mg wet wt) were sampled by piercing the posterior end of the animal with a needle while holding the specimen above a droplet of sea water on a microscope slide. The pierced end was then touched to the droplet as the animal was squeezed gently. A coverslip, supported at the corners by bits of modeling clay, was placed over the preparation. Ten females were sampled each month and for each female the first 50 oocytes encountered in the microscopic survey of the slide were measured. An average of 9 males (range, 5-13) was sampled each month for the presence of free coelomic sperm. Animals of both sexes in the 2 larger size classes in the density study and any excess animals from the collections for

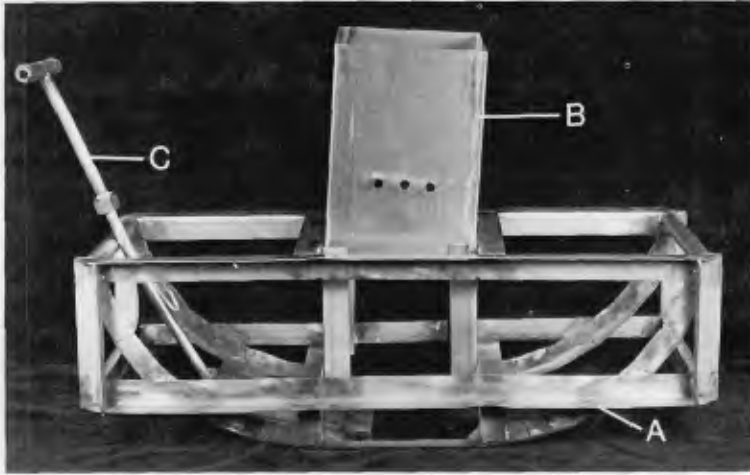


FIG. 2. Stainless steel sampling device for density study. Sampler is pushed into the sediment until stopped by rim (A) which is 5 cm above the bottom of the sampler. The 15×15 cm corer (B) is inserted and the shovel (C) is guided along the track to cut off the bottom of the core sample at 5 cm depth. The sampler is then raised and the sample dropped into an open 1 mm mesh bag for sieving.

reproductive measurements were maintained in the laboratory for 2 mo and observed for spawning.

Methods used in laboratory studies of behavior of *Phascolion cryptus* will be presented in the Results section along with an account of the observations.

DENSITY—The number of *Phascolion cryptus* per square meter ranged from 667 to 3,856 at the Link Port station from June 1976 to May 1977 (Fig. 3). Although measurements of density showed considerable monthly variability, a higher density was found in June 1976 at the beginning of the study than in May of the following year. The greatest decrease occurred between August and September 1976. A breakdown of total density into densities of each of the 3 size classes indicates that the decrease in September was due primarily to the diminished numbers of juveniles (Fig. 4). The lack of concomitant increase in the larger size classes points to a possible loss of juveniles from the population, rather than growth of individuals. During the last few months of the study (March through May) the relative numbers of juveniles and adults were essentially the same as those of the first few months (June through August), despite the overall decrease in actual densities of both large and small size classes during the year (Figs. 4, 5).

Monthly collections usually contained samples from both bare-sand areas and areas covered by seagrass beds comprised of *Halodule wrightii*. Densities were consistently higher throughout the year in seagrass beds than in sandy areas outside of the seagrass (Fig. 6).

SHELL OCCUPANCY—At the Link Port station *Phascolion cryptus* of the 2 upper size classes were commonly found in discarded shells of 5 species of gastropods. They were, in order of abundance at the collecting site:

Cerithium muscarum, *Nassarius vibex*, *Modulus modulus*, *Neritina virginea*, and *Marginella apicina*. The shells of *C. muscarum* occurred in the greatest numbers, constituting 84% of the shells available for occupancy by *P. cryptus*. Thirty-nine percent of the *C. muscarum* shells were actually occupied by *P. cryptus*. The abundance of *Modulus* and *Marginella* shells was markedly less than *Cerithium*, but the percentage occupancy of these shells by *Phascolion cryptus* was not significantly different from that of *Cerithium* (Table 1). The remaining 2 gastropod shells, *Nassarius vibex* and *Neritina virginea*, had a significantly lower occupancy by *P. cryptus* than *C. muscarum* (Table 1). The smallest sipunculans were found predominantly in shells of *Bittium varium*.

An examination of the percentage occupancy of shells in each of 3 size classes shows that with increasing shell size, there is an increasing percentage of available shells occupied (Fig. 7). This difference in percentage occu-

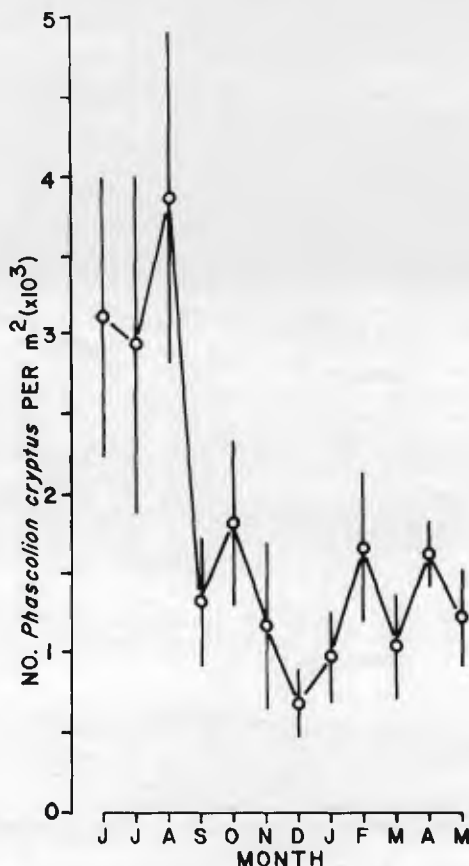


FIG. 3. Density of *Phascolion cryptus*. Monthly averages of the total numbers of individuals per square meter, including all size classes, from June 1976 to May 1977. Standard error bars are shown.

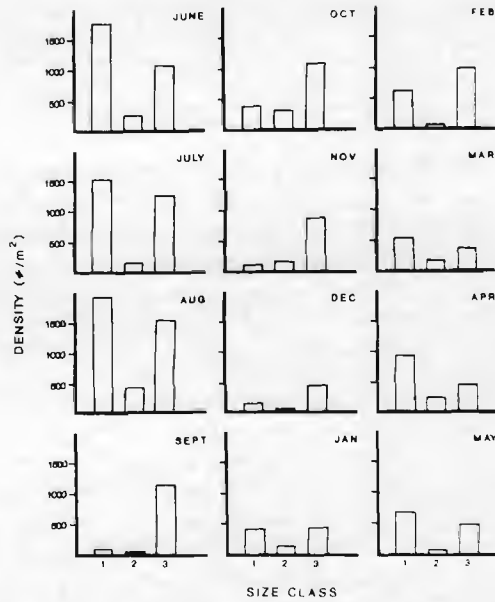


FIG. 4. Monthly densities of the 3 size classes of *Phascolion cryptus* from June 1976 to May 1977. Size classes 1, 2 and 3 represent *Phascolion* in gastropod shells of sizes from 1.0 to 2.0 mm, 2.0 to 2.8 mm and greater than 2.8 mm, respectively.

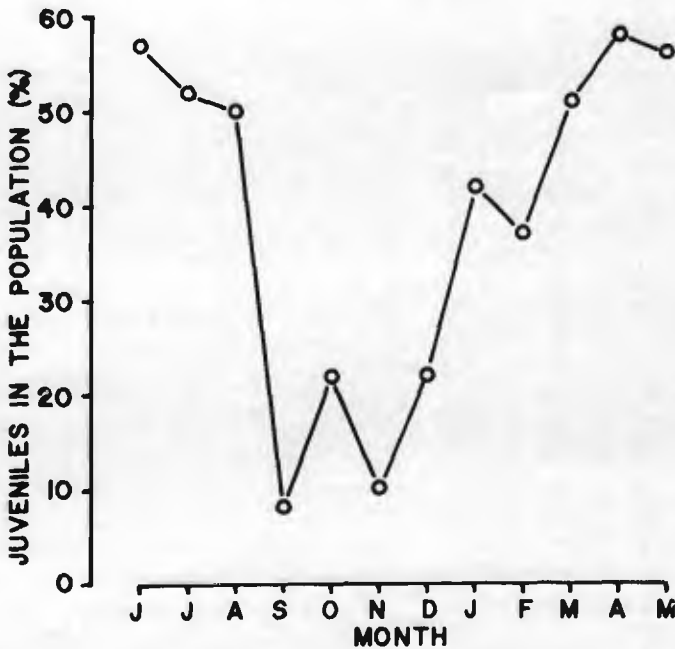


FIG. 5. Percent of *Phascolion cryptus* juveniles (in 1-2 mm shells) in the population from June 1976 to May 1977.

TABLE 1. Shell species most commonly inhabited by *Phascolion cryptus* (excluding the 1.0-2.0 mm size class). Tested differences (χ^2 , $df = 1$) in shell occupancy between *Cerithium muscarum* and each of the 4 other shell species are indicated.

Shell Species	Total No.	No. Occupied	% Occupied	χ^2	Significance
<i>Cerithium muscarum</i>	1198	464	39	--	--
<i>Modulus modulus</i>	85	28	33	1.18	ns
<i>Marginella apicina</i>	23	9	39	0.00	ns
<i>Nassarius vibex</i>	94	26	28	4.67	0.01 < P < 0.05
<i>Neritina virginea</i>	57	3	5	26.30	P < 0.01

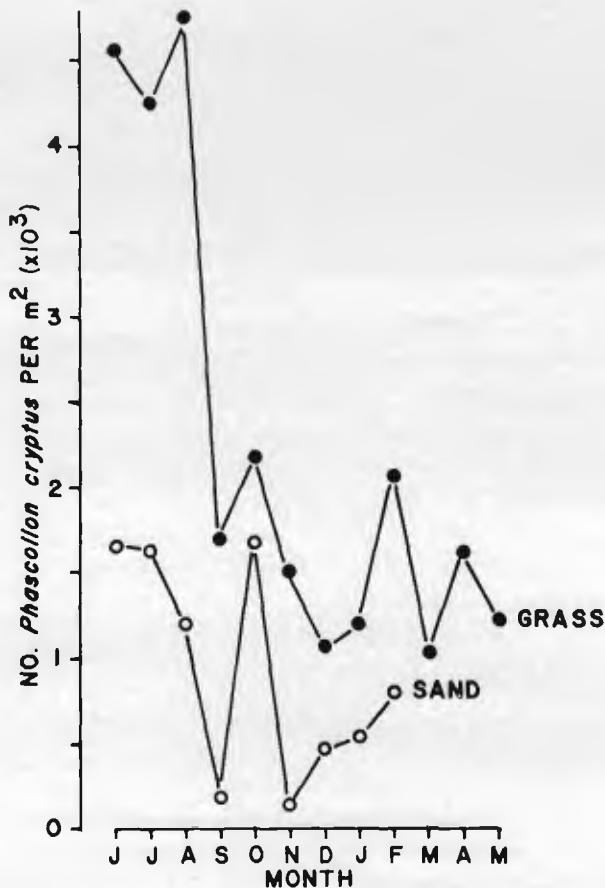


FIG. 6. Density of *Phascolion cryptus* in beds of *Halodule wrightii* (Grass) and bare sand (Sand) from June 1976 to May 1977.

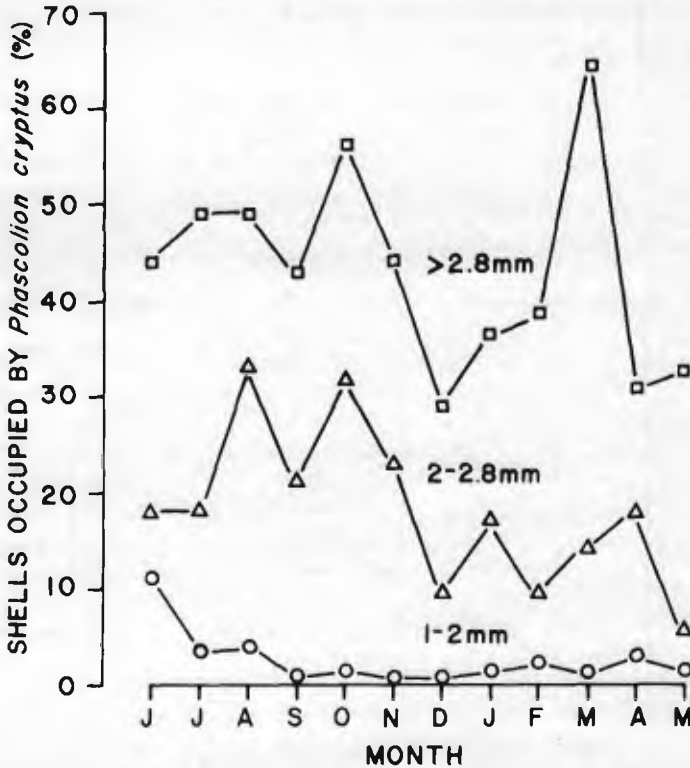


FIG. 7. Percent of discarded gastropod shells occupied by the 3 size classes of *Phascolion cryptus* from June 1976 to May 1977.

pancy in the 3 size classes persisted throughout the year in spite of monthly variations for each size class. Never were all of the available shells occupied. The highest percentage occupancy in any of the size classes was 66.5 which occurred in the largest size class in March.

The behavior of animals in relation to their shells was investigated in a series of 3 laboratory experiments. In the first 2 experiments, 12 animals (7 in experiment 1 and 5 in experiment 2) were extracted from their shells by cracking the shells in a vise. Each *Phascolion cryptus* was then immediately placed in a 10 cm culture dish in the center of a circle of 6 empty shells. The shell apertures were towards the center of the circle and were equidistant from the animal. Shell apertures presented to half of the animals were directed down against the bottom of the dish and those presented to the other half were directed upward. Shells used were of comparable size and of the same species as those from which the animals had been removed. In 11 dishes, the shells were *Cerithium muscarum* and in 1 dish *Marginella apicina*. Animals and shells were placed in dishes of sea water without substratum in experiment 1, and with substratum in experiment 2. The substratum, obtained from the Link Port collecting site, consisted of a thin

layer of silt overlying 1 cm of sand. Once the animals were exposed to the empty shells, they were watched continually and their behavior was recorded and timed.

In experiment 1, specimens which had been removed from their shells entered empty shells by inserting the introvert into the aperture and pulling the more posterior trunk into the shell. Of the 7 animals observed, the times for choosing a shell ranged from 14 min to over 7 hr, and the elapsed time from the beginning of entry until the animal disappeared completely into the shell ranged from 3 to 7 min. Once in a shell, the animal turned around and extended its introvert from the shell aperture. This turn-around time ranged from 11 to 18 min in the 6 cases in which animals entered *Cerithium* shells and was 6 min in the case of the animal that entered a *Marginella* shell.

In experiment 2, animals burrowed into the sediment and extended their introverts above the substratum to select the empty shells. Times for shell selection ranged from 30 to 86 min for the 5 animals observed. Once inside the shells, animals eventually buried themselves and the shells they inhabited 3-7 mm below the sediment level. Though all the animals in these 2 experiments entered empty shells, only 1 in 12 entered the first encountered shell.

In the third experiment, the spires of shells containing *Phascolion cryptus* were removed in a vise. The remaining shell was approximately one-half its original length and the posterior end of the animal was exposed. The 6 animals in this experiment were placed in culture dishes of sea water next to an intact empty shell of similar size and of the same species as that which it was inhabiting. Two empty shells were added to the 5 dishes in which no shell exchange had occurred by Day 2. An additional 2 shells were added to the 1 dish in which no shell exchange had occurred on Day 10. In time, all animals left the damaged shells and entered intact, empty shells. The time required for this exchange ranged from 1 to 9 da.

REPRODUCTIVE BIOLOGY—Samples of coelomic fluid taken at monthly intervals revealed that gametes in some stage of differentiation were present in most animals (greater than 20 mg in wt) throughout the year. Free spermatozoa were present in the coeloms of at least 70% of the male population except in August when the percentage was only 13 (Fig. 8). For 6 mo out of the yr, coelomic spermatozoa were found in 100% of the males examined. Small oocytes, from 20 to 110 μm in dia, were present throughout the year, suggesting that the ovary was continually productive. Large oocytes (110-140 μm) showed a general increase in percentage from a low in summer to a high in winter and spring (Fig. 9). This trend corresponded with the decrease in laboratory spawning activity in summer months and with the low percentage of juveniles in the population in the fall (Figs. 4, 5). Animals spawned in the laboratory in every month of the year, however, the lowest activity was in the summer and the highest in the fall.

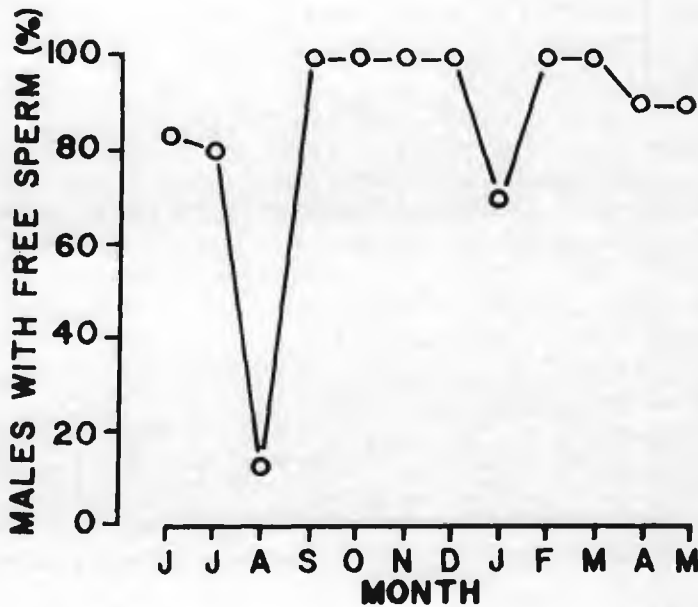


FIG. 8. Percent of *Phascolion cryptus* males with free coelomic sperm from June 1976 to May 1977. (Number of males observed each month equals, respectively, 12, 6, 8, 5, 5, 13, 10, 10, 10, 10, 10).

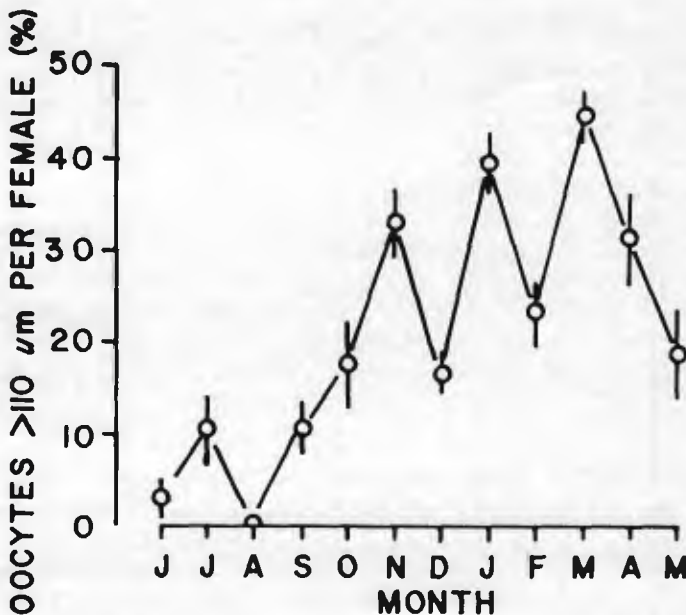


FIG. 9. Average monthly percentage of large oocytes (> 110 μm dia) per female. Each month, 50 oocytes from each of 50 females were measured (a total of 500 oocytes per month). Standard error bars are shown.

DISCUSSION

DENSITY—Densities for *Phascolion cryptus* have been measured by other investigators at the Link Port station, and such measurements fall within the range found in this study (667-3,856/m²). In a long-term survey of the benthic ecology of the Indian River, Virnstein (pers. comm.) found densities which averaged 2,271/m², the average for the same period in our study was 1,776/m². The density reported by Young and Young (1977, 1978) as a value for controls in their experimental studies was 2,400/m². These densities for *P. cryptus* are the highest recorded for any sipunculan species. Another species of the same genus and of comparable size, *Phascolion strombus*, was reported in densities ranging from 60 to 135/m² in waters 45 m in depth off the west coast of Sweden (Hylleberg, 1975). A large sand-burrowing species, *Sipunculus nudus*, which reaches lengths of 30 cm (Stephen and Edmonds, 1972) has been reported to have an average density of 4.6/m² on a sandy beach at Morgat, Bay of Douarnenez, Brittany, France (Edmonds, 1962). Rock-boring species from the Caribbean Sea, *Aspidosiphon brocki* and *Lithacrosiphon alticonum*, were found in densities as great as 900 and 500/m², respectively (Rice and Macintyre, 1982, Fig. 3).

The explanation for the overall decline of density in the population of *Phascolion cryptus* during our study is unclear. The sharpest reduction occurred in the juvenile population between the August and September measurements. Because the drop was unaccompanied by a corresponding increase in the larger size classes, we assume that it could not be due entirely, if at all, to growth of juveniles. Moreover, the abruptness of the decline leads us to speculate that some external factors, such as extremes of temperatures and salinity or heavy predation, were causative factors. An examination of readings made at the time of the September collection, show that the salinity was 16‰, lowest for the year and the temperature was 25°C, among the highest for the year. Further suggestion for the importance of these environmental factors comes from the experiment of Hylleberg (1975) on the cold-water population of *Phascolion strombus*. He demonstrated that this species could not tolerate combinations of high temperatures (above 16°C) and low salinities (below 23‰). Although *P. cryptus* occurs in warm waters, in view of these findings a further consideration of the tolerances of the species, especially of juveniles, would seem warranted.

The continued low numbers of juveniles from September through December (Figs. 4, 5) follows the summer period of low reproductive activity of adults and is most likely explained by a lack of production of young animals. The recovery of the juvenile population and its overall increase from December to May is consistent with increased reproductive activity of the population in fall and winter.

Our finding of *Phascolion cryptus* in greater densities among *Halodule wrightii* than in areas of bare sand agrees with other reports of high densities of macrobenthos in seagrass beds (O'Gower and Wacasey, 1967; Orth,

1977). In a study of animal communities associated with seagrass and sand beds in Biscayne Bay, O'Gower and Wacasey (1967) found a far greater abundance of species in seagrass. Among these enumerated was a species of *Phascolion*, later described as *Phascolion cryptus* (Hendrix, 1975) which occurred in *Halodule* beds in densities 13 times greater than in areas of bare sand in Virginia Key. Moreover, *P. cryptus* was the dominant benthic species in these *Halodule* beds.

Orth (1977) emphasized the importance of the stabilization of sediment by seagrass beds in Chesapeake Bay as a factor related to increased density of macrobenthos. He proposed that by impeding the flow of waves and currents and thus reducing erosion, the seagrass prevents juveniles and adults from being resuspended and transported away from their habitats. Young and Young (1978) further examined the sediment-stabilizing function of seagrass beds in studies at Link Port. In a series of field experiments testing the regulation of species densities of seagrass-associated macrobenthos, they tested the effect of removal of the blades of *Halodule wrightii*. They found that *Phascolion cryptus* differed from several other species in that it was not markedly affected by clipping of grass blades. The authors reasoned that stabilization of the sediment provided by the rhizomes was of greater importance to this species than protection or other factors provided by the blades. Other experiments in the same study compared the density of macrobenthos under caged and uncaged conditions in the field and showed little response by *P. cryptus* to the exclusion of predators by caging. More recently, however, Nelson (1981) has demonstrated that 2 species of decapod shrimp may prey on *P. cryptus*. He studied decapod and fish predation on macrobenthos associated with seagrass both in laboratory tanks and in predator inclusion cages in the field at the Link Port station. Of the predators tested, *Penaeus duorarum* and *Palaemonetes intermedius* significantly reduced the number of *P. cryptus* in laboratory tanks, though their effect in field experiments was not significant.

SHELL OCCUPANCY—Of the 37 reported species of *Phascolion*, most occupy discarded gastropod shells. The rest are found mostly in polychaete tubes or in mud and sand tubes of their own construction (Stephen and Edmonds, 1972; Hendrix 1975). Similar to the occupancy of shells by hermit crabs (cf., Reese, 1962; Scully, 1979; Bertness, 1980), the occurrence of *Phascolion* in certain species of shells may reflect, at least in part, abundance and diversity of available shells in the area. And, like hermit crabs, *Phascolion* may show some preference for certain species of shells within a habitat, although evidence is conflicting in this regard. Hylleberg (1975) found *P. strombus* to occur in shells of all species of gastropods as well as a scaphopod that inhabited the study area in the Gåsö Ränna Channel, Kristineberg, Sweden. No evidence for shell selection was detected for this species. *Phascolion cryptus* at the Link Port site was also found in all of the most commonly occurring shells. However, differences in the percentage occupancy by *P. cryptus* of the commonly available shells suggests that this

sipunculan might display some degree of selectivity for different species of shells (Table 1). Though *P. cryptus* showed by far the greatest percentage occupancy in the most abundant shell, *Cerithium muscarum*, its relative occupancy of the shells of *Nassarius vibex* and *Neritina virginea* was significantly lower. Percentage occupancy of 2 other shells, *Modulus modulus* and *Marginella apicina*, on the other hand, was not significantly different from that of *C. muscarum*. The reason for this apparent shell selection is not evident from our data. Morphology of shells, in terms of shape and size of aperture, length of spire, number of whorls and extent of cavity, is so variable among the 5 species that this seems an unlikely basis for shell selection. Future experimental observations, considering these and other factors such as size, shape, and weight of shells, are necessary before selectivity of different species of shells can be understood or verified in *P. cryptus*.

Selection of shells on the basis of size, or the exchange of smaller shells for larger shells, has been documented with greater certainty for *Phascolion* by both field and laboratory observations. The finding in the field of immature specimens of juveniles in smaller shells and of adults in larger shells indicates that *Phascolion* changes shells as it grows. Moreover, laboratory studies show that an animal will leave its protective habitat when space is diminished. Hylleberg (1975) maintained *P. strombus* in syringes from which the tip had been cut, and over a period of time he gradually decreased the space in the syringe by a periodic increase of pressure on the plunger. When the contracted animal completely filled the available space, it left the syringe. Similar results were found in our laboratory experiments on behavior of *P. cryptus* when the spire of the occupied shell was removed, thereby decreasing the size of the available habitat and exposing part of the animal. Under these circumstances the sipunculan left the damaged shell and entered an available intact shell.

Exchange of shells in the field has not been observed, nor have specimens without shells been found in field collections. Presumably during periods of exchange when the animals lack the protection of shells, or are in damaged shells, susceptibility to predation is increased. In our laboratory experiments, once animals were removed from their shells, the minimum time for them to enter other shells was 14 min and the maximum time over 7 hr. This was under presumably ideal conditions when empty shells were provided close to the shell-less animal within a small dish. In the field where empty shells might not be so readily available, the period without a shell or with a damaged shell might be prolonged, thus increasing the time of exposure to predation. Or perhaps in the field an animal retains its shell until it locates a more appropriate shell. Further investigations are indicated for an understanding of the significance of shell exchange in the avoidance of predation, and the developmental history of the individual.

Shell availability was not found to be a limiting factor for *Phascolion cryptus* in our study in which the highest percentage of occupied shells was found to be 66.5. However, the study by Hylleberg (1975) on *P. strombus*

off the west coast of Sweden suggests that shell availability may be limiting for that species. He found occupancy of available shells in the Swedish population to be 90%. As in hermit crabs (cf., Kellogg, 1976; Scully, 1979; Bertness, 1980), percentage occupancy by *P. cryptus* increased with increasing size of shells (Fig. 7). Although not noted in previous studies, our investigations of *P. cryptus* showed that the dominant shell species in the 2 larger size classes was *Cerithium muscarum*, whereas in the smallest size class it was *Bittium varium*. Thus the growth of this population of *P. cryptus* is dependent on the co-existence of at least 2 species of gastropods.

REPRODUCTIVE BIOLOGY—Most sipunculans, including *Phascolion cryptus*, are dioecious. Gametes are detached at an early stage of differentiation from a minute gonad attached to the body wall and complete their development as independent cells in the coelom. By assessing the state of differentiation of coelomic gametes (measuring oocytes or classifying stages of developing sperm) over 1 yr we found *P. cryptus* to be reproductively active throughout the year with a period of reduced activity in the summer. Annual reproductive cycles of 5 other species of sipunculans have been delineated by year-long observations of coelomic gametes. They are: the temperate species *Golfingia minuta* (Gibbs, 1975), *G. vulgaris* (Gonse, 1956), *G. pugettensis* (Rice, 1975a) and 2 populations of *Phascolosoma agassizi* (Towle and Giese, 1967; Rice, 1975a) and the tropical species *Phascolosoma arcuatum* (Green, 1975). In contrast to *Phascolion cryptus*, a subtropical species, all have definitive breeding seasons. Most of the species, including *P. cryptus*, have oocytes in the coelom throughout the year, suggesting that ovaries are continually active; however, oocytes of large sizes usually appear only prior to and during the breeding season. There are 2 exceptions, *Phascolosoma arcuatum* and a population of *P. agassizi* from Monterey Bay, California, in which the small oocytes disappear for 2 mo after the breeding season. Of these animals in which annual reproductive cycles have been ascertained, only *Phascolion cryptus* has large oocytes throughout the year, although in the summer the average percentage is low. Measurements of coelomic gametes from other temperate species, *Golfingia elongata*, *G. rimicola*, and *G. margaritacea*, made over only parts of the year but spanning spawning periods, suggest that breeding seasons for these species are also limited (Gibbs, 1976).

Estimates of reproductive activity have been made in other sipunculans by observations at all seasons of the year on spawning of animals maintained in the laboratory (see Rice, 1975a for review). By such observations, estimations of breeding seasons have been made with some degree of certainty for 5 additional species: *Phascolion strombus* (Akesson, 1958) and *Themiste pyroides* (Rice, 1975a) from temperate waters and *Phascolosoma perlucens*, *Themiste alutacea* (Rice, 1975b) and *Themiste lageniformis* (Rice, 1975a) from tropical or subtropical waters. The 2 temperate species have restricted breeding seasons, whereas the tropical/subtropical species appear to breed throughout much of the year. Thus, from the information available, it

would appear that *Phascolion cryptus* follows the pattern for most tropical and subtropical sipunculans in that it breeds during most of the year.

ACKNOWLEDGMENTS—This research was carried out at the Smithsonian Institution Smithsonian Marine Station at Link Port, in cooperation with Harbor Branch Foundation, Inc. in Fort Pierce, Florida. We acknowledge the assistance of Douglas Putnam in the collection and sorting of material and the skills of John Holt and Harbor Branch Foundation Research and Development Department in the construction of the sampling device.

LITERATURE CITED

- AKERSSON, B. 1958. A study of the nervous system of the Sipunculoidea with some remarks on the development of two species *Phascolion strombi* Montagu and *Golfingia minuta* Keferstein. *Undersökningar Över Öresund*. 38: 1-249.
- BERTNESS, M.D. 1980. Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama. *J. Exp. Mar. Biol. Ecol.* 48: 1-16.
- EDMONDS, S.J. 1962. Some notes on the abundance, environment and nutrition of *Sipunculus nudus* L. (Sipunculoidea) at Morgat, Brittany. *Cahiers de Biologie Marine*. III: 183-190.
- GIBBS, P.E. 1975. Gametogenesis and spawning in a hermaphroditic population of *Golfingia minuta* (Sipuncula). *J. Mar. Biol. Ass. U.K.* 55: 69-82.
- . 1976. Notes on the reproductive cycles of several *Golfingia* species (Sipuncula). *J. Mar. Biol. Ass. U.K.* 56: 909-915.
- GONSE, P. 1956. L'ovogenese chez *Phascolosoma vulgare*. II. Recherches biometriques sur les ovocytes. *Acta Zool.* 37: 225-233.
- GREEN, W.A. 1975. The annual reproductive cycle of *Phascolosoma lurco* (Sipuncula). Pp. 161-167. *In*: Rice, M.E. and M. Todorovic (eds.). *Proc. Intern. Symp. Biol. Sipuncula and Echiura*. Naucono Delo Press, Belgrade.
- HENDRIX, G.Y. 1975. A review of the genus *Phascolion* (Sipuncula) with the descriptions of two new species from the western Atlantic. Pp. 117-137. *In*: Rice, M.E. and M. Todorovic (eds.). *Proc. Intern. Symp. Biol. Sipuncula and Echiura*. Naucono Delo Press, Belgrade.
- HYLLEBERG, J. 1975. On the ecology of the sipunculan *Phascolion strombi* (Montagu). Pp. 241-250. *In*: Rice, M.E. and M. Todorovic (eds.). *Proc. Intern. Symp. Biol. Sipuncula and Echiura*. Naucono Delo Press, Belgrade.
- KELLOGG, C.W. 1976. Gastropod shells: a potentially limiting resource for hermit crabs. *J. Exp. Mar. Biol. Ecol.* 22: 101-111.
- NELSON, W.G. 1981. Experiment studies of decapod and fish predation on seagrass macrobenthos. *Mar. Ecol. Prog. Ser.* 5: 141-149.
- O'GOWER, A.K., AND J.W. WACASEY. 1967. Animal communities associated with *Thalassia*, *Diplanthera*, and sand beds in Biscayne Bay I. Analysis of communities in relation to water movements. *Bull. Mar. Sci.* 17: 175-210.
- ORTH, R.J. 1977. The importance of sediment stability in seagrass communities. Pp. 281-300. *In*: Coull, B.C. (ed.). *Ecology of marine benthos*, Vol. VI. Univ. So. Carolina Press, Columbia, South Carolina.
- REESE, E.S. 1962. Shell selection behaviour of hermit crabs. *Animal Behavior*. 10: 347-360.
- RICE, M.E. 1975a. Sipuncula. Pp. 67-127. *In*: Giese, A. and J. Pearse (ed.). *Reproduction of marine invertebrates*, Vol. I. Academic Press, New York.
- . 1975b. Observations on the development of six species of Caribbean Sipuncula with a review of development in the phylum. Pp. 141-160. *In*: *Proc. Intern. Symp. Biol. Sipuncula and Echiura*. Naucono Delo Press, Belgrade.
- , and I. G. Macintyre. 1982. Distribution of Sipuncula in the coral reef community, Carrie Bow Cay, Belize. *Smithsonian Contr. to the Mar. Sci.* 12: 551-565.
- SCULLY, E.P. 1979. The effects of gastropod shell availability and habitat utilization by the intertidal hermit crab *Pagurus longicarpus* Say. *J. Exp. Mar. Biol. Ecol.* 37: 139-152.
- STEPHEN, A.C., AND S.J. EDMONDS. 1972. *The Phyla Sipuncula and Echiura*. The British Museum (Natural History). London.
- TOWLE, A., AND A.C. GIESE. 1967. The annual reproductive cycle of the sipunculid *Phascolosoma agassizii*. *Physiol. Zool.* 40: 229-237.

- YOUNG, D.K., AND M.W. YOUNG. 1977. Community structure of the macrobenthos associated with seagrass of the Indian River estuary, Florida. Pp. 359-381. In: Coull, B.C. (ed.). Ecology of the marine benthos. Univ. of So. Carolina Press, Columbia, South Carolina.
- _____. 1978. Regulation of species densities of seagrass-associated macrobenthos: Evidence from field experiments in the Indian River estuary, Florida. J. Mar. Res. 36: 569-593.

Florida Sci. 46(3/4):382-396. 1983.

Academy Symposium

A PHYSICAL DESCRIPTION OF LONG-PERIOD
NET DISPLACEMENT VARIATION WITHIN THE
SOUTHERN INDIAN RIVER LAGOON, FLORIDA

MARK S. STERNBERGER

Harbor Branch Foundation, R.R. 1, Box 196, Fort Pierce, Florida 33450

ABSTRACT: Meteorological and hydrographic data were recorded over a 29-day period in the summer of 1981 to describe wind effects on long-period net displacement of water along the navigational channel of the southern Indian River lagoon, Florida. Tidal motions decreased with increasing distance from the ocean inlets at either end of the study area, enhancing wind effects. Tidal current speeds in the middle of the study area were 50% of those at the Fort Pierce Inlet, while the nontidal current variance increased by 27% over the same distance, and by 64% over that at the St. Lucie Inlet. A net displacement of water toward the north throughout the study area was coherent with windstress over time scales in excess of 2 da.

DYER (1973) reviewed criteria established by Pritchard (1955) and Cameron and Pritchard (1963) to classify estuaries by their stratification and salinity characteristics. Since 1960, descriptions of estuaries have shifted toward dynamic characteristics based upon net circulation as well as stratification (Hansen and Rattray, 1960, Bowden, 1978). In this study, a description of net flow is based upon low-frequency wind effects. Current data reveal characteristics similar to those described by Dyer (1973) for coastal lagoons. Compared to other parts of the Indian River (Smith, 1982), the southern Indian River lagoon has fewer spoil islands, less variation in the orientation of the navigation channel, greater width and no point sources of fresh water. Smith (1982) observed flow characteristics between the Fort Pierce and Sebastian Inlets and found that areas distant from ocean inlets exhibit periods of slight net displacement related to variability in local winds. My research supports this finding, although net displacement in the southern Indian River is larger and more consistent in direction from one station to the next. Hydrographic differences from one study to the next may account for observed differences in flow patterns.

The Indian River lagoon extends 195 km along the central Florida Atlantic coast. The southern Indian River is that portion between the 2 southern-