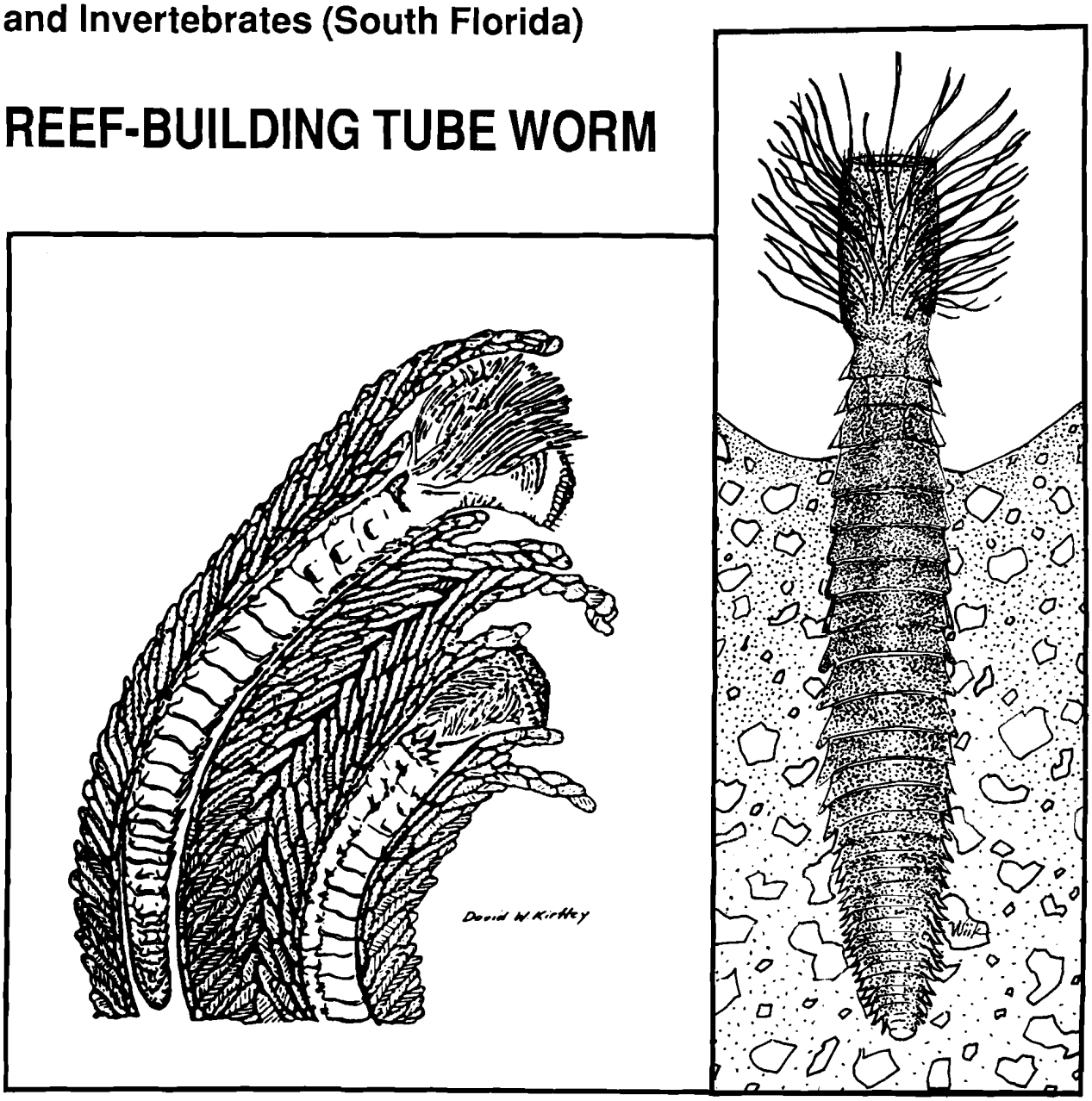
Biological Report 82(11.115)
December 1989

TR EL-82-4

Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)

REEF-BUILDING TUBE WORM



Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)

REEF-BUILDING TUBE WORM

by

Alexander V. Zale
and
Susan G. Merrifield

Oklahoma Cooperative Fish and Wildlife Research Unit
Department of Zoology
404 Life Sciences West
Oklahoma State University
Stillwater, OK 74078

Project Officer
David Moran
U.S. Fish and Wildlife Service
National Wetlands Research Center
1010 Gause Boulevard
Slidell, LA 70458

Performed for

U.S. Army Corps of Engineers
Waterways Experiment Station
Coastal Ecology Group
Vicksburg, MS 39180

and

U.S. Department of the Interior
Fish and Wildlife Service
Research and Development
National Wetlands Research Center
Washington, DC 20240

This series may be referenced as follows:

U.S. Fish and Wildlife Service. 1983-19__. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates. U.S. Fish Wildl. Serv. Biol. Rep. 82(11). U.S. Army Corps of Engineers, TR EL-82-4.

This profile should be cited as follows:

Zale, A.V., and S.G. Merrifield. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida)--reef-building tube worm. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.115). U.S. Army Corps of Engineers, TR EL-82-4. 12 pp.

PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

Information Transfer Specialist
U.S. Fish and Wildlife Service
National Wetlands Research Center
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458

or

U.S. Army Engineer Waterways Experiment Station
Attention: WESER-C
Post Office Box 631
Vicksburg, MS 39180

CONVERSION TABLE

Metric to U.S. Customary

Multiply	*By*	*To Obtain*
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (° C)	1.8 (° C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces	28.35	grams
pounds (lb)	0.4536	kilograms
pounds	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (° F)	0.5556 (° F - 32)	Celsius degrees

CONTENTS

ACKNOWLEDGMENTS

Drafts of this species profile were critically reviewed by Kevin Eckelbarger, Harbor Branch Foundation, Inc., Fort Pierce, Florida, Michael Hatfield, Kewalo Marine Laboratory, Honolulu, Hawaii, Paul H. Eschmeyer, Editorial Office, U.S. Fish and Wildlife Service, Fort Collins, Colorado, and the Coastal Ecology Group, U.S. Army Corps of Engineers, Vicksburg, Mississippi. Copies of several rare reports were graciously provided by Walter G. Nelson, Department of Oceanography and Ocean Engineering, Florida Institute of Technology, Melbourne, Florida. Sheila G. Johnson, Edmon Low Library, Oklahoma State University, provided exceptional assistance with literature searches and interlibrary loan. H. Franklin Percival of the Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, and O. Eugene Maughan of the Oklahoma Unit provided administrative assistance.

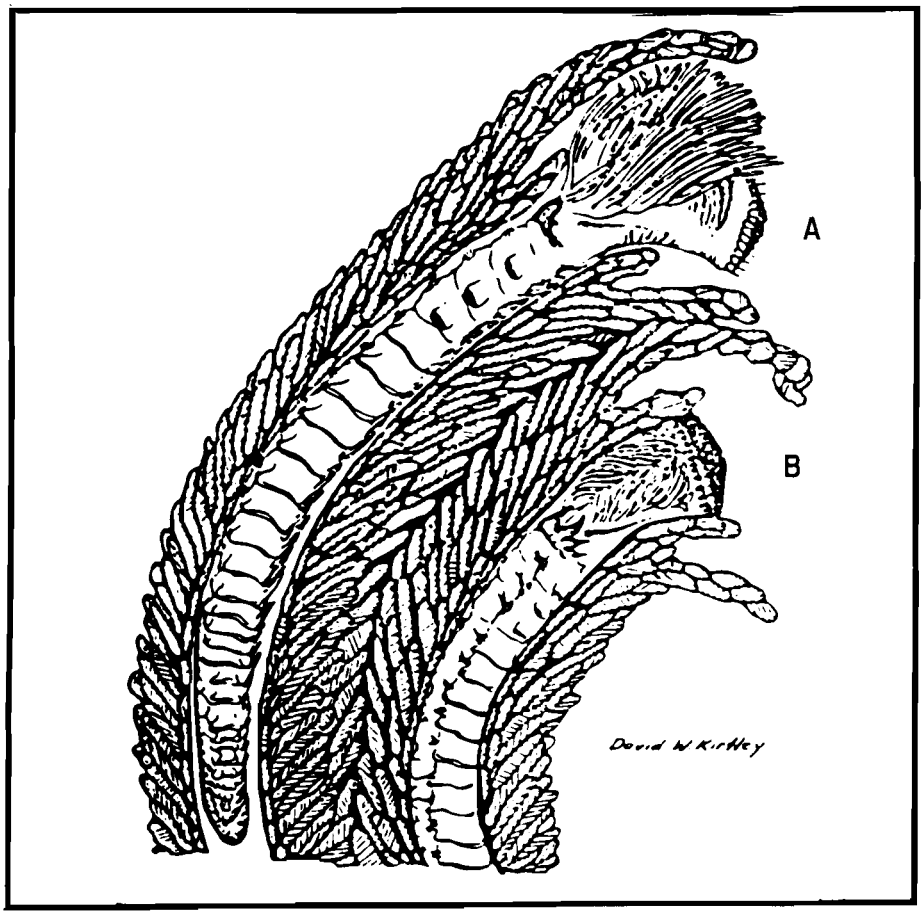

Figure 1. Reef-building tube worm: a. feeding position; b. withdrawn into tube.

REEF-BUILDING TUBE WORM

NOMENCLATURE/TAXONOMY/RANGE

Scientific name .....*Phragmatopoma lapidosa* Kinberg 1867

Preferred common name.....reef-building tubeworm (Figure 1)

Other common names.....sand-tube worm, honeycomb worm, reef-building polychaete, tube-building marine polychaete

Phylum.....Annelida
Class.....Polychaeta
Order.....Terebellida
Family.....Sabellariidae

Reciprocal crosses of *P. lapidosa* gametes with gametes of the northeast Pacific congener, *P. californica*, suggest the two taxa are conspecific subspecies (Pawlik 1988).

Geographic range: western Atlantic from east coast of Florida to Rio Grande do Sul near Santa Catarina in Brazil (Hartman 1944; Kirtley and Tanner 1968; DeJorge et al. 1969); also present, but rare, along coast of Gulf of Mexico (Potts 1979). Distribution in Florida extends about 320 km from Cape Canaveral, Brevard County, to Key Biscayne, Dade County (Kirtley 1966; Kirtley and Tanner 1968). Typically intertidal or subtidal (i.e., within or just seaward of the surf zone) along exposed beaches

subject to high-energy wave action (Multer and Milliman 1967; Kirtley and Tanner 1968; DeJorge et al. 1969), but present to depths of 100 m (Kirtley and Tanner 1968). Present also along channels at inlets (e.g., Sebastian, Fort Pierce, and St. Lucie Inlets in Florida) characterized by swift tidal currents (Gore et al. 1978). The distribution of the reef-building tube worm in southern Florida is illustrated in Figure 2.

MORPHOLOGY AND IDENTIFICATION AIDS

Sabellariids are obligate agglutinated-sand tube-dwelling colonial polychaetes (as opposed to annelids that secrete calcareous or membranous tubes) that have elongate, segmented, cylindrical bodies divided into four parts (proceeding posteriorly): the "head" or opercular stalk (consisting of a prostomium or pre-oral region fused to a peristomium or post-oral region), and the parathoracic, abdominal, and caudal regions. The head of the reef-builing tube worm has an anterior opercular disk that serves as a "stopper" when the worm retracts into its tube. An array of hard, clawlike paleae (setae) on the operculum are used to manipulate sand grains being cemented into the tube. Two rows of ciliated feeding tentacles run lengthwise ventrally along the head. The ventral mouth, with its pair of feeding palps, lies behind and between the rows of feeding tentacles. The lower lip of the mouth is surrounded by the horseshoe-shaped building organ that supplies the proteinaceous cement for tube construction. The parathoracic region consists of three segments, each with biramous parapodia (fleshy lateral appendages, each with a dorsal and ventral cirrus), simple branchiae (gills), and a ventral muscular plate. About 32 segments make up the abdomen; these possess notopodia (dorsal branches of the parapodia), neuropodia (ventral branches of the parapodia), branchiae, and numerous small hook-like uncini (setae) on the parapodia that anchor the body to the surrounding tube wall. The cylindrical caudal region terminates in the anus. Maximum total length is about 30 to 40 mm. Worms 15 to 25 mm long are 30 to 40 mg wet weight. The preceding description was summarized from Kirtley (1966, 1968), Kirtley and Tanner (1968), DeJorge et al. (1969), and Parker (1982).

In southeastern Florida, identification of the reef-building tube worm is facilitated by recognition of the unique mound-like reefs built up by successive colonizations of the worms. These may range from fist-sized lumps attached to pilings to extensive reefs several hundred meters wide and several kilometers long, paralleling the beach (Kirtley 1966; Kirtley and Tanner 1968). Individual heads are typically low and rounded, resembling cushions. They may rise as much as 2 m above the surrounding substrate, but the "living" portion is seldom as much as 1 m high (Kirtley 1966). The reefs are generally a dark, drab brown resulting from the aggregate coloration of sand, shell hash, and mineral grains from which they are constructed. The mounds are friable and easily broken by hand. The vertically arranged, parallel worm tubes give the reefs a honeycomb appearance. Tube densities average about $5/cm^2$ (Multer and Milliman 1967). Internal diameters of the tubes are about 2 to 4 mm; external diameters at the aperture range from 4 to 10 mm, depending on worm density (Multer and Milliman 1967; Kirtley 1968). Individual tubes are curved but intertwine little (Multer and Milliman 1967). A hood-like protrusion extends partly around the rim of each tube (Kirtley 1966; Multer and Milliman 1967). The lower ends are sealed. Kirtley (1966) stated that under optimal conditions, individual tubes reach a maximum length of about 10 cm, but Gram (1968) reported that tubes are generally 15 to 30 cm long.

REASON FOR INCLUSION IN SERIES

The reefs constructed by reef-building tube worms along the southeast coast of Florida are significant both geologically and biologically. Reefs of the sand tubes of reef-building tube worms extend within their geographic range for hundreds of kilometers of coastline (Kirtley and Tanner 1968). The ability of the worms to thrive under high-energy breaker conditions and to extend their colonial tube masses upward and seaward by extraction and agglutination of littoral drift materials makes them important vectors in coastline development. Beachrock, converted from the reefs, and sand impounded on their landward sides provide for actual progradation of beaches (Kirtley and Tanner 1968). By sorting out flat shell fragments and the heavier suspended particles in littoral drift, tube construction by the worms results in the retention of beach sediment (Emery 1963; Multer and Milliman 1967; Gram 1968). The cracks and crevices of the reefs act as traps for sediment and shell fragments, thereby further contributing to sediment retention (Gram 1968). Being wave resistant, the reefs protect the shore

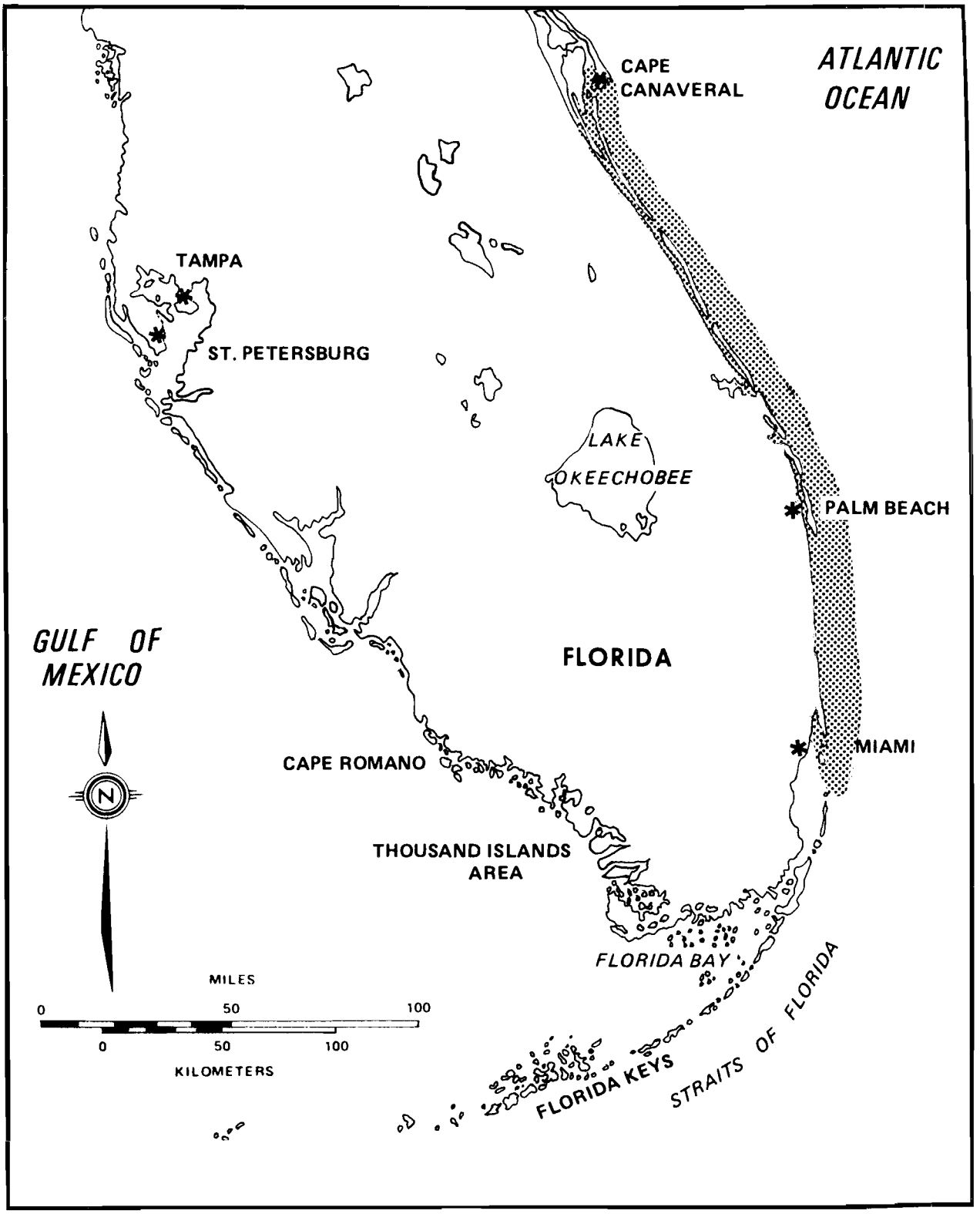

Figure 2. Distribution of the reef-building tube worm in south Florida.

against wave attack and retard erosion (Multer and Milliman 1967; Mehta 1973). It appears likely that reef-building tube worms are at least in part responsible for the formation and maintenance of beaches and barrier islands in southeast Florida (Kirtley and Tanner 1968).

The reefs are the primary basis for an elaborate and stable marine community (Kirtley and Tanner 1968; Narchi 1973, 1974; Gore et al. 1978; Gilmore et al. 1981; van Montfrans 1981). They provide hard and stable substrate, shelter, and food, and thereby allow many species to inhabit the surf zone, an area where most would normally be unable to survive (Gore et al. 1978).

LIFE HISTORY

Spawning

Florida populations of reef-building tube worms may spawn semicontinuously (without a seasonal trend) throughout most of the year; Eckelbarger (1976) recovered viable gametes from worms throughout the year; he collected larvae in plankton tows in February, August, and October; and he observed larval settlement in May, September, and December. Gore et al. (1978) observed settlement in March. This semicontinuous spawning periodicity differs markedly from the polytelic spawning (with a seasonal trend) of all other sabellariids (Smith and Chia 1985).

Fertilization occurs in the water (Kirtley 1966). Males release sperm into their sand tubes through a series of bilaterally arranged nephridia throughout the gamete-bearing abdominal segments; sperm are expelled into the water column in short bursts by rapid withdrawal of the head region into the tube (Eckelbarger 1984). Initiation of sperm release by one male generally stimulates releases by adjacent males; females release eggs in response to the presence of sperm in the water (Eckelbarger 1984). Mature sperm have distinctive long, tapering, curved acrosomes and laterally displaced flagella (Eckelbarger 1984). Total length of sperm is about 42 µm; the head, including the acrosome, is about 6 µm long (Eckelbarger 1976). Females expel eggs from their tubes much as males expel sperm (Eckelbarger 1984). Diameters of spawned oocytes are 97 to 103 µm (Eckelbarger 1976). The eggs are sticky and adhere to sand grains upon expulsion; this property may be an adaptation to restrict transport in the turbulent surf zone (Eckelbarger 1984).

Larvae

Larvae of the reef-building tube worm are common in the nearshore plankton along the east coast of Florida (Eckelbarger 1976) and may be an ecologically significant component of the planktonic community (Kirtley and Tanner 1968). A key to larvae of Florida sabellariids was published by Eckelbarger (1977). Mauro (1975) and Eckelbarger (1976) described in detail development of reef-building tube worm larvae maintained in the laboratory. The following description is drawn largely from Eckelbarger (1976); larvae were maintained at 21 to 23 °C in circulating or aerated cultures. Descriptions of larvae derived by scanning electron microscopy (SEM) by Eckelbarger and Chia (1976) confirmed Eckelbarger's (1976) light microscopy observations, except that SEM revealed the presence of "sensory tufts" on the dorsal surface of the larval tentacles; these may play a role in the selection of a substrate on which to settle.

Freshly shed ova are irregular in shape and have a clear, conspicuous germinal vesicle. Within minutes, the eggs become round and develop a wrinkled vitelline membrane. The germinal vesicle breaks down 10 to 15 min after fertilization. The first and second polar bodies appear in about 50 to 55 and 60 to 65 min after fertilization and the first and second cleavages occur within 75 to 78 and 80 to 85 min of fertilization. From 10 to 12 h after fertilization, the embryo loses its sticky coat and hatches as a simple top-shaped trochophore that possesses a prototroch (ciliated girdle) and an apical tuft consisting of short, fine cilia. At 17 to 20 h, a single reddish eyespot is formed and a stiff cilium appears posteriorly. At 20 to 21 h, the larva develops a pair of small barbed provisional setae that begin to protrude through the body wall on each side. At this stage, the larva is opaque and granular in appearance; groups of irregular, yellow-green pigment specks are scattered over its surface. At 22 to 24 h, 3 pairs of provisional setae are present, distinct chromatophores have formed, and a mouth and digestive system have developed; active feeding begins at this stage. At 40 to 42 h, the larva is more elongate and shows faint indications of segmentation. It has 4 to 7 provisional setae on each side and two eyespots; a second ciliated girdle, the telotroch,

circles its anus. At about 6 days, the larva is clearly elongate and has 4 eyespots and as many as 20 provisional setae. Between 7 and 10 days, the larva develops a pair of dorsal tentacle buds and abdominal uncini. Three clearly defined parathoracic segments and 3 less clearly defined abdominal segments are present. At 12 days, the tentacles have lengthened and dorsal parapodial lobes of the parathoracic segments are clearly defined; each has 4 setae. One to three primary (settling) paleae and two pairs of opercular spines appear. At about 19 days, the tentacles are about half the length of the body and have ciliated food grooves; segmentation of the robust larva is distinct. At this stage, the larvae alternately crawl over or swim close to the surface of the substrate. During crawling, they are oriented head-downward and frequently contact the substrate with the mouth and tentacles.

Juveniles

Metamorphosis and settlement occur 14 to 30 days after fertilization in circulating or aerated cultures at 21 to 23 °C; length ranges from 0.6 to 1.0 mm at settlement (Eckelbarger 1976). Metamorphosis usually requires the presence of conspecific tubes or sand and is triggered by the presence of free fatty acids, a requirement which accounts for the gregariousness of the species (Pawlik 1988). Pawlik's study (1988) showed that when larvae were cultured with sand that came from conspecific tubes, frequency of metamorphosis was 50% at 15 °C about 28 hours after hatching and also 50% at 20 °C about 17 hours after hatching.

Metamorphosis involves an elongation of the body and dramatic changes in the head region: the tentacles rotate anteriorly until they project forward, the provisional setae are replaced by 6-10 pairs of primary paleae, the entire head shrinks in relative size, the building organ appears around the mouth, and various appendages develop on a number of segments (Eckelbarger 1976). The telotroch is still present at this stage but the prototroch has disappeared. After settlement, development continues rapidly; within one month, the juvenile closely resembles the adult worm (Eckelbarger 1976).

Upon settling, the larva actively moves over the substrate, presumably evaluating possible attachment sites (Kirtley 1966). A wide variety of natural and artificial settlement sites are used (Kirtley 1966; Multer and Milliman 1967; Eckelbarger 1976). Existing worm reefs, both "dead" and "living," are perhaps the most common attachment sites (Eckelbarger 1976). Established reefs are therefore essentially permanent. Settlement occurs over the entire surface of dead, wave-eroded worm mounds, but only between the openings of existing and occupied adult tubes of sparsely populated reefs. No recruitment occurs on the surfaces of mounds consisting of closely packed tubes of adults; successful settlement on such mounds is limited to their periphery (Eckelbarger 1976). Adult and juvenile worms use their operculum to scrape away algal growths, fouling organisms, and debris located around the openings of their tubes; this activity probably serves to preclude the settlement of new larvae (Eckelbarger 1976).

Upon selection of a site, the metamorphosing larva secretes and attaches a cylindrical, muco-proteinaceous tube to which it begins cementing small fragments; the initial fragments often consist largely of small, dark grains of heavy minerals (Kirtley 1966; Eckelbarger 1976). Tubes of juveniles can therefore be readily distinguished from those of adults by their color from a considerable distance; adults use larger, lighter-colored sand grains and shell fragments. Multer and Milliman (1967) and Gram (1968) demonstrated that the median size of particles incorporated in the tubes increases with worm size. Other materials used by young worms include small quartz grains, foraminiferal tests, sponge spicules, and silt (Kirtley 1966). Larger worms use correspondingly larger materials including ostracod carapaces, small mollusk shells, fragmented pieces of larger mollusk shells, large quartz grains, large foraminiferans, and echinoid spines (Kirtley 1966; Multer and Milliman 1967). Generally, worms prefer sediments of 250 to 500 µm in diameter (Main and Nelson 1988a) or 125 to 500 µm (Multer and Milliman 1967) for tube construction; depending on the diameters of available materials, they therefore preferentially concentrate finer or coarser grains than they would if selection were random (Main and Nelson 1988a). Significant amounts of sediment finer than 62 µm in diameter (silt) are incorporated into tubes, probably serving as "mortar" to fill cracks between larger grains (Multer and Milliman 1967). Flat mollusk-shell fragments are typically used to line the inner wall of the

tube; more rounded grains are incorporated in the outer layers (Multer and Milliman 1967). Platy shell fragments are incorporated much more frequently than quartz sand grains, perhaps because the shell fragments are less dense and less spherical in form and hence more easily suspended in the water column (Main and Nelson 1988a). Construction materials are grasped from the water column by the oral tentacles or opercular paleae, passed to the building organ, coated with proteinaceous cement, and implanted into the tube with the opercular paleae (Kirtley 1966).

The size, shape, and orientation of the tube are influenced by hydrodynamic and sedimentary conditions prevailing at the site and the presence or absence of other organisms or obstructions (Kirtley 1966). Kirtley (1966) speculated, on the basis of few data, that strong positive correlations exist between worm size, intensity of turbulence, and available particle size. The worms constantly enlarge and repair their tubes, especially the delicate "hood" at the aperture. Damaged tubes are quickly repaired; human footprints on reefs are not detectable after 24 h (Kirtley 1966).

Adults

Reef-building tube worms are dioecious. Populations are composed of equal proportions of males and females (Eckelbarger 1976). Sex products first develop in both sexes about 6 to 8 weeks after larval settlement and the worms are fully mature after 4 months (Eckelbarger 1976). Sexes are easily distinguished; the gamete-containing abdominal segments of mature males and females are creamy-white and steel-blue respectively, corresponding to coloration of sex products (Kirtley 1966, 1968; DeJorge et al. 1969; Eckelbarger 1976). The sexes are otherwise morphologically identical. The testes and ovaries are bilaterally arranged organs in the abdominal segments (Eckelbarger 1979, 1984). Eckelbarger (1979, 1984) described oogenesis and spermatogenesis. Removal of sexually mature worms from their tubes induces expulsion of gametes (Kirtley 1966; DeJorge et al. 1969; Mauro 1975; Eckelbarger 1976), and thus facilitates artificial fertilization in the laboratory.

AGE AND GROWTH CHARACTERISTICS

No information is available on the longevity of reef-building tube worms in Florida, but Kirtley (1966) suggested that "it does not seem probable that the organisms would survive for more than one or two years." However, Wilson (1971, 1974) estimated that the life span of a similar species, *Sabellaria alveolata*, in southwestern England is commonly 5 years and may exceed 10 years.

Eckelbarger (1976) monitored growth rates of newly settled juveniles at 2-week intervals at Walton Rocks, Martin County, Florida. On 26 March, modal length of the population was less than 1 mm, and no worms exceeded 2 mm in length. Modal lengths were 2-3, 3-4, and 4-5 mm on 14 April, 25 April, and 8 May. Corresponding ranges were 1-5, 2-7, and 2-8 mm. Average length 6 weeks after settlement was 5.2 mm.

Eckelbarger (1976) also monitored monthly growth rates of a population at Hutchinson Island in Martin County. The colony probably settled in early September. Modal lengths (ranges in parentheses) were as follows: October, 5 mm (1-12); November, 5 mm (2-10); December, 9 mm (2-14); January, 8 mm (2-16); February, 13 mm (6-22); March, 15 mm (10-26); April, 15 mm (8-24); and May, 15 mm (8-22). Mean length in May was 15.5 mm. Tube lengths of these animals were 1.0-1.7 cm on 30 October, 1.8-2.5 cm on 12 November, and 1.5-6.0 cm on 11 December.

The mean daily growth increment of worm tubes was 1.45 mm at Punta Moron, Venezuela (Merida and Penchaszadeh 1982). Accretion rates of tubes of worms from this population in the laboratory were 2.03, 3.18, and 0.97 mm per day at 22, 26, and 30 °C, respectively. Gore et al. (1978) reported that 6 months after settlement in March, new reefs were indistinguishable from older colonies that had been established in previous years. Kirtley (1968) reported that a newly settled reef attained a thickness of about 25 cm within 6 weeks.

Maximum total length is about 40 mm (Kirtley and Tanner 1968). Body length varies annually and by locality, perhaps depending on food availability or physical conditions; tube diameters and body lengths are highly correlated (Eckelbarger 1976).

ECOLOGICAL ROLE

Feeding Behavior and Food

Kirtley (1966) described the feeding behavior of adult reef-building tube worms. The organism lies on its dorsum, partly extended into the "hood" of its tube. The operculum is turned backward and downward, and the ciliated prostomial tentacles are extended upward and outward. Water currents produced by the cilia convey small suspended particulate matter toward a rapidly revolving bolus of mucus just above the mouth. The bolus is periodically ingested. The worms also feed on algae and other organisms encrusting sand and shell fragments. The fragments are grasped with the opercular paleae and then directed with the aid of the prostomial tentacles to the mouth where the organic materials are removed. If the fragment is suitable for tube construction, it may then be passed along to the building organ. The prostomial feeding tentacles may also be used to seize small sand particles and transport them toward the building organ for tube building. Feeding and tube-building are highly integrated and complementary functions.

The food of reef-building tube worms consists primarily of planktonic microorganisms, including diatoms, foraminiferans, and algae; encrusting organisms adhering to sand and silt are also eaten (Kirtley 1966).

Predators

Reef-building tube worms are eaten by crustaceans (including the grapsid crab *Pachygrapsus transversus* and the xanthid crabs *Mennipe nodifrons*, *Pilumus dasypodus*, and *Panopeus bermudensis)*, gastropods, and fishes (Kirtley 1966; Gore et al. 1978). The worms appear to be the primary forage of a number of species of crabs that live on or within the reefs (Gore et al. 1978).

Competitors

Barnacles *(Tetraclita squamosa)* colonizing worm reefs compete with reef-building tube worms for space (Multer and Milliman 1967). The crab *Pachycheles monilifer*, which is an abundant inhabitant of worm reefs in southeastern Florida (Gore et al. 1978), feeds on suspended material and plankton and may compete with reef-building tube worms for food.

Associated Species

Worm reefs are the primary basis for an elaborate and stable marine community that includes crustaceans, mollusks, sponges, bryozoans, anthozoans, and fishes (Kirtley and Tanner 1968; Narchi 1973, 1974; Gore et al. 1978; Gilmore et al. 1981; van Montfrans 1981). Reefs provide hard and stable substrate, shelter, and food, thereby allowing many species to inhabit the surf zone, in which most of these organisms would normally be unable to survive (Gore et al. 1978). Crustaceans, many of them cryptic and slow moving, make up about 90% of the macroinvertebrate fauna associated with worm reefs in southeastern Florida (Gore et al. 1978).

Gore et al. (1978) collected 96 species (in 52 genera and 22 families) of decapod and stomatopod crustaceans within, on, or associated with worm reefs in southeastern Florida. In contrast, only six species inhabited the surrounding surf zone. The six most abundant species associated with the reefs, about 80% of the total number of individuals collected, were the porcellanid crab *Pachycheles monilifer*; the grapsid crab *Pachygrapsus transversus*; the alpheid pistol shrimp *Synalphus fritzmuelleri*; and the xanthid crabs *Menippe nodifrons*, *Pilumnus dasypodus*, and *Panopeus bermudensis*. Two of these, *Pachycheles monilifer* and *M. nodifrons*, are restricted to worm reefs in southeastern Florida.

Narchi (1973, 1974) found the bivalves *Hiatella solida* and *Petricola typica* living in worm reefs on the coast of Brazil; worm reefs appeared to be the preferred habitat of *Petricola.*

Gilmore et al. (1981) collected a total of 107 species of fish from worm reef habitats in Florida; adjacent surf zone habitats yielded 91 species. Collections in the worm reef were numerically dominated by two demersal species (hairy blenny *Labrisomus nuchipinnis* and molly miller *Scartella cristata*) and three semi-demersal species (spottail pinfish *Diplodus holbrooki*, porkfish *Anisotremus virginicus*, and sailor's choice *Haemulon parrai*). A total of 40 fishes of commercial or sport value were "frequent," "common," or "abundant" in the worm reef habitat, compared with 35 in the adjacent open surf zone; 27 of these species were found exclusively (at these frequencies) in the reef habitat and 22 in open habitats. Although the species richness of fishes of the

worm reef habitat is not remarkably higher than that of the adjacent open surf zone, the large number of habitat-specific species indicates that the presence of worm reefs substantially enhances the overall diversity of commercially and recreationally important fishes in the beach zone.

ENVIRONMENTAL REQUIREMENTS

Temperature

Gilmore et al. (1981) reported that water temperatures at reef-building tube worm colonies in southeastern Florida ranged from 18 to 27 °C. Water temperatures at reefs studied by Gore et al. (1978) ranged from 11 to 32 °C over a 2-year period. However, these extremes are probably exceeded within tubes of reefs exposed at low tide during exceptionally hot or cold weather. Extreme air temperatures may stress reef-building tube worms in intertidal reefs. Wilson (1971) observed massive die-offs of *Sabellaria alveolata* after severe frosts in southwestern England; also, *S. vulgaris* has suffered heavy winter mortality in Delaware Bay (Curtis 1973). Eckelbarger (1976) believed that elevated summer temperatures may have resulted in the death of a reef-building tube worm colony in Florida. The tropical and subtropical distribution of the reef-building tube worm suggests that it is intolerant of temperate climates. Cape Canaveral, the northern extreme of the range of the species, marks the approximate center of a transition zone between the warm-temperate Carolinian and tropical Caribbean faunal regions (Briggs 1974; Gilmore 1977).

Eckelbarger (1976) maintained experimental cultures of artificially fertilized reef-building tube worm eggs at temperatures of 10 to 35 °C. No development occurred at the extreme temperatures, and 48%, 65%, 82%, 95%, and 47% of the eggs developed at 15, 18, 21, 25, and 30 °C, respectively. Eckelbarger (1976) concluded that larval development was optimal at 24 to 26 °C.

Salinity

Water salinities measured at reef-building tube worm reefs studied by Gore et al. (1978) and Gilmore et al. (1981) ranged from 28 to 39 ppt. In the laboratory, the worms survived at salinities as low as about 10 ppt for several days (Mauro 1977). This tolerance is probably adaptive in southeastern Florida, where heavy rains and freshwater runoff may appreciably dilute salinities within worm tubes between high tides.

Substrate

Stable settlement substrate is a critical environmental requirement of reef-building tube worms. Beaches composed entirely of shifting sands afford larval worms no opportunity for settlement. Unstable objects subject to rolling or burial by sands are unsatisfactory. However, a wide variety of natural and artificial substrates can be colonized, including living and dead shells of mollusks and horseshoe crabs *(Limulus polyphemus)*, coquina rock, sea walls, piers, jetties, peat, and beach debris (Kirtley 1966; Multer and Milliman 1967; Eckelbarger 1976). Existing "living" and "dead" worm reefs are common attachment sites (Eckelbarger 1976). Complete removal of a reef or reef sand will probably delay recolonization considerably because the larvae usually require, for metamorphosis, a chemical stimulus produced by conspecific worms (Pawlik 1988).

In addition to providing stable settlement, substrates surrounding the colonization site must be composed of sand and similar-sized particles suitable for tube construction (Multer and Milliman 1967). Habitats such as exposed rocky shorelines that have adequate wave action and stable substrates are unsuitable environments for reef-building tube worms because they lack the amounts of suspended particles needed for tube building.

Depth

Habitats occupied by reef-building tube worms are primarily intertidal (DeJorge et al. 1969) and nearshore (Kirtley and Tanner 1968). Kirtley (1966) suggested that optimal habitat extends from mid-tide level to a depth of about 2 m. Reefs occasionally occur above mid-tide, but only if suitable substrate and strong wave action are present (Kirtley 1966). At depths greater than 2 m, wave action is generally insufficient to maintain the required turbulent conditions. However, colonies have been reported to occur to depths of 100 m (Kirtley and Tanner 1968), perhaps at sites with strong submarine currents.

Current

Reef-building tube worms require constant high-energy wave action to supply food, remove metabolic wastes, and maintain the suspension of sand grains and other particles for tube building (Kirtley 1966; Multer and Milliman 1967). Average breaker heights along the east coast of Florida where worm reefs are well developed are 50-75 cm (Kirtley and Tanner 1968). Worm reefs may also form at the mouths of inlets where tidal currents are strong enough. South of Dade County, the turbulent, silt and sand laden conditions required by the worms do not exist; such habitats foster the formation of coral reefs.

Suspended Solids

Reef-building tube worms showed no indication of a negative response to experimental suspended-solid levels as high as two orders of magnitude greater than maximum levels reported from surf zones in Florida (Nelson and Main 1985). Habitats having the intense turbulence and shifting-sand (surrounding) substrate required by reef-building tube worms are high in suspended solids. However, high suspended solid loads alone may not provide habitat suitable for reef-building tube worms if particle size of the suspended materials is too small. Habitats having high silt loadings only are unsuitable; sand-sized particles must be present.

Pollution and Contaminants

Mulhern (1976) examined the short-term tolerances of adult reef-building tube worms in their tubes to three refined fuel oils mixed with sea water in the laboratory. The estimated 48 h LC_{50} for kerosene was 44% (by volume); mean mortality rates after 48 h exposures to 10%, 20%, 30%, 38%, and 46% concentrations were 5%, 18%, 38%, 55%, and 61%, respectively. Mean mortality rates of worms exposed to 10%, 40%, and 46% concentrations of diesel fuel for 48 h were 5%, 11%, and 16%, respectively. Many surviving worms exposed to kerosene or diesel fuel suffered lost or damaged feeding tentacles. No significant mortality was observed among worms exposed to furnace fuel (Bunker "C") for 48 h at concentrations as high as 40%. Worms exposed to furnace fuel did not suffer damaged tentacles. Total submersion in these fuel oils for 24 h resulted in mortalities of only 8%, 2%, and 4% in kerosene, diesel fuel, and furnace fuel, respectively, but tentacles of worms in kerosene and diesel fuel were damaged or lost. Mulhern (1976) inferred that reef-building tube worms are relatively resistant to short-term oil pollution and appear capable of surviving typical oil spills; however, he acknowledged that worms suffering from lost or damaged feeding tentacles may have reduced long-term survival.

Kavanagh (1979) determined that the tolerance of reef-building tube worms to cadmium varied ontogenetically. The 96 h LC_{50} values for adults and larvae were 10.9 ppm and 3.0 ppm, respectively. Fertilization success and growth and development of larvae were significantly reduced at cadmium concentrations exceeding 1.0 ppm. Adult worms exposed to cadmium concentrations of 0.5 ppm and 1.0 ppm for 240 h remained in apparent good health with no morphological differences from controls, but adults exposed to 2.5 ppm cadmium exhibited tentacle deterioration within 48 h and died within 216 h.

The 48 h LC_{50} of adult reef-building tube worms for the reference toxicant dodecyl sodium sulfate is 460 mg/l (Mulhern 1976).

Dredging

Strong currents and high sediment loadings characteristic of coastal inlets provide excellent habitat for reef-building tube worms. Accordingly, worm reefs grow well on bulkheads, jetties, and along the bottoms of channels at some inlets, eventually making them navigable only by shallow-draft watercraft (Kirtley 1968). The narrowed channels also increase the velocity of tidal currents, thereby making passage dangerous. Dredging of worm reefs required to keep such inlets navigable is deleterious to reef-building tube worms and associated fauna directly affected by dredging.

Beach Nourishment

Burial, siltation, and exposure to sulfides are all factors which may be present due to beach nourishment or disposal of dredged sediments. Clark (1978) reported that total mortality of reef-building tube worms occurred at reefs adjacent to beaches nourished by spoil dredged from nearby Sebastian Inlet, Florida. The presence of large quantities of drifting sand over the reefs suggested

that mortality was the direct result of overwash with sand and consequent smothering of worms. Nelson and Main (1985) reported that reef-building tube worms tolerated burial by sediments for up to 72 h at 17 to 23 °C in the laboratory, but exhibited increased mortality as compared with coarser sediments. Further laboratory experiments showed tolerance of burial for 72 h at winter temperatures (18.5-21.5 °C) but only for 25 h of summer temperatures (29.2 °C) (Main and Nelson 1988b). Reef-building tube worms showed no negative response to extremely high silt levels (up to 6.0 g/l) over a 4-day period (Main and Nelson 1988b). The tube worms showed 50% mortality between 24 and 48 h of exposure to high levels of sulfide (about 4.3 mg/l) simultaneously with low initial oxygen levels (<0.2 mg/l) (Main and Nelson 1988b).

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50272-101

REPORT DOCUMENTATION PAGE	1. REPORT NO. Biological Report 82(11.115)*	2.	3. Recipient's Accession No.

4. Title and Subtitle
Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)--Reef-building Tube Worm

5. Report Date
December 1989

6.

7. Author(s)
Alexander V. Zale and Susan G. Merrifield

8. Performing Organization Rept. No.

9. Performing Organization Name and Address
Oklahoma Cooperative Fish and Wildlife Research Unit
404 Life Sciences West
Oklahoma State University
Stillwater, OK 74078

10. Project/Task/Work Unit No.

11. Contract(c) or Grant(G) No.
(C)
(G)

12. Sponsoring Organization Name and Address
National Wetlands Research Center
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

U.S. Army Corps of Engineers
Waterways Experiment Station
P.O. Box 631
Vicksburg, MS 39180

13. Type of Report & Period Covered

14.

15. Supplementary Notes
*U.S. Army Corps of Engineers Report No. TR EL-82-4.

16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, distribution, life history, habitats, and environmental requirements of coastal species of fishes and aquatic invertebrates. They are designed to assist in environmental impact assessment. The reef-building tube worm is an ecologically and geologically significant invertebrate inhabiting the coastal zone of southeastern Florida. The reefs constructed by the worms retain beach sediments, protect shorelines from storm damage, and are the basis for an elaborate marine community of fishes and invertebrates. The reefs provide substrate, shelter, and food in the relatively inhospitable surf zone. Reef-building tube worms require stable settlement substrates within sandy beach habitats and intense turbulence to maintain suspension of sand grains and other particles for tube building.

17. Document Analysis a. Descriptors

Annelida
Feeding habits
Growth
Temperature
Suspended sediments
Contaminants
Competition
Salinity
Life cycles

b. Identifiers/Open-Ended Terms

Reef-building tube worm
Phragmatopoma lapidosa
Spawning
Environmental requirements

c. COSATI Field/Group

18. Availability Statement
Unlimited distribution

19. Security Class (This Report)
Unclassified

21. No. of Pages
vi + 12

20. Security Class (This Page)
Unclassified

22. Price

(See ANSI-Z39.18)

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
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National Wetlands Research Center
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458