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Distribution, habitat use and ecology of deepwater Anemones (Actiniaria) in the Gulf of Mexico

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ABSTRACT

The distribution of deepwater Actiniaria is poorly known. Rarely are these organisms identified to family, as this requires both well-preserved specimens and taxonomic expertise. Ecological information is similarly lacking. From the results of a comprehensive surveying program in the deep Gulf of Mexico, we report the occurrence of nine species of Actiniaria. For the most abundant four of these, we plot distributions and discuss habitat use, morphological variation, and feeding strategies. Actiniaria in the Gulf appear to have broad, basin-wide distributions with little depth preference. Faunal biomass is highest in the NE Gulf within submarine canyons or at the base of slope escarpments. Attachment mode is mostly opportunistic on various types of hard substrata, including trash. Sediment-dwelling forms are very abundant at an organically rich site within a large submarine canyon.

1. Introduction

Among deep-sea benthic organisms, anthozoans comprise a significant and often dominant fraction throughout the world's oceans, with representatives known from depths greater than 6000 m (e.g., Carlgren, 1956; Menzies et al., 1973). Members of the Orders Pennatulacea (sea pens) and Ceriantharia (tube anemones) often dominate numerically, being specially adapted for living in soft sediments. True sea anemones (Order Actiniaria) are patchier in distribution, as many members require hard substrata for attachment. As much of the deep sea lacks such substrate, actiniarian species that must attach to substrata settle opportunistically, if at all.

Although deepwater trawls may yield biased results regarding community structure (M. Wicksten, personal communication), they remain among the few tools available to deep-sea biologists for carrying out zoogeographic surveys (Gage and Tyler, 1991). The Deepwater Program: Gulf of Mexico Continental Slope Habitats and Benthic Ecology Project (DGoMB) conducted such a sampling program and its many trawls, covering a wide diversity of habitats, provide a rare opportunity to examine community structure at a basin-wide scale.

A small oceanic basin bordered on three sides by continents, the Gulf of Mexico covers only 1.5 million km^2, but possesses most of the geomorphic features found in larger basins. The continental margins are structurally complex, containing numerous canyons, hills, knolls, enclosed basins, and escarpments. Two-thirds of the Gulf's terrigenous inputs come from the Mississippi River, which deposits the bulk of its sediments over the Mississippi Fan (Pequegnat, 1983). This feature covers over 10% of the seafloor and plays a significant role in benthic faunal structure throughout most of the northcentral and northwestern Gulf. This and the myriad topographic features of the Gulf create a high diversity of benthic habitats within a relatively confined and isolated biogeographic area. Such an area is ideal for studying large-scale ecological processes.

Actiniaria comprises over 1100 species worldwide (Fautin, 2006). Most species are sessile, attached to hard substrates. As with many marine invertebrates, shallow-water Actinaria are much better known than their deep-sea counterparts, which have been the focus of relatively few biogeographic or ecological studies. Many deepwater actiniarians have burrowing lifestyles. True burrowing actiniarians (i.e. *Edwardsia*) use a bulb-like physa to dig and anchor into sediments, in *lieu* of a broad, flattened pedal disc. In the deep Gulf of Mexico (and other basins), some epilithic species live in sediments by grasping a ball of mud with the pedal disc. We consider this epipelic lifestyle ecologically similar to that of true burrowing species. Additional attachment substrates in the Gulf of Mexico include other animals and trash; we discuss the biogeographical, morphological, and ecological implications of these strategies.

2. Methods

Deepwater trawls were carried out as part of the DGoMB 2000–2002. A 12.2 m otter trawl with 3.8-cm mesh was deployed from R.V. *Gyre* at 39 stations (Fig. 1) along the northern

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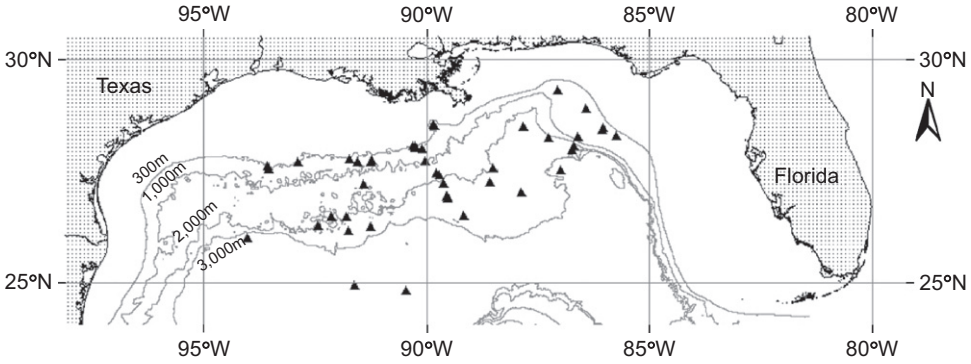

Fig. 1. Locations of DGoMB survey trawls. Water depths in m.

Table 1
DGoMB station data for voucher specimens of Actiniaria

Species	Station	Lat. °N	Long. °W	Depth (m)	Date
Actinauge longicornis	NB5	26.250693	91.240297	2100–2110	9-May-00
	B3	26.168170	91.748757	2300–2620	10-May-00
	S41	28.072240	86.677498	2955–3030	9-June-00
	MT1	28.529045	89.816425	420–501	17-June-00
	2MT1	28.552447	89.838332	461	3-June-01
Chondrophellia coronata	MT5	27.263362	88.564210	2025–2410	4-June-00
	MT6	27.037953	87.861228	2680–2790	5-June-00
	MT1	28.529045	89.816425	420–501	17-June-00
Paraphelliactis sp.	S35	29.316083	87.045490	645–695	12-June-00
Stephanauge nexilis	B3	26.168170	91.748757	2300–2620	10-May-00
	MT5	27.263362	88.564210	2025–2410	4-June-00
	MT6	27.037953	87.861228	2680–2790	5-June-00
Monactis vestita	B3	26.168170	91.748757	2300–2620	10-May-00
Actinoscyphia sp.	B2b	26.613773	92.326848	2140–2330	19-June-00

continental slope (37 trawls) and abyssal plain (5 trawls), recovering 321actiniarian specimens. These were immediately sorted to morphotype in the field, enumerated, weighed, and then fixed in 4% buffered formalin for storage at Texas A&M University. When possible, anemone mass was determined using volume displacement. This technique is commonly used for zooplankton hauls, provides more consistent measurements than wet weights, and can be performed quickly with many samples. Voucher specimens (Table 1) were identified by taxonomic specialists; then returned to Texas A&M University and used to identify the remaining specimens.

Additional records for anemones in the Gulf of Mexico were gathered from expedition reports (1983–1985) of the Northern Gulf of Mexico Continental Slope Study (NGoMCSS). *In situ* observations were provided by close-up anemone and seafloor photographs taken in November 2000 from DSV *Alvin* during *Atlantis* voyage 3, leg 58 (“Edge of the Gulf Cruise”, chief scientist I. MacDonald). This cruise was partially funded by the DGoMB project, and visited sites in the Gulf of Mexico adjacent to many of the trawling areas.

3. Results

3.1. Actiniaria of the Gulf of Mexico

Nine species of Actiniaria have been identified from the deep Gulf of Mexico (Table 2). Six of these, comprising the majority of the individuals encountered, belong to family Hormathiidae. Three other families (Actinoscyphiidae, Actinostolidae, Halcuriidae) also are reported from the region. Of these, only Actinoscyphiidae was encountered in the DGoMB trawls. Of the 86 deep-sea trawls, ranging in depth from 175 to 3720 m, 44 (51%) sampled actiniarians.

3.2. Hormathiidae

In terms of diversity and biomass, the majority of deepwater Actiniaria we sampled from the Gulf of Mexico belong to Hormathiidae. Members of this family share many features, including a thick-walled column, a strong mesogleal marginal sphincter, and relatively short tentacles, and thus must be differentiated based on histological and anatomical details (Carlgren, 1949).

Specimens belonging to *Actinauge longicornis* collected from DGoMB are white and moderate to large sized (50–220 mm length; Fig. 2A). Unless wrapped around a sponge or a pennatulacean stalk, the diameters of the pedal disc and column are roughly equal. In its contracted state, a member of *A. longicornis* is ovoid or a squat cylinder. The oral disc is broad, with short, stout, pale violet marginal tentacles. The column bears small tubercles and a deciduous cuticle, giving it a rough texture. In many specimens of *A. longicornis*, the tubercles are fused distally; this is most pronounced in the largest specimens.

A. longicornis is known from several sites in the west Atlantic and Caribbean, at depths 220–580 m (summarized in Fautin, 2006). We found members of *A. longicornis* in three sites, at depths from 420 to 2620 m. This species was unusually abundant at the head of the Mississippi Submarine Canyon (station MT1), a site with highly flocculent sediments. A repeat trawl in June 2001 confirmed the abundance of *A. longicornis* at MT1. Virtually all *A. longicornis* specimens (117 out of 120) from this site were epipelic rather than epilithic/epizooic. In terms of megafaunal biomass at the head of the Mississippi Submarine Canyon, *A. longicornis* comprised more than twice that of all other trawl organisms combined.

Chondrophellia coronata is another moderate-sized anemone, with specimens ranging from 20 to 50 mm in diameter. Like *A. longicornis*, specimens of *C. coronata* collected in the DGoMB are white and bear tubercles that are fused distally (Fig. 2B). The two are distinguished by the presence of gametogenic tissue on the older mesenteries in members of *Chondrophellia*. The tentacles of freshly caught specimens of *C. coronata* were orange; this differs from the pale purple tentacles of *A. longicornis*.

C. coronata is widespread. It is reported from the eastern and western North Atlantic and eastern Pacific, at depths from 600 to 3570 m (Verrill, 1883; Carlgren, 1942; Wolff, 1961; summarized in