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AN AGGREGATION OF THE PANDALID SHRIMP, HETEROCARPUS ENSIFER, ON DEEP REEF HABITATS OF THE WEST FLORIDA SLOPE, EASTERN GULF OF MEXICO

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ABSTRACT: Heterocarpus ensifer A. Milne–Edwards (1881) (Crustacea: Pandalidae), armed nylon shrimp, is widely distributed in the western and eastern North Atlantic Ocean. In the western Atlantic this shrimp occurs from off North Carolina to Brazil and in the Gulf of Mexico (GOM), western Bahamas, and Caribbean Sea at depths of 170–885 m. Despite its widespread occurrence, ecology or biology information for this species are sparse, and *in situ* observations of abundance, behavior and habitat preferences are particularly lacking. During extensive submersible and ROV observations on and near deep–reefs in the north–central and eastern GOM, a remarkably large aggregation of *H. ensifer* was observed on the West Florida Slope (WFS). On one ROV dive it was estimated that thousands of these shrimp occupied an area <100 m². They were most abundant on transition (near reef) and prime high–profile reef habitats composed of dead and live *Desmophyllum pertusum*, sponges, rocks, and other coral species. Collected males (n=14) exhibited a broader size range, 17.74–33.72 mm CL, than females (n=12, 23.08–30.15 mm CL); however, mean carapace length was similar for both sexes at 27.47 mm (females) and 26.40 mm (males). All but 3 collected females were ovigerous with Stage 1 embryos, and ROV video revealed that many of the shrimp were ovigerous females with clearly visible dark blue embryo masses on the abdomen. Evidence supports that the purpose of this aggregation was likely for mating and spawning. Although the frequency and locations of such aggregations are unknown, they are further indication of the importance of deep–sea complex habitats.

KEY WORDS: cold-water corals, deep-sea corals, shrimp reproduction, spawning aggregation, Pandalidae

INTRODUCTION

Heterocarpus ensifer A. Milne-Edwards (1881) (Crustacea: Decapoda: Caridea: Pandalidae), the armed nylon shrimp, is widely distributed, occurring in the western and eastern North Atlantic, Caribbean Sea, and western Mediterranean Sea over a depth range of 88-1,278 m (Escobar-Briones and Villalobos-Hiriart 2003, Tuset et al. 2009). Although also reported from the Indo-west Pacific, southwestern Indian Ocean and Hawaii, there is some uncertainty that these are all H. ensifer (Crosnier 1988, Poupin et al. 2012). In the western Atlantic this shrimp occurs from off North Carolina to Brazil and in the Gulf of Mexico (GOM), the western Bahamas, and Caribbean Sea in depths of 170-885 m (Briones-Fourzán et al. 2010). As with other pandalid shrimp, H. ensifer has been suggested as a potential commercial resource (Holthuis 1980, Wehrtmann et al. 2012); however, no large fisheries for it are yet developed.

Despite its widespread occurrence, there is little information on the ecology or biology of this species, aside from some data on its reproduction. Briones–Fourzán et al. (2010) characterized *H. ensifer* as a gonochoristic, iteroparous species that likely spawns year–round on the Yucatan slope of the southern GOM. They also reported that fecundity increased with size of females and ranged from 3,339 to 24,788 extruded eggs with sizes of 0.030–0.064 mm³. In the eastern Atlantic, Tuset et al. (2009) observed ovigerous females year around but reported mass spawning in spring and summer. Males and females are morphologically similar, with a high degree of rostral polymorphism after sexual maturity (Lozano–Alvarez et al. 2007). Females grow larger than males (Briones–Fourzán et al. 2010), but males exhibited faster growth in the eastern Atlantic (Tuset et al. 2009).

This pandalid shrimp is known from scattered locations in the GOM, especially in the southern GOM (Briones-Fourzán et al. 2010, Gracia et al. 2010). Hopkins et al. (1989) reported this species to be uncommon in the eastern GOM and assumed it might undergo diurnal migrations, but their data were limited. In the GOM (Felder et al. 2009) and islands of the northeastern Atlantic (Tuset et al. 2009) this shrimp was listed as a benthic, soft bottom species. However, in situ observations of abundance, behavior and habitat preferences are particularly lacking throughout its range. Note the submersible observations from Hawaii (Gooding et al. 1988) may not be of H. ensifer due to taxonomic uncertainty. Extensive submersible and ROV observations in the north-central and eastern GOM provided opportunities to record deep-sea species and community data otherwise unattainable, especially from complex habitats not easily sampled with conventional methods (e.g., nets). Observations of a remarkably large aggregation of H. ensifer on deep reefs of the West Florida Slope (WFS) and subsequent specimen collection during a 2010 research cruise are the basis of this note on abundance, distribution, and behavior.

METHODS AND METHODS

This paper focuses on the massive aggregation of *Hetero-carpus ensifer* observed on deep—sea coral bioherms and rocky ledges at WFS study sites (Figure 1). Data on shrimp aggregations were collected during a fall (20 September–3 October 2010) cruise using the R/V *Cape Hatteras* and the *Kraken II* ROV (Remote Operated Vehicle, University of Connecticut).



Figure 1. Multibeam sonar close up of the West Florida Slope deep–reef area relevant to the aggregation of Heterocarpus ensifer observed in September 2010. Submersible (JSLII) and ROV (Kraken II = KROV and Jason II = JROV) bottom dive tracks from 2009 and 2010 illustrate the degree of observational coverage. A single Tucker trawl (TT) track which impacted the bottom is mapped, and the arrow indicates direction of tow. Locations of CTD transects (data presented in Ross et al. 2017) are noted. Depth contours are in meters.

Details of this and other relevant GOM cruises as well as habitat and oceanographic analyses for the WFS region are presented in Ross (2017) and Ross et al. (2017).

Fauna occurrence and bottom habitat data were largely acquired by video and still cameras mounted to the ROV. Paired scaling lasers 10 cm apart were mounted on the ROV video camera. Video methods were standardized to the extent possible (see Ross and Quattrini 2007). When the ROV was moving, the video camera was set to predetermined pan/ tilt positions, zoomed to wide angle, and the vehicle moved at slow speeds as near to bottom as possible. This was modified as needed in heavy coral/rock areas and as lighting needs changed. Transects were run across all habitat types, including reef and non-reef areas. At times during most dives, specimens were collected by using the manipulator arm or suction device mounted on the ROV. A SeaBird SBE 19plus was mounted to the ROV downweight (≤ 15 m off bottom) and recorded conductivity (µS/cm), temperature (°C), depth (pressure), salinity, and dissolved oxygen (ml/l) once per second. A Tucker trawl (2x2 m, 1.59 mm mesh size) was used for midwater sampling, but on one occasion this net impacted the bottom and collected bottom-associated species.

Specimens from all collections were preserved at sea in 10% formalin in seawater solution. After the cruises, specimens were rinsed in water and stored in 50% isopropanol and later were identified to the lowest taxonomic level possible. All collected specimens of *H. ensifer* were deposited in the Invertebrate Zoology Collections of the Harvard Museum of Comparative Zoology (MCZ) and include the catalogue numbers MCZ:IZ:169904, MCZ:IZ:169905, MCZ:IZ:169906, and MCZ:IZ:169907.

In the lab, videos from the ROV cameras were viewed multiple times to document habitat and identify fauna (to species if possible). One of 3 general habitat categories was assigned to each fauna observation as in Ross and Quattrini (2007): Prime reef (variable, but rugged profile of ≥ 1 m, which could be rocky formations or dense stands of living and dead coral), Transition reef (mostly dead coral rubble and/or scattered small rocks with profiles ≤ 1 m, often with sandy bottom showing in places), and Off—reef (relatively flat bottom composed mostly of soft substrata). The dominant coral on the 2 reef categories was *Desmophyllum pertusum* (= *Lophelia pertusa*). Species occurrence was compared among the 3 general habitat types.

In a few places the resolution of the scaling lasers allowed for density of observed H. ensifer to be estimated. Appropriate video frames (clear view of habitat, shrimp, and lasers) were frozen, an area based on lasers estimated, and all shrimp in that area were counted. Even when area could not be estimated, counts of individuals were made by enumerating individuals in video frames as the vehicle moved through different habitats. In many places the video resolution did not allow exact counts because the shrimp were too dense, they blended with the background habitat, the ROV was too far away or moving too fast. Even so, the presence and general quantity of shrimp was usually obvious, and in these cases qualitative estimates of abundance were defined as follows: Few (10s of individuals), Common (100s of individuals), Abundant (1000s of individuals). Blue embryo masses were often visible in the video on the abdomens of females, and where possible, numbers of females in the view were estimated. Collected specimens (n = 26) were sexed (see King and Moffitt 1984, Gayathri and Chakraborty 2024) and measured to the nearest 0.01 mm with dial calipers for carapace length (CL, from the posterior margin of the orbit to the posterior dorsal edge of the carapace) and for rostrum length (RL, from the tip to the base of the rostrum).

Embryos from ovigerous females were examined under a compound microscope to identify 3 stages of development following Echeverria–Saenz and Wehrtmann (2011), Kuberan et al. (2021) and Gayathri and Chakraborty (2024). Embryos that were recently extruded after mating (Stage 1) lack an eye spot and are yolk filled. Embryos mostly filled with yolk but exhibiting a faint eye spot are Stage 2, while a dominant eye spot and reduced yolk are Stage 3.

Results

Multiple cruises (2008–2012) to the WFS mapped the complex habitats, collected oceanographic data, and conducted 11 manned submersible and ROV dives (67.7 h of bottom observations) to document fauna and habitats. The portion of the WFS with dense coral and rock reefs illustrated in the Figure 1 inset is the best surveyed part of this region, and observations from the 6 dives accomplished there are described below. *Heterocarpus ensifer* was observed on only 2 dives in 2010 (ROV–2010– CH–007 and 009). All dives but one (*Jason II*, November 2010) took place during daylight.

TABLE 1. Numerical estimates (No.) of Heterocarpus ensifer from video analysis of 2 ROV dives on deep reefs of the West Florida Slope, 28 and 30 September 2010. Area was estimated from lasers mounted 10 cm apart on the video camera. Few = 10s of individuals; Common = 100s of individuals; Abundant = 1000s of individuals. Prime Habitat = variable, but rugged profile of \geq 1 m, which could be rocky formations or dense stands of living and dead coral; Transition Habitat = mostly dead coral rubble and/or scattered small rocks with profiles < 1 m, often with sandy bottom showing in places; Off-reef Habitat = relatively flat bottom composed mostly of soft substrata.

Dive	Depth (m)	No.	Area (m²)	No. females	Habitat
ROV-2010-CH-007	518	3			Prime
	518	Few			Prime
	517	2			Transition
	491	11		3	Prime
	495	6			Prime
	493	1			Prime
ROV-2010-CH-009	549	92			Off–reef
	549	187	0.5		Off–reef
	549	52	0.1222	8	Transition
	549	Common			Prime
	543	Common			Prime
	545	Common			Prime
	545	Common			Prime
	543	86	0.1925	8	Transition
	543	Common			Prime
	543	Common			Transition
	547	Abundant			Transition
	547	213	0.5		Transition
	547	Few			Prime
	547	64	0.5		Prime
	543	Few			Prime
	543	Common			Prime
	542	Common			Prime
	543	Few			Prime
	543	Abundant			Transition
	539	Abundant			Transition
	539	Few			Prime
	539	Common			Transition
	541	Few			Prime

On the 28 September 2010 dive KROV-2010-007 surveyed a reef complex between 485-522 m over 9.5 h (Figure 1). A total of 21 H. ensifer were observed on Prime reef habitat (491-518 m) and 2 were observed on Transition habitat (517 m) at approximately 26° 12.464' N, 84° 43.550' W (Table 1). None were observed on the flat, sandy bottom type. There was an additional qualitative observation of Few on Prime habitat. These shrimp did not occur in dense aggregations but were either single individuals or loose groups of 3-10 individuals; in all cases they were closely associated with reef structures (Figure 2). Although a few females could be distinguished by the blue embryo masses (Table 1), video resolution and cryptic behavior (Figure 2) hindered resolution of the numbers of ovigerous females. During this dive mean bottom temperature was 8.5°C (range = $8.1-9.1^{\circ}$ C), mean bottom salinity was 35.0 (range = 35.0-35.1), and mean bottom dissolved oxygen was 2.7 ml/l (range = 2.7 - 2.8 ml/l).

The next dive in this area (KROV–2010–008, 29 September 2010, Figure 1) occurred on deeper (530–584) rock and coral reef. During the 9.4 hrs of bottom observation no *H. ensifer* were observed.



Figure 2. Heterocarpus ensifer observed on West Florida Slope reef dive ROV–2010–CH–007 at 491 m on 28 September 2010. Photographs are from ROV video frame grabs. Underlying habitat is course sand, sponge, rock, and living and dead coral. Red arrows in bottom frame indicate H. ensifer closely associated with a mostly dead Desmophyllum pertusum colony.



Figure 3. Heterocarpus ensifer observed on West Florida Slope reef dive ROV–2010– CH–009, at 541–547 m on 30 September 2010. Photographs are from ROV video frame grabs. Note the bluish colored abdomens visible in most frames indicate ovigerous females. A. Close view of Prime reef habitat with 6 H. ensifer visible. B. Heterocarpus ensifer scattered over Transition reef habitat adjacent to Prime reef. Laser dots (center left) spaced 10 cm apart are outlined in red. C. High density of H. ensifer on Transition reef habitat. D. Prime reef habitat with high density of H. ensifer.

Dive KROV-2010-009 (30 September 2010) was closer to dive 007, occurring in 519-549 m (Figure 1) with a bottom time of 8.3 hrs. Within a few minutes of the ROV arriving on the bottom (sandy rubble Transition reef adjacent to Prime reef) a massive aggregation of H. ensifer was observed covering the bottom (Figure 3) at approximately 26° 12.281–12.243' N, 84° 43.967–43.953' W (540–547 m). This dive spent about 2.78 h exploring the area (estimated to be $\leq 100 \text{ m}^2$) containing the H. ensifer. Although 279 individuals were counted on sandy, Off-reef, habitat, these only occurred in 2 adjacent places very near the reef habitats (Table 1). The great majority of H. ensifer were observed on Transition Reef habitat (353 counted) and the abutting Prime Reef habitat (85 counted). Common and abundant qualitative numerical estimates were most noted on the Transition habitats (Table 1). Ovigerous females with blue embryo masses were frequently observed (Table 1, Figure 3); however, the estimated number of females is conservative as many could not be counted or viewed clearly. Mean bottom temperature was 8.3°C (range = 8.1-8.6°C), mean bottom salinity was 35.0 (range = 34.8–35.1), and mean bottom dissolved oxygen was 2.7 ml/l (range = 2.7-2.7 ml/l).

The few density counts that were possible (Table 1) docu-

mented high shrimp biomass packing. These counts are conservative as shrimp were so dense in several places that individuals were often difficult to distinguish. In addition, many shrimp were embedded deep within the coral branches (Figure 3A) and were not visible unless the video was zoomed in. In reef areas with the highest densities, individuals were touching each other and were often layered on top of each other (Figure 3C and D). Despite not being able to count all shrimp nor fully estimate density, it is likely this aggregation included tens of thousands of individuals in an area < 100 m². The remainder of this dive covered a large area of diverse habitat, but no additional *H. ensifer* were observed.

On dives 007 and 009 observed individuals did not exhibit much activity. Mostly they sat on the bottom or within coral or rock crevices, moving very little. Because of their density, they were often in close contact with one another. Under the ROV lighting their colors appeared to be pale reds to pink (e.g., Figure 3), but when photographed on the surface soon after capture, both sexes were a dark red (Figure 4).

On 10 Nov 2010 the Jason II ROV conducted a 5.3 h nighttime dive on the WFS reefs between the tracks of Kraken II dives 008 and 009 (492–555 m, Figure 1). Heterocarpus. ensifer were

not observed. Likewise, during the 2 JSLII dives in this area in September 2009 (Figure 1) no *H. ensifer* were observed.

Specimens (n=127) of *H. ensifer* were collected non–selectively by suction during dive 009 (19 retained, Table 2). In one suction collection split between 2 containers (B1/2, Table 2) 57



Figure 4. Freshly collected Heterocarpus ensifer (MCZ:IZ:169907) from Kraken II ROV dive 2010–CH–009 from deep–coral reefs of the West Florida Slope. A. Berried female (top), 30.15 mm CL, and male (bottom), 30.01 mm CL. B. closer view of abdomen of female from top photo illustrating dark blue embryos.

males and 58 females were collected; however, only 10 females were retained (Table 2). Two female *H. ensifer* were also collected during one Tucker trawl tow that impacted the bottom early in the tow (Figure 1). This trawl collection and the observations in dive 007 were the only indication that *H. ensifer* occurred away from the main aggregation observed in ROV dive 009. Males (n=14) exhibited a broader size range, 17.74–33.72 mm CL, than females (n=12), 23.08–30.15 mm CL; however, mean carapace length was similar for both sexes at 27.47 mm (females) and 26.40 mm (males) (Table 2).

Nine of the 12 females collected carried dark blue embryo masses on the abdomen (Figure 4). All embryos examined on all 9 females were in Stage 1, recently extruded after mating. Female exoskeletons were soft suggesting they had recently molted.

DISCUSSION

Direct observations of mass aggregations of adult H. ensifer have not been reported previously in the Atlantic Ocean, and only rarely for other pandalid shrimp. However, even though the occurrence of H. ensifer in Hawaii is questionable (Crosnier 1988), using a submersible Moffitt and Parrish (1992) reported that this nominal species occurred in diffuse groups around relief features. In contrast, Gooding et al. (1988), also using a submersible off Hawaii, observed nominal H. ensifer in abundance on sandy bottoms, but not densely aggregated. In Palau (Western Pacific) H. ensifer was observed in large numbers near deep reefs, and Saunders and Hastie (1992) suggested that they were gregarious and may follow scent trails in swarms for feeding. Pandalidae and Hippolytidae shrimps were observed off Alaska to form aggregations around large anemones (Stevens and Andersen 2000). Aggregations for feeding or reproductive purposes were inferred for Plesionika spp. in the Mediterranean Sea (Fanelli and Cartes 2004). During numerous cruises and hundreds of hours of underwater observations conducted by the author in depths ranging from 200–1000 m from North Carolina through the GOM (1991–2010; e.g., Sulak and Ross 1996, Gartner et al. 2008, Partyka et al. 2007, Ross et al. 2012, Demopolous et al. 2017) H. ensifer were rare or not observed (S.W. Ross, pers. obs.; unpubl. data), the one exception being described here. As in other studies (Moffitt and Parrish 1992, Gooding et al. 1988), they did not appear to react to the ROV.

The overall size range of *H. ensifer* collected (17.74–33.72 mm CL, both sexes) was within the range of other studies with 3 exceptions. The 23.08 mm CL ovigerous female collected is smaller than the smallest egg–bearing females reported from the southern GOM (23.5 mm CL, Briones–Fourzan et al. 2010; 24.5 mm CL, Lozano—Alvarez et al. 2007). In addition, an even smaller (22.7 mm CL) ovigerous female was reported from off the eastern Yucatan Peninsula (Escobar—Briones and Villalobos—Hiriart 2003). As in Briones—Fourzan et al. (2010) mean size of males and females exhibited little difference from each other. All but one of the collected shrimp were well within the size ranges reported for the onset of sexual maturity (females, 23–24 mm CL; males,

TABLE 2. Specimens of Heterocarpus ensifer collected on deep reefs of the West Florida Slope, 30 September 2010, using a Tucker trawl (TT) which hit the bottom and the ROV Kraken II suction sampler (B). CL = carapace length; RL = rostrum length.

Station	Depth (m)	Gear	CL (mm)	RL (mm)	Sex	Stage
CH-2010-081	525	TT	24.97	*	F	ovigerous
CH-2010-081			26.18	*	F	ovigerous
ROV-2010-CH-009	542	B3	27.63	30.57	F	ovigerous
ROV-2010-CH-009		В3	28.71	28.99	м	
ROV-2010-CH-009		В3	33.72	21.52*	м	
ROV-2010-CH-009		В3	25.23	28.16	М	
ROV-2010-CH-009		В3	26.22	26.97	М	
ROV-2010-CH-009		В3	17.74	22.79	М	
ROV-2010-CH-009	543	B1/2	28.88	27.78	F	ovigerous
ROV-2010-CH-009		B1/2	28.85	26.65	F	ovigerous
ROV-2010-CH-009		B1/2	30.07	*	F	ovigerous
ROV-2010-CH-009		B1/2	28.82	*	F	ovigerous
ROV-2010-CH-009		B1/2	27.78	22.29	F	
ROV-2010-CH-009		B1/2	28.84	*	F	
ROV-2010-CH-009		B1/2	24.44	26.67	F	
ROV-2010-CH-009	545	B2	23.08	20.04	F	ovigerous
ROV-2010-CH-009		B2	30.15	24.99	F	ovigerous
ROV-2010-CH-009		B2	28.62	27.82	м	
ROV-2010-CH-009		B2	28.08	27.46	М	
ROV-2010-CH-009		B2	30.01	29.92	М	
ROV-2010-CH-009		B2	25.39	15.02*	М	

21–22 mm CL; Lozano-Alvarez et al. 2007). Although the sizes of *H. ensifer* observed in ROV video could not be accurately measured, the observed specimens appeared to be large adults similar in size to those collected.

The purpose of this H. ensifer aggregation is not explicitly clear. Saunders and Hastie (1992) proposed that H. ensifer moves in swarms following scent trails; however, the extreme size of the aggregation reported here does not seem to support a mass feeding event. Also, feeding behavior was not observed. The presence of males and females in close proximity, the large number of ovigerous females observed, all collected ovigerous females with Stage 1 embryos, and the soft carapace of the females which is evidence of recent molting required before mating (Bauer 1976, Lacoursiere–Roussel and Sainte–Marie 2009) most likely argue for this being a mating and spawning aggregation. This aggregation fits the Pure Searching mating system (Correa and Thiel 2003, Bauer 2011), characterized by large aggregations or schools, individual mobility, and high population density. In such aggregations the newly molted females emit sex pheromones, and mating with males soon follows; however, proximity of the 2 sexes is required (Bauer 2011). The mating process (i.e., transfer of sperm from males to females) often takes \leq 120 min, depending on the caridean species, and is closely followed by the release of eggs from the ovaries which are fertilized as they pass to attachment on the pleopods (Correa and Thiel 2003). This aggregation appeared to be quite localized in a small area on this section of WFS deep—reef, which would facilitate mating, and association with reef structures may offer predator protection during a vulnerable period. Like other deep—sea *Heterocarus* spp. (Kuberan et al. 2021, Gayathri and Chakraborty 2024), *H. ensifer*, appears to spawn year—round in the southern GOM (Lozano—Alvarez et al. 2007, Briones—Fourzan et al. 2010), but Briones—Fourzan et al. (2010) noted lower reproductive output in the fall season. It releases thousands of small eggs per spawning event which are likely planktotrophic exhibiting prolonged larval development (Briones—Fourzan et al. 2010).

Habitat use in *H. ensifer* is apparently more diverse than previously reported. Tuset et al. (2009) stated that this shrimp was only known from sandy or muddy bottoms. Briones–Fourzan et al. (2010) noted that their small trawl and trap catches of *H. ensifer* on the GOM Yucatan slope were related to lack of soft bottom substrate in an area of complex topography. However, complex topography is difficult or impossible to sample with most surface deployed gear; thus, it is possible, considering the potential close association of *H. ensifer* with coral/rocky reef habitats (this study), that these shrimp could have occupied the unsampled reef areas. As noted above, use of complex reef habitats, especially during mating and spawning, provides some protections from predation and perhaps also provides enhanced feeding opportunities.

The persistence or regularity of such shrimp aggregations cannot be determined from this study. Despite the large amount of direct observation time over a wide area of the southeastern US and GOM (see above), these observations are often one—time visits to a site, and even when there are multiple visits they are usually widely spaced in time (e.g., once per year). Thus, there is a low probability and low predictability of observing events of short duration, like mating or spawning.

While several species of *Heterocarpus* are commercially fished

or have potential for fisheries, especially in the Pacific and Indian oceans (King 1986, Echeverria-Saenz and Wehrtmann 2011, Wehrtmann et al. 2012, Kuberan et al. 2021), H. ensifer has been considered to be too small or not abundant enough for a fishery (Saunders and Hastie 1992, Briones-Fourzan et al. 2010). The 792 specimens (Lozano-Alvarez et al. 2007) and the 816 specimens (Briones–Fourzan et al. 2010) collected by extensive trawling and trapping off the Yucatan Peninsula (311–715 m) were thought to be the largest samples of H. ensifer yet from the GOM. As noted here, aggregations of this shrimp possibly in the tens of thousands can occur in the GOM but may also be too sporadic or unpredictable to support a fishery. Even so, this aggregation of biomass, the largest yet observed, indicates that H. ensifer could have a significant impact on localized ecosystems, such as deep—coral reefs, by providing prey (themselves and their offspring) and by being predators. They were reported as prey for some sharks near Brazilian seamounts (Vaske Junior et al. 2009), for pelagic stingray off Brazil (Veras et al. 2009), for wreckfish on the Charleston Bump (Goldman and Sedberry 2011) and for giant isopods on the Yucatan slope (Lozano–Alvarez et al. 2007).

The close association of *H. ensifer* with the deep—coral (mostly D. *pertusum*) habitat during this proposed mass spawning aggregation is further evidence of the importance of complex deep—sea ecosystems. While studies of deep—sea coral ecosystems have expanded greatly over the last 20 years, it is clear that new discoveries are not only possible but are common (e.g., Young 2009, Sowers et al. 2024, this study). The same is true for other deep—sea complex habitats, including seamounts, methane and hydrothermal seeps, submarine canyons, shipwrecks, and sponge grounds. Increasing interests from bottom fisheries, mining, and energy exploration and development in the deep sea compounded by the growing threats from climate change strongly suggest that additional research and monitoring are needed.

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