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coral reef paper

Benthic hydroids (Cnidaria, Hydrozoa) from Alacranes Reef, Gulf of Mexico, Mexico

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ABSTRACT.—Here, we provide the first list of shallow-water hydroids for Alacranes Reef, Mexico, comprising 49 species in 33 genera. The most speciose superorder was Leptothecata (36 species), with three particularly diverse families: Clytiidae, Sertulariidae, and Plumulariidae. Three species were recorded for the first time in the Gulf of Mexico (GoM), and 13 for the south-central GoM. The majority of fauna was substrate generalist with specific distributions: 38 hydroid species occurred on natural reefs, 18 on artificial reefs, 9 on drifting *Sargassum* spp., and 8 on the seagrass *Thalassia testudinum* K.D. Koenig. Our results significantly increase knowledge of the hydroids from Mexican waters. This is an important step toward detecting non-native species in the near future, as well as for improving and designing new conservation programs in the area.

Benthic hydroids from Mexican waters of the Atlantic Ocean are poorly known, and most records come from the Caribbean coast (Calder and Cairns 2009, and references therein). The hydroid fauna of shallow waters of the Gulf of Mexico (GoM), south of Texas, remains almost entirely unstudied. Few data are available for species in the planktonic stage (cf. Segura-Puertas et al. 2003, Gasca and Loman-Ramos 2014). For benthic hydroids, conspicuous hydrocorals have been noted in the Lobos-Tuxpan reef system (De la Cruz-Francisco et al. 2016, González-González et al. 2016). Jerónimo (2016) recorded 39 species of benthic Hydrozoa, of which 60% represented new records in the region. This highlights the general lack of knowledge of hydrozoan and medusozoan diversity in Mexican waters, which is particularly evident when comparing better studied areas, for example the 400 species (Siphonophora excluded) of planktonic and benthic Hydrozoa reported in the Mediterranean Sea (cf. Gravili et al. 2013).

Hydroids play a significant role in energy transfer from plankton to benthos. Hydroids have different modes of propagation: sexual (planula and actinula larvae) vs asexual (buds, frustules, colony fragments) (Gili and Hughes 1995), with rapid settlement and growth, respectively (Boero 1984, Migotto et al. 2001). They occur in a variety of habitats on a diversity of substrates (Calder 1991, Gili and Hughes 1995, Genzano and Rodríguez 1998). They are a common component of fouling communities (Ronowicz et al. 2013) and coral reef fauna (Gravier-Bonnet and Bourmaud 2006).

Coral reefs support a high diversity of species (e.g., mollusks, Kohn 1967; fish, Wilson et al. 2007). Several coral reef systems can be found in the GoM, such as the large areas of the Veracruz, Campeche and Alacranes Reefs. Alacranes is an atoll-like bank-reef system covering 650 km^2 and includes a relatively deep lagoon (5–40 m depth) located 137 km north of Progreso harbor and Campeche Bank (Jordán-Dahlgren and Rodríguez-Martínez 2003) (Fig. 1). This reef is particularly important in terms of marine biodiversity in Mexico, and its relevance was recognized by the creation of a marine protected area there in the early 1990s (Diario Oficial 1994). The reef supports a variety of recreational (scuba diving and sport fisheries) and commercial activities, including fisheries for spiny lobster (Palinuridae), queen conch (Strombidae), groupers (Serranidae), and other economically-important species (Canela-Rojo 1992, INE 1996, Ríos-Lara et al. 2007). Despite its acknowledged value, little is known about benthic and sessile invertebrates inhabiting the Alacranes Reef, with only sponges (Ugalde et al. 2015) and sea anemones (González-Muñoz et al. 2013) having been studied in detail.

As part of a project focused on the diversity of shallow water benthic invertebrates around Mexico, a survey of different habitats (natural and artificial reefs, seagrass meadows, and drifting macroalgae) within this reef area was conducted. The current contribution represents our first effort to study the richness and diversity of hydroid colonies in a variety of different habitats and microhabitats within the Alacranes Reef system. Here, we provide a first list for the Alacranes Reef region, with specific ecological notes for each species of benthic hydroids.

Material and Methods

The study was conducted during May 17–29 and June 22–26, 2016, through two collection efforts along the Alacranes Reef aiming to maximize the representation of natural (NR) and artificial substrates (AR) within the system. In total, 42 sampling efforts (scuba diving, 3–40 m depth) were performed along coral (NRs: algae, sponges, hydroids, stony and soft corals, mollusks, ascidians, rocks) and artificial reefs (ARs: shipwreck, buoys, chains) (Table 1, Fig. 1). In addition, hydroids were collected from 20 randomly selected fragments of drifting *Sargassum* sp. (SA). Also, leaves and roots with hydroid colonies were gathered from *Thalassia testudinum* K.D. Koenig meadows (TT) along three 120-m transects.

All samples were preserved in 96% ethanol, except for some hydrocorals, which were identified in situ and photographed underwater. When necessary, specimens were analyzed using molecular techniques to corroborate their identity at the species level, according to the protocol established in Cunha et al. (2015). Voucher specimens were deposited in the collection of Cnidarians of Gulf of Mexico and Mexican Caribbean "Lourdes Segura" (Faculty of Science, Multidisciplinary Teaching and Research Unit, Sisal, Yucatán) under the code: YUC–CC–254–11. Sequences were deposited in GenBank (see accession numbers in Table 2).

Table 1. Sampling sites for the present study on Alacranes Reef off Mexico. Depths with single value were sampled at only one depth, while ranges included sampling at multiple depths. Asterisks indicate repeated sampling efforts at the same site. Dash indicates no specific coordinates.

Station	Latitude (N)	Longitude (W)	Depth (m)	Date
1	21°22′54.81″	89°41′36.6″	6.0	17/05/2016
2	22°23′44.2″	89°42′6.3″	14.0–15.0	17/05/2016
3	22°29′42.8″	89°46′20.5″	5.0–7.5	18/05/2016
4	22°22′56.3″	89°40′57.2″	5.0–9.4*	18/05/2016
5	22°22′57.1″	89°40′46.6″	0.0–15.0	18/05/2016
6	22°23′45.2″	89°42′08.8″	5.0–8.6	19/05/2016
7	22°22′55.8″	89°41′43.2″	5.0–8.6	19/05/2016
8	22°23′24.0″	89°40′48.0″	0.5	20/05/2016
9	22°23′41.4″	89°41′57.2″	7.5	20/05/2016
10	22°22′35.4″	89°40′18.1″	0.0–10.0	20/05/2016
11	22°22′56.3″	89°40′57.2″	1.5–2.7*	21/05/2016
12	22°23′50.4″	89°40′39.6″	20.0	21/05/2016
13	22°23′23.8″	89°40′45.4″	15.0	21/05/2016
14	22°22′3.5″	89°40′13.2″	9.0	21/05/2016
15	22°25′3.1″	89°44′23.8″	22.0	22/05/2016
16	22°21′56.0″	89°39′40.9″	5.0–7.0	23/05/2016
17	22°23′1.3″	89°41′4.5″	1.5	23/05/2016
18	22°22′36.7″	89°40′24.2″	0.0–9.0	24/05/2016
19	22°22′3.3″	89°40′13.4″	5.0–7.6	24/05/2016
20	22°22′1.5″	89°39′13.2″	4.0–5.0	25/05/2016
21	22°22′20.1″	89°40′25.7″	7.0–8.0	25/05/2016
22	22°22′57.9″	89°41′42.5″	7.0–8.0	25/05/2016
23	22°22′20.1″	89°40′25.7″	7.0–8.0	26/05/2016
24	22°22′48.3″	89°39′13.9″	5.0–16.0	26/05/2016
25	22°22′05.0″	89°39′17.5″	5.0–8.0	27/05/2016
26	22°23′31.5″	89°40′4.1″	4.0–8.0	27/05/2016
27	22°22′25.2″	89°40′34.1″	8.0–10.0	27/05/2016
28	22°22′40.3″	89°41′41.7″	18.0–20.0	28/05/2016
29	22°22′56.3″	89°40′57.2″	1.0*	28/05/2016
30	22°22′38.3″	89°41′37.2″	16.0–21.0	29/05/2016
31	22°28.98′0″	89°46.35′0″	30.0	22/06/2016
32	22°32′32.8″	89°44′55.1″	10.0	22/06/2016
33	22°35′08.3″	89°44′34.2″	40.0	23/06/2016
34	22°30′08.6″	89°47′15.2″	6.0	23/06/2016
35	22°34.64′0″	89°42.95′0″	36.0	24/06/2016
36	22°34.64′0″	89°42.95′0″	23.5	24/06/2016
37	22°29.90′0″	89°47.60′0″	28.6	24/06/2016
38	22°35.18′0″	89°45.00′0″	14.6	25/06/2016
39	22°34.80′0″	89°45.84′0″	24.6	25/06/2016
40	22°24′56.2″	89°44′14.2″	36.7	26/06/2016
41	22°27′08.7″	89°45′47.8″	17.3	26/06/2016
42	–	–	16.0	26/06/2016

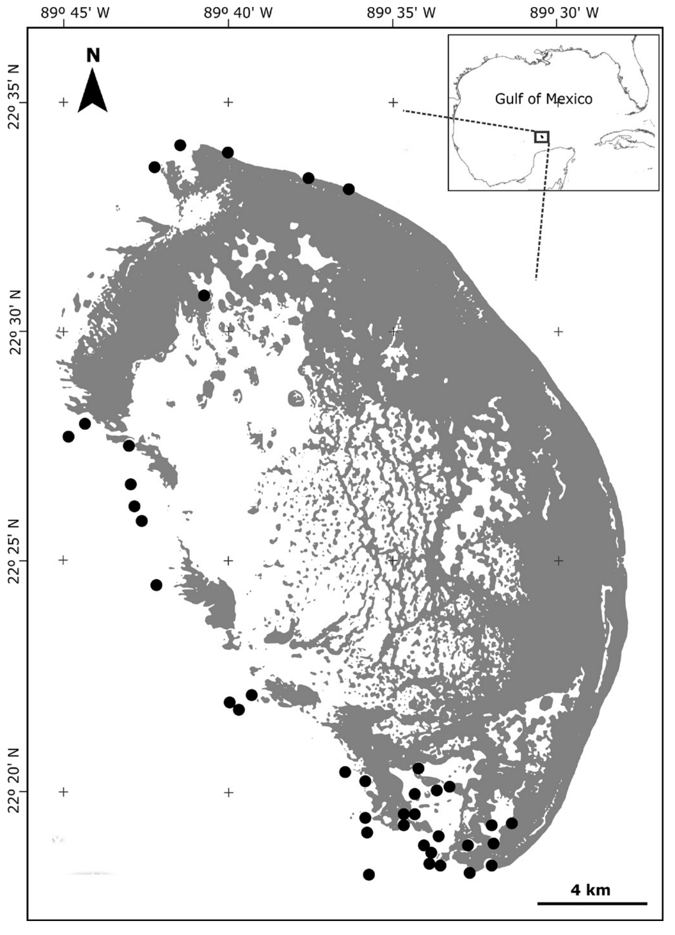

Figure 1. Map of sampling areas in Alacranes Reef, south-central Gulf of Mexico. Circles indicate specific sites where species were sampled and gray area indicates submerged habitats.

Results

In total, 270 samples (212 NRs, 25 ARs, 20 SA, 13 TT) was collected over a temperature range of 27–29 °C, yielding 49 hydroid species (13 "Anthoathecata" and 36 Leptothecata) distributed among 33 genera (Table 2). Some colonies were not identifiable to the species level because the specimens were damaged and occurred at low abundance; for some of these, molecular data allowed identification to the genus level. Clytiidae and Sertulariidae were the most speciose families of Leptothecata, followed by Plumulariidae. Three species were first records for the GoM, and 13 species were recorded for the first time in shallow waters of the southern GoM basin. Twenty species have both polyp and free medusa stages in their life cycle, while the remaining 29 have only the polyp stage with fixed gonophores (Table 2). Fertile colonies were observed in all habitats, and few hydroids were substrate specialists, e.g., *Hydractinia* sp. (two substrates) and *Turritopsoides* sp. (one substrate) (Tables 3, 4).

Table 2. Taxonomic list of benthic Hydroidolina species (Cnidaria, Hydrozoa) from Alacranes Reef. New record is for: NR_SGoM = in the southern Gulf of Mexico; NR_GoM = in the Gulf of Mexico. P = with polyp stage; M = with medusa stage; - not applicable; * GenBank Accession Number 16s rDNA. Registration code is YUC-CC-254-11 + no.

Taxon	Registration code	New record	Life cycle strategy
Superorder "Anthoathecata"			
Order Capitata, sensu stricto			
Family Sphaerocorynidae			
Sphaerocoryne agassizii (McCrady, 1859)	740, 863*MF538730, 868	-	P/M
Family Milleporidae			
Millepora alcicornis Linnaeus, 1758	801, 802	x	P/M
Millepora complanata Lamarck, 1816	not collected	x	P/M
Millepora spp.	not collected	-	P/M
Family Pennariidae			
Pennaria disticha Goldfuss, 1820	748–750, 764–773, 796–799, 827, 893, 926, 936, 946–949, 957, 958, 965, 967	x	P/M
Family Zancleidae			
Zanclea migottoi Galea, 2008	744, 805*MF538731, 876	x	P/M
Order "Filifera"			
Family Eudendriidae			
Eudendrium capillare Alder, 1856	742	x	P
Eudendrium cf. *capillare* Alder, 1856	832	-	-
Eudendrium carneum Clarke, 1882	739, 741, 864, 865, 925, 930, 932, 956, 959, 962, 969, 978, 982	x	P
Eudendrium spp.	901, 952, 983	-	-
Myrionema amboinense Pictet, 1893	867, 872, 975, 977, 994	x	P
Family Hydractiniidae			
Hydractinia sp.	717*MF538732, 718*MF538733, 736, 870	-	P/M
Family Oceaniidae			
Corydendrium parasiticum (Linnaeus, 1767)	714, 715, 727, 811, 866, 869, 889	x	P
Turritopsis dohrnii (Weismann, 1883)	862*MF538734	x	P/M
Turritopsoides sp.	716*MF538735, 735, 743, 871*MF538736, 873	NR_GoM	P
Family Stylasteridae			
Stylaster roseus (Pallas, 1766)	800, 964	x	P
Superorder Leptothecata			
Order incertae sedis			
Family Hebellidae			
Hebella cf. *furax* Millard, 1957	782	-	P/M
Hebella cf. *scandens* (Bale, 1888)	783	-	P/M
Hebella cf. *venusta* (Allman, 1877)	823	-	P/M
Order Lafoeida, sensu novum			
Family Lafoeidae			
Filellum spp.	780, 781, 980, 986	-	-

Table 2. Continued.

Taxon	Registration code	New record	Life cycle strategy
Family Syntheciidae			
Hincksella cylindrica (Bale, 1888)	981	NR_SGoM	P
Synthecium tubithecum (Allman, 1877)	976	NR_SGoM	P
Order Macrocolonia			
Suborder Haleciida, sensu novum			
Family Haleciidae			
Halecium bermudense Congdon, 1907	729, 730, 734, 941, 979	NR_SGoM	P
Halecium cf. *bermudense* Congdon, 1907	721–723, 725, 732, 733, 804, 814, 900, 902, 966, 968, 972, 974	-	-
Nemalecium lighti (Hargitt, 1924)	720, 726, 728, 731, 737, 950	x	P
Suborder Sertulariida			
Family Sertulariidae			
Dynamena disticha (Bosc, 1802)	751, 784, 788, 790, 841, 884, 888, 895, 912, 961	x	P
Dynamena quadridentata (Ellis and Solander, 1786)	892, 897, 907	NR_SGoM	P
Sertularia loculosa Busk, 1852	922, 923	NR_GoM	P
Sertularia distans (Lamouroux, 1816)	935, 996	NR_SGoM	P
Sertularia marginata (Kirchenpauer, 1864)	775, 785, 786, 787, 789	x	P
Sertularia turbinata (Lamouroux, 1816)	890, 934	NR_SGoM	P
Family Sertularellidae			
Sertularella diaphana (Allman, 1885)	791, 938	x	P
Family Thyroscyphidae			
Thyroscyphus marginatus (Allman, 1877)	883, 896, 909, 916, 917, 919, 951	x	P
Suborder Plumupheniida			
Infraorder Aglaopheniida			
Family Aglaopheniidae			
Aglaophenia latecarinata Allman, 1877	753, 757, 763, 776, 779, 803, 831	x	P
Infraorder Plumulariida, sensu novum			
Family Halopterididae			
Antennella secundaria (Gmelin, 1791)	761, 774, 835, 903, 933, 953	x	P
Halopteris carinata Allman, 1877	899, 910, 914, 920, 927, 945, 947, 963	NR_SGoM	P
Halopteris diaphana (Heller, 1868)	984	NR_GoM	P
Monostaechas quadridens (McCrady, 1859)	894, 908, 911, 918	NR_SGoM	P
Family Kirchenpaueriidae			
Kirchenpaueria halecioides (Alder, 1859)	747, 885	x	P

Table 2. Continued.

Taxon	Registration code	New record	Life cycle strategy
Family Plumulariidae			
Dentitheca dendritica (Nutting, 1900)	756, 944, 955, 971, 995	x	P
Monotheca margaretta (Nutting, 1900)	778, 954, 960	NR_SGoM	P
Plumularia floridana Nutting, 1900	719, 754, 760, 762, 795, 924	x	P
Pumularia setacea (Linnaeus, 1758)	752, 915, 921, 940, 943	NR_SGoM	P
Plumularia strictocarpa Pictet, 1893	745, 746, 755, 758, 759, 777	NR_SGoM	P
Plumularia spp.	792, 793, 794	-	-
Order Statocysta			
Suborder Campanulinida, sensu novum			
Incertae sedis sp. 1	997	-	-
Family Campanulinidae			
Lafoeina tenuis Sars, 1874	985	NR_SGoM	P/M
Suborder Proboscoida, sensu novum			
Infraorder Obeliida			
Family Clytiidae			
Clytia cf. *gracilis* (M Sars, 1851)	817, 824, 849	x	P/M
Clytia hemisphaerica (Linnaeus, 1767)	808, 815, 826, 886, 891	x	P/M
Clytia cf. *hummelincki* (Leloup, 1935)	839	-	P/M
Clytia linearis (Thorneley, 1900)	818, 898, 905, 942	x	P/M
Clytia paulensis (Vanhöffen, 1910)	816, 833, 848, 854	NR_SGoM	P/M
Clytia sp. 1	834, 836-838, 840, 843, 844, 846, 850–853, 855–861, 973	-	P/M
Clytia sp. 2	845, 847, 988	-	P/M
Clytia spp.	904, 929	-	-
Family Obeliidae			
Obelia dichotoma (Linnaeus, 1758)	807, 809, 810, 812, 813, 819-822, 825, 828-830, 842, 875, 928, 931, 937, 970, 987	x	P/M

Obelia dichotoma (Linnaeus, 1758) was the most frequently encountered species, occurring in four of the five sampled habitats (Table 3).

The highest number of hydroid species was found on NRs (38), followed by ARs (18), SAs (9), and the TT (8) (Table 3). On NRs, the hydroids were found on a variety of taxa, mainly sponges [e.g., *Aplysina* sp., *Callyspongia vaginalis* (Lamarck, 1814), and *Niphates erecta* Duchassaing and Michelotti, 1864 (23 species in total] and soft corals (19), followed by algae (e.g. *Halimeda* sp., *Sargassum* sp.; 14) (Table 4). The majority of the colonies from ARs were recovered from the shipwreck (13), followed by buoys and chains (8) (Table 4).

Of the SA samples analyzed, 55% were colonized by 10 hydroid species, mainly *Aglaophenia latecarinata* Allman, 1877 (25% of the SA samples), followed by *O. dichotoma* (20% of the SA samples) (Tables 3, 4). Usually several species were found

Table 3. Relative abundance and frequency of the hydroid species in the different analyzed habitats on Alacranes Reef off Mexico (NR = natural reefs; AR = artificial reefs; SA = *Sargassum* sp. drifting algae; TT = *Thalassia testudinum*). Small circle = scarce (1–3 colonies); medium circle = moderately abundant (4–6 colonies), and large circle = abundant (>6 colonies). Empty circle = infertile colonies; full circle = fertile colonies. [(1)] For the hydrocorals it was not possible to determine the reproductive stage; * as a general substrate, all polyps were found on specific substrates within this group.

		AR*			
Species	NR	Buoys and chains	Shipwreck (Marisol)	SA	TT
Sphaerocoryne agassizii	○	–	–	–	–
Millepora alcicornis [(1)]	◯	○	○	–	–
Millepora complanata [(1)]	○	–	–	–	–
Pennaria disticha	⬤	○	–	–	–
Zanclea migottoi	–	–	–	•	–
Eudendrium capillare	•	–	–	–	–
Eudendrium carneum	•	•	○	–	–
Myrionema amboinense	●	–	–	–	–
Hydractinia sp.	●	–	–	–	–
Corydendrium parasiticum	●	○	–	–	–
Turritopsis dohrnii	○	–	–	–	–
Turritopsoides sp.	●	–	–	–	–
Stylaster roseus [(1)]	○	–	–	–	–
Hebella cf. *furax*	○	–	–	–	–
Hebella cf. *scandens*	–	–	–	•	–
Hebella cf. *venusta*	–	–	–	–	○
Hincksella cylindrica	○	–	–	–	–
Synthecium tubithecum	○	–	–	–	–
Halecium bermudense	●	•	–	–	–
Nemalecium lighti	●	○	–	–	–
Dynamena disticha	◯	–	○	–	⬤
Dynamena quadridentata	○	–	○	–	–
Sertularia loculosa	○	–	–	–	–
Sertularia distans	–	–	○	–	–
Sertularia marginata	–	–	–	•	•
Sertularia turbinata	–	–	○	–	–
Sertularella diaphana	•	–	–	–	–
Thyroscyphus marginatus	◯	–	–	–	–

Table 3. Continued.

Species	NR	AR*		SA	TT
		Buoys and chains	Shipwreck (Marisol)		
Aglaophenia latecarinata	○	–	–	◯	–
Antennella secundaria	●	–	○	–	–
Halopteris carinata	◯	–	–	–	–
Halopteris diaphana	–	–	•	–	–
Monostaechas quadridens	◯	–	–	–	–
Kirchenpaueria halecioides	–	–	–	–	○
Dentitheca dendrítica	◯	–	–	–	–
Monotheca margaretta	○	–	–	○	–
Plumularia floridana	◯	–	–	○	○
Plumularia setacea	◯	–	–	–	–
Plumularia strictocarpa	◯	–		○	–
Incertae sedis sp. 1	–	–	○	–	–
Lafoeina tenuis	–	–	○	–	–
Clytia cf. *gracilis*	•	–	–	–	○
Clytia hemisphaerica	–	–	○	•	•
Clytia cf. *hummelincki*	○	–	–	–	–
Clytia linearis	◯	–	–	–	–
Clytia paulensis	◯	–	–	–	–
Clytia sp.1	●	○	–	–	–
Clytia sp. 2	○	–	○	–	○
Obelia dichotoma	◯	•	◯	◯	–
Total	38	8	13	9	8

attached to the same drifting algal fragment, and only the colonies of *Zanclea migottoi* Galea, 2008, *Hebella* cf. *furax* Millard, 1957, and *Clytia hemisphaerica* (Linnaeus, 1767) possessed gonophores. Remarkably, *Z. migottoi* and *Hebella* cf. *scandens* (Bale, 1888) were found only on SA. Conversely, only 98 samples of *T. testudinum* supported epibionts; seven species of hydroids were found growing on part of the leaves or roots (Table 3), most corresponding to infertile and some fertile colonies of *Dynamena disticha* (Bosc, 1802) (approximately 50% on the leaves). *Hebella* cf. *venusta* (Allman, 1877) and *Kirchenpaueria halecioides* (Alder, 1859) were found exclusively on this marine spermatophyte. *Plumularia floridana* Nutting, 1900, and *C. hemisphaerica* were found together on the same leaf of sampled TT.

Table 4. Substrate types colonized by hydroid colonies on Alacranes Reef off Mexico. + present; – absent; * as a general substrate, all polyps were found on a specific substrate within this group.

Species	Algae	Seagrass	Sponges	Hydroids	Stony corals	Soft corals	Mollusks	Gastropod shell with hermit crabs	Ascidea	Rocks	Artificial reefs*	Total type of substrate
Sphaerocoryne agassizii	–	–	+	–	–	–	–	–	–	–	–	1
Millepora alcicornis (1)	–	–	–	–	+	+	–	–	–	–	+	3
Millepora complanata (1)	–	–	–	–	–	–	–	–	–	+	–	1
Pennaria disticha	–	–	+	–	+	+	+	–	+	+	+	7
Zanclea migottoi	+	–	–	–	–	–	–	–	–	–	–	1
Eudendrium capillare	+	–	–	–	–	–	–	–	–	–	–	1
Eudendrium carneum	–	–	+	–	+	+	+	–	+	+	+	7
Myrionema amboinense	+	–	+	–	+	–	–	–	–	+	–	4
Hydractinia sp.	–	–	–	–	–	–	+	+	–	–	–	2
Corydendrium parasiticum	–	–	+	–	+	+	+	–	+	–	+	6
Turritopsis dohrnii	–	–	–	–	–	–	–	–	+	–	–	1
Turritopsoides sp.	–	–	–	–	–	–	+	–	–	–	–	1
Stylaster roseus(1)	–	–	–	–	+	–	–	–	–	+	–	2
Hebella cf. *furax*	+	–	–	–	–	–	–	–	–	–	–	1
Hebella cf. *scandens*	+	–	–	–	–	–	–	–	–	–	–	1
Hebella cf. *venusta*	–	+	–	–	–	–	–	–	–	–	–	1
Hincksella cylindrica	–	–	+	–	–	–	–	–	–	–	–	1
Synthecium tubithecum	–	–	–	–	+	–	–	–	–	–	–	1
Halecium bermudense	–	–	+	–	+	+	–	–	–	–	–	3
Nenmalecium lighti	–	–	+	–	–	+	–	–	–	–	+	3
Dynamena disticha	+	+	–	–	+	+	–	–	–	+	+	6
Dynamena quadridentata	–	–	+	–	–	–	–	–	–	+	+	3
Sertularia loculosa	–	–	+	–	–	+	–	–	–	–	–	2
Sertularia distans	–	–	–	–	–	–	–	–	–	–	+	1
Sertularia marginata	+	+	–	–	–	–	–	–	–	–	–	2
Sertularia turbinata	–	–	–	–	–	–	–	–	–	–	+	1

Table 4. Continued.

Species	Algae	Seagrass	Sponges	Hydroids	Stony corals	Soft corals	Mollusks	Gastropod shell with hermit crabs	Ascidea	Rocks	Artificial reefs*	Total type of substrate
Sertularella diaphana	–	–	–	–	–	–	–	–	–	+	–	1
Thyroscyphus marginatus	–	–	+	–	+	+	+	–	–	+	–	5
Aglaophenia latecarinata	+	–	+	–	–	–	–	–	–	–	–	2
Antennella secundaria	+	–	+	–	–	–	–	–	+	–	+	4
Halopteris carinata	–	–	–	–	+	+	+	–	–	+	–	4
Halopteris diaphana	–	–	–	–	–	–	–	–	–	–	+	1
Monostaechas quadridens	–	–	+	–	+	+	–	–	–	+	–	4
Kirchenpaueria halecioides	–	+	–	–	–	–	–	–	–	–	–	1
Dentitheca dendrítica	–	–	–	–	–	+	–	–	–	–	–	1
Monotheca margaretta	+	–	–	–	–	+	–	–	–	–	–	2
Plumularia floridana	+	+	+	–	–	+	–	–	–	–	–	4
Plumularia setacea	–	–	–	+	+	+	+	–	–	–	–	4
Plumularia strictocarpa	+	–	+	–	–	+	–	–	–	+	–	4
Incertae sedis sp. 1	–	–	–	–	–	–	–	–	–	–	+	1
Lafoeina tenuis	–	–	–	–	–	–	–	–	–	–	+	1
Clytia cf. *gracilis*	–	+	+	–	–	–	–	–	–	–	–	2
Clytia hemisphaerica	+	+	–	–	–	–	–	–	–	–	+	3
Clytia cf. *hummelincki*	–	–	+	–	–	–	–	–	–	–	–	1
Clytia linearis	–	–	+	–	–	+	–	–	–	+	–	3
Clytia paulinensis	–	–	+	–	–	+	–	–	–	–	–	2
Clytia sp.1	–	–	+	–	–	–	–	–	–	–	+	2
Clytia sp. 2	–	–	+	–	+	–	–	–	–	–	+	3
Obelia dichotoma	+	–	+	+	–	+	–	–	+	+	+	7
Total of species	14	7	23	2	14	19	8	1	6	14	17	

Discussion

Knowledge of fauna inhabiting coral reefs is of utmost importance for monitoring and identifying non-native species, and for the success of conservation programs. There are few faunal studies in the south-central reefs of the GoM, and those that exist were based on a small number of taxa. In Alacranes Reef, there are comprehensive inventories of fish species richness (González-Gándara et al. 1999), but information on invertebrates is scarce. González et al. (1991) noted 49 bivalve and 114 gastropod species, and 3 species of sea anemones, 31 amphipods, three caridean shrimps, 6 shrimps, 37 heterobranch sea slugs, and 12 sponges (González-Muñoz et al. 2013, Paz-Ríos et al. 2013, Santana-Moreno et al. 2013, Duarte et al. 2014, Ortigosa 2015, Ugalde et al. 2015). Our data suggest that hydroids are one of the most diverse groups of sessile invertebrates in the area, and represent 23% (with 49 species) of the 214 hydroid species previously reported for the whole GoM (Calder and Cairns 2009).

Most of the species studied were previously reported from tropical and subtropical waters surrounding the GoM system (Calder and Cairns 2009, Jerónimo 2016). Leptothecata dominated the collections, representing 74% of the fauna (Fig. 2), similar to other studies from tropical areas (Calder and Kirkendale 2005, Gravier-Bonnet and Bourmaud 2006, Iglesias et al. 2011). The only species that occurred across nearly all studied habitats was *O. dichotoma*, a supposedly cosmopolitan hydrozoan found on a variety of natural and artificial substrates (Millard 1975, Ruiz et al. 2000, Gaonkar et al. 2010, Orejas et al. 2013, Fernandez et al. 2014); it is invasive in some regions (e.g., Australia; Wyatt et al. 2005). Low abundance or absence from certain habitats and/or substrates of some species is probably associated with seasonality and accumulation of species through time (Fernandez et al. 2014). Future studies are needed to examine in detail the role of biotic and abiotic variables and their seasonality with respect to the hydroid fauna of the region.

We were unable to identify some specimens to species level using morphology or molecular data, because we did not find close sequence matches in GenBank. Validation of species identification based on genetic taxonomy is restricted by the limited number of published sources of genetic sequences (Laakmann and Holst 2014). Therefore, it is necessary to gather more information about morphological and molecular genetic taxonomy, particularly for Mexican hydroids.

It has been widely recognized that "Anthoathecata" is usually found in the planktonic stage, while Leptothecata is more commonly recorded in the benthic stage. In the southern GoM, 86 species of hydromedusae have been identified (Segura-Puertas et al. 2003, 2009, Loman-Ramos et al. 2007, Mendoza-Becerril et al. 2009, Martell-Hernández et al. 2014), of which 55% are "Anthoathecata" (with metagenetic life cycles). Thirty-seven benthic hydroid species have been reported from the southern GoM (Jerónimo 2016); of these, 57% are Leptothecata, which mostly consists of species with only a benthic stage. The Mediterranean Sea supports the best known biodiversity of hydrozoans globally: Gravili et al. (2013) reported approximately 58 species of "Anthoathecata" and 112 species of Leptothecata. It still is unclear why so many anthoathecates are represented by only their medusa stages in GoM and other areas, but it may be related to the fact that many athecate polyps are unknown, rare, fragile, miniscule, cryptic, short-lived, and display pronounced seasonality (Genzano et al. 2009). Bias resulting from the paucity of hydroid studies and the different methodologies used to collect the medusa and polyp stages might also explain the lack of

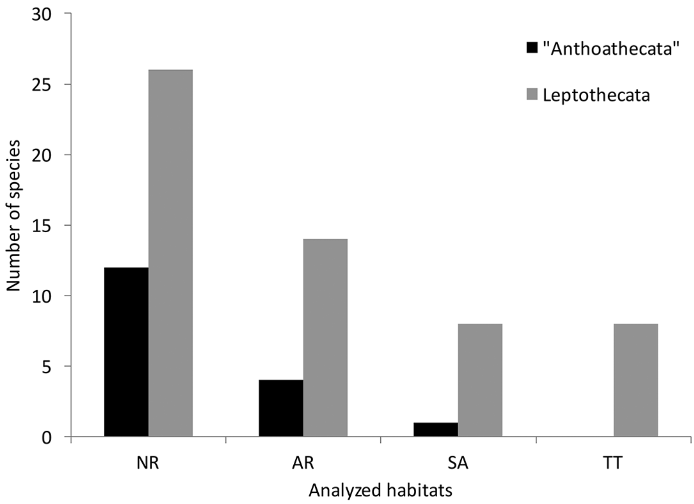

Figure 2. Number of hydroid species in the different analyzed habitats (NR = natural reefs, AR = artificial reefs, SA = *Sargassum* spp. drifting algae, TT = *Thalassia testudinum*).

knowledge about many anthoathecate polyp species. In coral reefs, the benthic colonies are usually directly collected by snorkeling and scuba diving; therefore, their collection depends on the number and expertise of the sampling researchers in the field. By contrast, medusae are collected by nets that can cover a larger sampling area in less time, and they can be collected by non-experts.

Through extensive sampling of diverse substrates, we were able to better characterize species richness of the Alacranes Reef (Tables 3, 4). A wide range of structural features can affect the settlement and growth forms of benthic invertebrates (e.g., spatial orientation, structural complexity, composition, and substrate texture) (Moura et al. 2006, Perkol-Finkel et al. 2006, Thanner et al. 2006, Genzano et al. 2011, Buss et al. 2016), and the substrates can impact species composition, diversity, abundance, and distribution of these benthic organisms (Calder 1991). The ARs offer a high degree of structural and spatial complexity, habitat heterogeneity, and varied niche sizes, providing substrates at several vertical levels where currents provide a consistent supply of food, and sedimentation is reduced (Genzano et al. 2011). They also act as shelter and feeding grounds for different marine species (Krohling et al. 2006, Israel et al. 2016). Benthic hydroids are considered particularly well-adapted to a diversity of such artificial structures, including ship hulls and buoys (Kirkendale and Calder 2003, Farrapeira et al. 2011).

Many of the hydroids species collected were non-specific epibionts (Table 4). The substrate-specific or general distribution of settled hydroid species may relate to selection by the planula larvae (cf. Calder 1991) and/or abiotic conditions. In variable environments, hydroids tend to be predominantly substrate generalists (Calder 1976, Gili et al. 1989). For example, many hydroid species use sponges as a substrate (Boero and Fresi 1986, Puce et al. 2005). Gorgonian colonies act as substrate-multiplier species by generating habitats for diverse hydroid colonies (Schuchert 2001, Gili et al. 2006, Puce et al. 2008). Spermatophyte meadows are commonly used as substrates by hydroids (e.g., Boero 1981, Lewis and Hollingworth 1982, Hughes et al. 1991, García 1992), such as the fertile and abundant *D. disticha* reported by Calder (1991) on the same seagrass species as the present study, and by Boero (1981) on *Posidonia oceanica* (Linnaeus) Delile.

Other hydrozoans have been reported on various floating substrata, including macroalgae. Calder (1995) found 10 species on the thalli of holopelagic *Sargassum* spp., and Morris and Mogelberg (1973) considered hydroids as diverse and common taxa on floating *Sargassum.* On SA, *Clytia* and *Aglaophenia* were well represented genera in our study, and Smith et al. (1973) considered them among the numerically and functionally most important animals on drifting *Sargassum*.

Habitat specificity in hydroids is less common. For example, hydractiniids are usually epibionts on gastropod shells occupied either by hermit crabs or other animals (Mills 1976, Schuchert 2008), though some species grow on algae or rocks (Miglietta et al. 2009). Polyps of *Turritopsoides,* on the other hand, were described on *T. testudinum* (Calder 1988), but we found this polyp only on gastropod shells. We also observed some hydroids growing on the perisarc of other hydroids (Table 4), a common association in some Leptothecata (Puce et al. 2008). Further analyses are needed to clarify and describe the roles of both partners involved in all epibiotic associations.

The results of the present study increase our general knowledge of benthic hydroid diversity on NRs, ARs, SA, and TT of the coral reef region in the GoM. It is necessary to increase taxonomic and ecological studies in neighboring areas as well, because the hydroid fauna of the region remains largely unknown. It is also important to increase research into both stages of the life cycle (polyp and medusa), which are often sampled using different techniques. A large geographic coverage is recommended for the medusa stages to gauge non-indigenous species distributions (Cangussu et al. 2010, Marques et al. 2013). Future hydroid studies of Alacranes Reef are necessary for the development of new management policies and conservation strategies, as the first plan for the area was designed more than two decades ago (Ardisson et al. 1996).

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