Associations between hydroid species assemblages and substrate types in the mangal at Twin Cays, Belize

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Received October 31, 1990

CALDER, D. R. 1991. Associations between hydroid species assemblages and substrate types in the mangal at Twin Cays, Belize. Can. J. Zool. **69**: 2067–2074.

Hydroid species composition on various substrates in a mangrove ecosystem was investigated during the winter of 1987 at Twin Cays, Belize, Central America. Soft sediments, on which hydroids were either depauperate (peat) or not observed at all (silt, sand, mud), predominated in the study area. However, firm substrates, including submerged prop roots of red mangrove (*Rhizophora mangle*), turtle grass (*Thalassia testudinum*), benthic algae (Chlorophyta and Rhodophyta), floating algae (*Turbinaria turbinata* and *Sargassum fluitans*), epibenthic invertebrates (especially sponges, hydroids, molluscs, and crustaceans), wood, and rope, supported a moderately diverse hydroid fauna (48 species). More hydroid species (22) were found on mangrove prop roots than on any other substrate. Six substrate groups and 11 species groups were recognized in numerical analyses of hydroid–substrate frequency data. Constancy of species groups for substrate groups was mostly low or very low, reflecting the low frequency of occurrence of most hydroid species in collections from Twin Cays. Fidelity of some species groups for certain substrate groups was high, especially for those groups occurring on drifting algae and rope. Although most hydroid species were relatively facultative with respect to substrate, bottom type was an important factor influencing their distributions.

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En 1987, la composition spécifique des hydroïdes a été étudiée sur différents substrats dans une mangrove, à Twin Cays, dans le Belize, en Amérique centrale. Les sédiments mous, dans lesquels ont trouve peu d'hydroïdes (tourbe), ou d'où ils sont complètement absents (limon, sable, boue), prédominent dans la région étudiée. Cependant, les substrats fermes, notamment les racines-échasses submergées du manglier *Rhizophora mangle*, les hydrocharitacées *Thalassia testudinum*, les algues benthiques (Chlorophytes et Rhodophytes), les algues flottantes *Turbinaria turbinata* et *Sargassum fluitans*, les invertébrés suprabenthiques (notamment des éponges, des hydroïdes, des mollusques et des crustacés), le bois et les cordages supportent une faune moyennement diversifiée d'hydroïdes (48 espèces). C'est sur les racines-échasses plus que sur tout autre substrat qu'a été trouvé le plus grand nombre d'espèces d'hydroïdes (22). Six groupes de substrats et 11 groupes d'espèces ont été reconnus au cours d'analyses numériques des données de fréquence d'hydroïdes sur les divers substrats. Les affinités entre les groupes d'espèces et les groupes de substrate étaient peu ou très peu constantes, ce qui reflète la fréquence plutôt faible de la plupart des especes d'hydroïdes dans les récoltes de Twin Cays. La fidélité de certains groupes d'espèces à certains groupes de substrats était élevée, particulièrement celle des groupes qui se tiennent dans les algues flottantes ou les cordages. Bien que la plupart des espèces d'hydroïdes se soient avérées peu sélectives dans le choix de leur substrat, le type de fond constitue un facteur déterminant de leur répartition.

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Introduction

The nature of the substratum significantly influences species composition, diversity, abundance, and distribution of benthic organisms, including hydroids. With the possible exception of certain habitats in deep waters (Pérès 1982; Gili *et al.* 1989), hydroids are generally more diverse and abundant on firm or hard substrata, such as aquatic vegetation, invertebrate exoskeletons, and rocks, than on unconsolidated sand, mud, or clay. Although some species of Hydroida exhibit marked substrate selectivity (e.g., see Picard 1952; Dales 1957; Nishihira 1965; Rees 1967; Millard 1973, 1975), a majority appear to be substrate generalists.

Accumulated soft sediments usually predominate in mangrove swamps, occurring in sheltered coastal areas of the tropics and subtropics. Such substrata are unfavourable for most hydroids, and the group has seldom been mentioned as a significant component of the mangal biota (see Macnae 1968; Rützler 1969; Por and Dor 1984; Sasekumar 1984; Price *et al.* 1987). Moreover, mangrove habitats in many parts of the world are exposed at low tide, and few hydrozoan species tolerate extended exposure to air. Furthermore, reduced or widely fluctuating salinities within estuarine mangrove systems may limit hydroid diversity.

In addition to arboreal and intertidal mangal habitats, permanently subtidal environments frequently occur within creeks and channels of high-salinity mangrove systems in the western Atlantic (Rützler 1969; Rützler and Feller 1987). Substrates including mangrove prop roots and attached and motile biota, as well as grass beds and mats of macroalgae, exist in relative abundance within these subtidal areas. In the euhaline Caribbean mangal at Twin Cays, Belize, hydroids were abundant and diverse subtidally in areas exposed to wave action or tidal water motion (Calder 1991*b*). The hydroid fauna was depauperate in still-water areas, even where suitable subtidal substrates were available. The only common hydroid species in the intertidal zone at Twin Cays was the thecate *Dynamena crisioides* (Calder 1991*c*).

The objective of this study was to characterize some associations between hydroid species and their substrates in the mangal at Twin Cays, Belize.

TABLE 1. The hydroids and their frequencies of occurrence on major substrates in the mangal at Twin Cays, January–February 1987

	Rm	Th	ST	Ba	Sp	Hy	Mo	OI	MS	WP
Athecates										
Turritopsis fascicularis	1	.	.	.	.	.	.	.	.	.
Turritopsis nutricula	6	1	.	1	4	.	.	1	.	.
Turritopsoides brehmeri	.	1	.	.	1	.	.	.	.	.
Millardiana longitentaculata	2	.	.	.	.	.	1	.	.	.
Pachycordyle napolitana	.	.	.	.	.	.	.	1	.	.
Bougainvillia sp.	.	.	.	.	.	.	.	1	.	.
Stylactaria arge	.	.	.	.	.	.	.	2	.	.
Amphinema sp.	.	1	.	.	.	.	.	.	.	1
Leuckartiara sp.	.	.	.	.	.	.	.	2	.	.
Eudendrium bermudense	4	.	.	.	.	.	.	.	.	4
Myrionema amboinense	10	1	.	1	.	.	.	.	.	.
Zyzzyzus warreni	.	.	.	.	2	.	.	.	.	.
Sphaerocoryne bedoti	.	.	.	.	3	.	.	.	.	.
Coryne sargassicola	.	.	1	.	.	.	.	.	.	.
Cladonema radiatum	.	1	.	1	.	.	.	.	1	4
Zanclea alba	.	.	5	.	.	.	.	.	1	.
Millepora alcicornis	6	.	.	.	.	.	.	.	2	.
Millepora complanata	4	.	.	.	.	.	.	.	1	.
Thecates										
Halecium nanum	.	2	1	2	.	.	.	.	.	.
Halecium tenellum	2	.	.	.	.	.	.	.	.	1
Halecium sp. (n.sp.)	.	.	1	.	.	.	.	.	.	.
Nemalecium lighti	24	11	.	1	2	.	4	.	1	6
Phialella sp.	.	.	.	.	.	1	1	.	1	.
Eirene sp.	.	.	.	1	.	.	.	.	.	.
Lafoeina amirantensis	.	.	.	.	.	.	.	.	.	1
Aequorea sp.	.	.	.	.	.	.	.	1	.	.
Orthopyxis sargassicola	.	.	1	.	.	.	.	.	.	.
Clytia hemisphaerica	4	4	2	6	1	2	2	2	.	6
Clytia latitheca	1	.	.	.	1	.	.	.	.	.
Clytia linearis	4	.	.	1	.	1	.	1	1	3
Clytia macrotheca	2	.	.	.	.	.	.	1	1	4
Clytia noliformis	.	.	4	.	.	.	.	.	1	.
Clytia paulensis	.	.	1	.	.	.	1	.	.	.
Obelia bidentata	3	.	.	1	.	2	.	1	1	.
Obelia dichotoma	5	2	4	2	.	3	2	.	3	6
Symmetroscyphus intermedius	.	5	1	.	.	.	.	.	.	.
Dynamena crisioides	21	.	.	.	.	.	3	.	.	.
Dynamena disticha	.	8	2	1	.	.	.	.	1	.
Sertularella peculiaris	.	.	1	.	.	.	.	.	.	.
Tridentata distans	4	1	.	.	.	.	.	1	.	.
Tridentata marginata	1	1	.	.	.	.	.	.	.	.
Tridentata turbinata	7	.	.	2	1	.	.	1	1	.
Antennella secundaria	3	.	.	.	.	.	.	.	.	1
Halopteris diaphana	9	2	4	1	1	.	1	.	.	.
Ventromma halecioides	22	.	1	1	.	1	3	.	.	3
Monotheca margaretta	.	.	1	.	.	.	.	.	.	.
Plumularia strictocarpa	.	.	3	.	.	.	.	.	.	.
Aglaophenia latecarinata	.	.	2	.	.	.	.	.	.	.
Total number of records	145	41	35	22	16	10	18	15	16	40
Total number of species	22	14	17	14	9	6	9	12	13	12

NOTE: Substrate abbreviations: Rm, *Rhizophora mangle*; Th, *Thalassia testudinum*; ST, floating *Sargassum* and *Turbinaria*; Ba, benthic algae; Sp, sponges; Hy, hydroids; Mo, molluscs, OI, other invertebrates (decapods, polychaetes, bryozoans, echinoderms, ascidians); MS, miscellaneous substrates (wood, peat, rope); WP, wooden test panels.

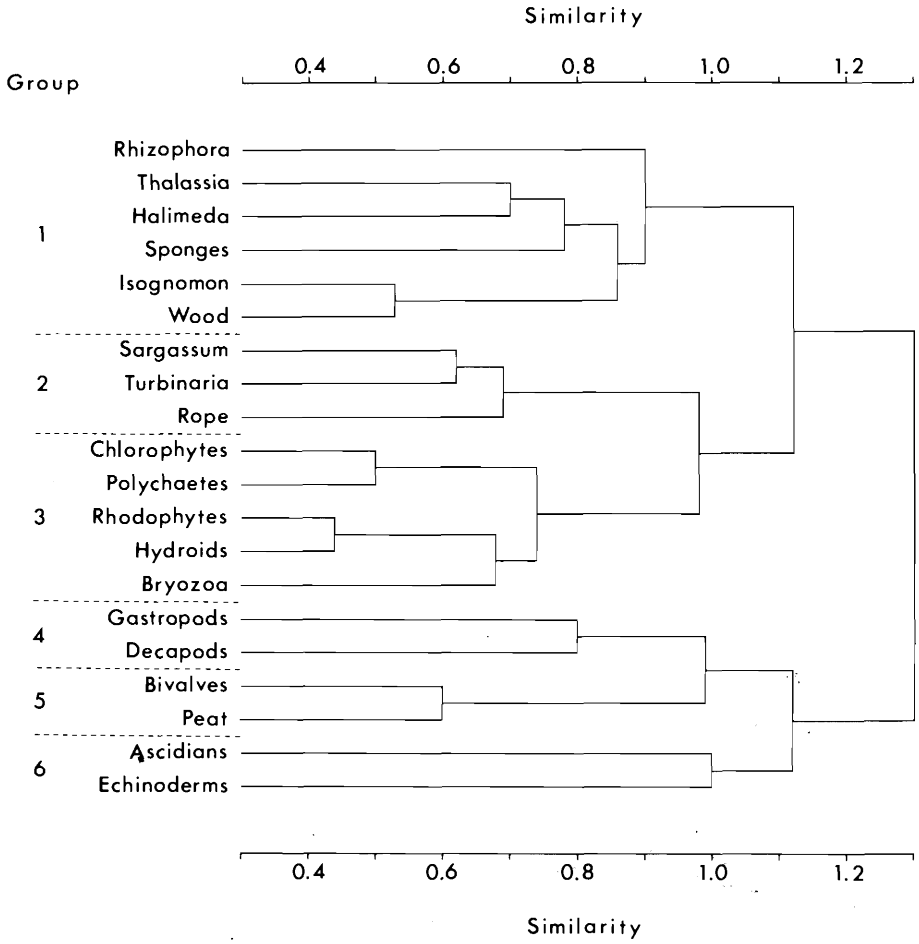

FIG. 1. Substrate groupings in a normal cluster analysis of hydroid–substrate frequency data from Twin Cays.

Materials and methods

Hydroids were collected in the mangrove system at Twin Cays, Belize (Calder 1991*b*), between 29 January and 22 February 1987. Thirty-nine qualitative collections were made along the shoreline of Twin Cays, including its bays, channels, creeks, and surrounding seagrass beds (within 100 m of shore). Data on substrate type were recorded for each species. Predominant firm substrates included red mangrove (*Rhizophora mangle*) prop roots and attached biota (especially macroalgae and sessile invertebrates), as well as beds of turtle grass (*Thalassia testudinum*) and mats of the chlorophyte *Halimeda incrassata*. Hydroids were collected from clumps of Sargassaceae (*Sargassum fluitans* and *Turbinaria turbinata*) drifting within the mangrove system and from wooden test panels immersed in Cuda Cut at depths of 0.1, 0.5, 1.0, 1.5, 2.0, and 2.5 m between 29 January and 19 February 1987. Other substrata for hydroids in the mangal included exoskeletons of motile invertebrates, as well as rope, wood, and peat.

Normal (substrate group) and inverse (species group) cluster analyses were performed on species–substrate frequency data using the program SAHN (Rohlf 1988). Clustering was undertaken using the Bray–Curtis coefficient of similarity, flexible sorting, and a beta value of −0.25. Nodal analyses (Boesch 1977) measuring the coincidence of species groups and substrate groups were undertaken for constancy (the frequency with which a given species group is associated with a particular substrate group) and fidelity (the degree to which a species group is restricted to a substrate group). Principal components analysis was computed on the data using the program PRINCOMP and employing a correlation matrix of variables (Podani 1988).

Results

Sediments in and adjacent to the Twin Cays mangal consisted almost entirely of silt, mud, sand, or peat. Of these substrates, hydroids were found only on peat (Table 1). Nevertheless, firm substrates were widespread and supported a moderately diverse hydroid fauna (48 species). The only hard bottoms in the study area were a few small scleractinian coral patches occurring around the periphery of the islands, but no hydroids were found on these patches other than *Eirene* sp.

Some associations between hydroid species collected during the study and their substrates are apparent in a species–substrate frequency analysis (Table 1). Nine species (*Turritopsis nutricula, Nemalecium lighti, Clytia hemisphaerica, Clytia linearis, Obelia bidentata, Obelia dichotoma, Tridentata turbinata, Halopteris diaphana,* and *Ventromma halecioides*) were recorded from half or more of the 10 major substrate categories. The substrate with the largest number of both athecate and thecate hydroid species, and by far the most individual records (145), was prop roots of *Rhizophora.* Hydroids were also prevalent, and taxonomically varied, on leaves of *Thalassia* and on floating thalli of *Turbinaria* and *Sargassum.* Nearly two-thirds of the 48 species were found on two or more substrate types.

Six major substrate groups for hydroids were recognized in a normal cluster analysis (Fig. 1) of hydroid–substrate frequency data. Substrate group 1 was made up of a heterogeneous

TABLE 2. Species groups recognized in an inverse numerical analysis

Group A
Turritopsis fascicularis
Clytia latitheca
Tridentata marginata

Group B
Millardiana longitentaculata
Halecium tenellum
Clytia macrotheca
Eudendrium bermudense
Millepora complanata
Antennella secundaria
Millepora alcicornis
Tridentata distans
Clytia linearis
Obelia bidentata

Group C
Turritopsis nutricula
Myrionema amboinense
Tridentata turbinata
Halopteris diaphana
Clytia hemisphaerica
Obelia dichotoma
Nemalecium lighti
Dynamena crisioides
Ventromma halecioides

Group D
Turritopsoides brehmeri
Zyzzyzus warreni
Sphaerocoryne bedoti

Group E
Amphinema dinema
Lafoeina amirantensis
Phialella sp.

Group F
Eirene sp.

Group G
Cladonema radiatum
Halecium nanum
Symmetroscyphus intermedius
Dynamena disticha

Group H
Pachycordyle napolitana
Bougainvillia sp.

Group I
Stylactaria arge
Aequorea sp.
Leuckartiara sp.
Clytia paulensis

Group J
Coryne sargassicola
Halecium sp. (n.sp.)
Sertularella peculiaris
Monotheca margaretta

Group K
Zanclea alba
Clytia noliformis
Orthopyxis sargassicola
Plumularia strictocarpa
Aglaophenia latecarinata

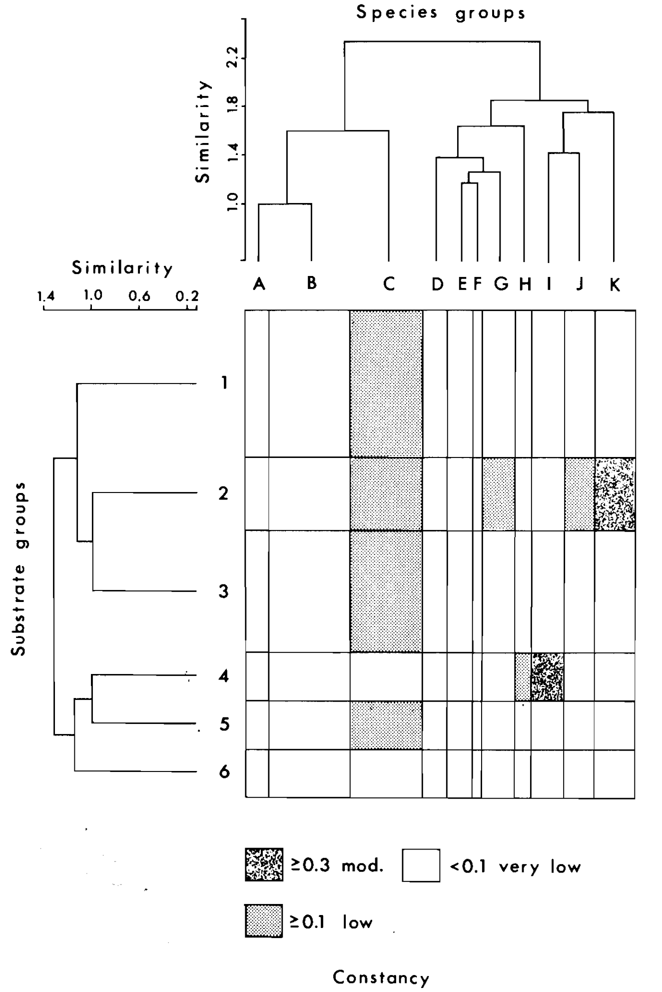

FIG. 2. Nodal diagram for constancy, associating 11 hydroid species groups with six major substrate groups at Twin Cays.

assemblage of substrates. Prop roots of *Rhizophora* were classified together with others in this group, including *Thalassia*, although similarity of *Rhizophora* to the other five substrates faunistically was quite low. Substrate group 2 included floating substrates allochthonous to the mangal (pelagic *Sargassum*, detached *Turbinaria*, and drifting rope found tangled in mangroves along the shore). Substrate group 3 comprised epibenthic algae and sessile invertebrates. The remaining three groups were dissimilar to the others. Each of these groups contained two major substrate types, with gastropod and decapod exoskeletons in substrate group 4, bivalves (other than *Isognomon*) and peat in substrate group 5, and ascidian tests and echinoderm spines in substrate group 6.

Eleven species groups were distinguished in an inverse cluster analysis (Table 2). Those in species groups A, B, and C occurred partly or entirely on prop roots of *Rhizophora.* Species in group A were found only once or twice in the samples, those in group B were more frequent and occurred predominantly on *Rhizophora*, and those in group C were abundant substrate generalists at Twin Cays. The remaining eight species groups included hydroids that were recorded on substrates other than mangroves. Species group D included three species linked by their occurrences on sponges, whereas those of species group E shared occurrences on wood (including pilings and wooden test panels). Species group F included only *Eirene* sp., collected on coralline algae encrusting a small coral patch west of the West Island. A primary substrate for hydroids in species group G was *Thalassia*. The two hydroids in species group H were found only on the crab *Mithrax* sp., and those in species group I shared occurrences on shells of gastropods. Species group J comprised four hydroid species found only on floating *Turbinaria*, and those in species group K were found either on pelagic *Sargassum*, on floating *Turbinaria*, or on discarded and drifting rope tangled among mangrove prop roots.

Constancy of most species groups was low or very low for most substrate groups (Fig. 2), largely because of the low overall frequency of occurrence of most hydroid species at Twin Cays. The highest constancy value (0.38) was for species group K on substrate group 2, reflecting the moderate frequency of this species assemblage on floating *Sargassum, Turbinaria*, and rope.

The degree to which some species groups were restricted to certain substrate groups in collections from Twin Cays was high in several instances (Fig. 3). As expected, fidelity of species groups G, J, and K for floating substrates (substrate group 2) was high. Similarly, species groups H and I were largely or entirely restricted to gatropods or crabs (substrate group 4) in the collections. Species group D comprised species most prevalent on sponges, a component of substrate group 1. Other high values of fidelity may have been due, at least in part, to the low frequency with which constituent species were present in the collections.

Results from principal components analysis (Fig. 4) reflected

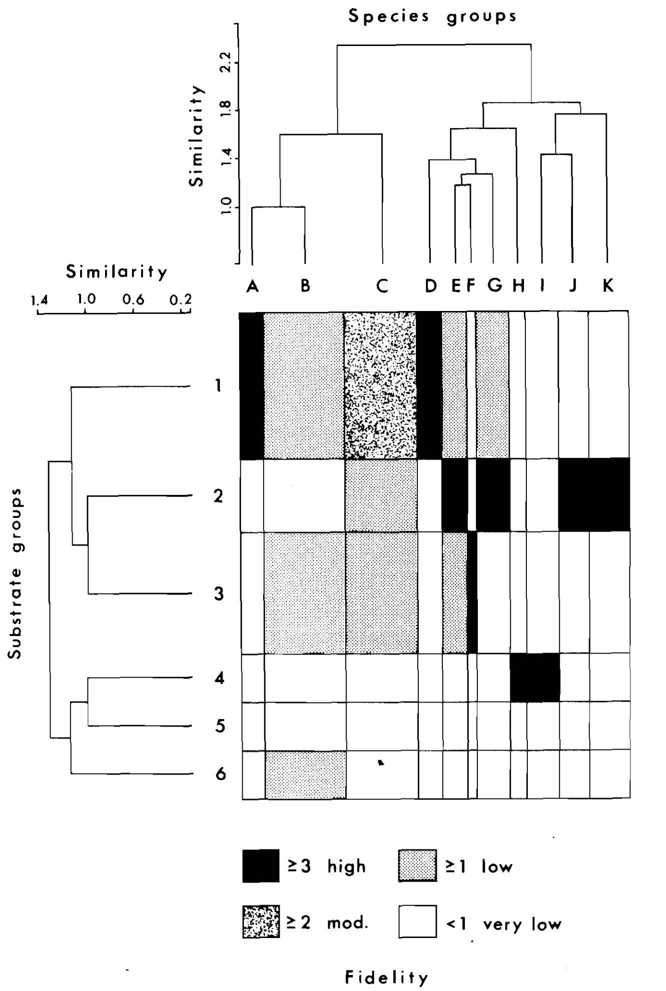

FIG. 3. Nodal diagram for fidelity, associating 11 hydroid species groups with six major substrate groups at Twin Cays.

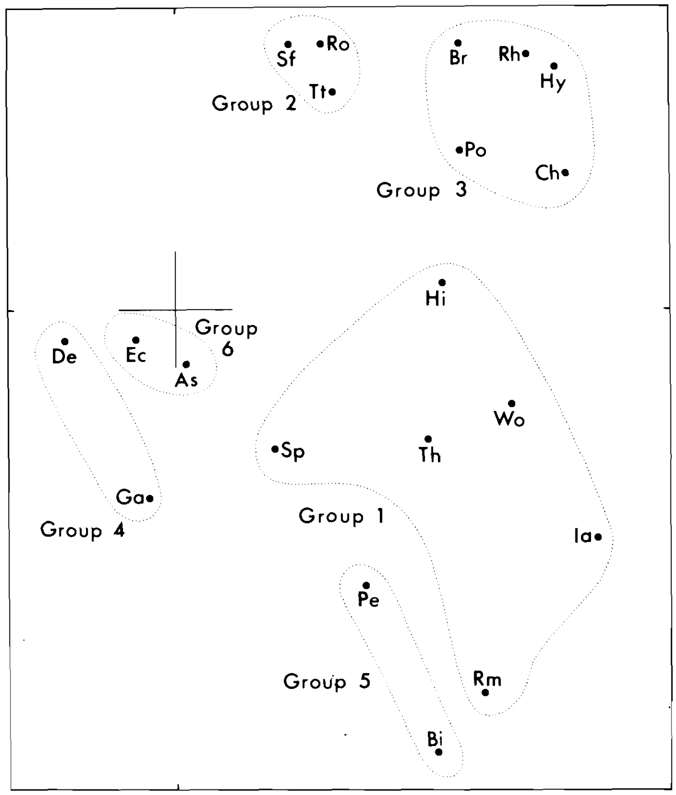

FIG. 4. Principal components analysis of 20 hydroid substrates at Twin Cays. Dotted lines enclose constituents of substrate groups 1–6 as defined by cluster analysis. Sf, *Sargassum fluitans*; Ro, rope; Tt, *Turbinaria turbinata*; Br, Bryozoa; Rh, rhodophytes; Hy, hydroids; Po, polychaete tubes; Ch, chlorophytes; De, decapods; Ga, gastropods; Ec, echinoderm spines; As, ascidians; Hi, *Halimeda incrassata*; Wo, wood; Sp, sponges; Th, *Thalassia testudinum*; Ia, *Isognomon alatus*; Rm, *Rhizophora mangle*; Pe, peat; Bi, bivalves.

the general distinctness of the six substrate groups as classified in the cluster analysis. The relatively high internal similarity of substrate groups 2 and 3, and the similarity of those two groups to each other, is reflected in this analysis. Conversely, the general dissimilarity of constituents within substrate group 1, especially between *Rhizophora* and other substrates, is also apparent. Algal substrates, together with hydroids, bryozoans, tubes of polychaetes, and floating rope (groups 2 and 3), were located on the upper right quadrant of the diagram, whereas motile invertebrates (group 4) were on the lower left. Such separation reflected the major differences in hydroid species composition between these groups of substrates. *Rhizophora* and other substrates in group 1 (except *Halimeda*) were scattered over the lower right quadrant, together with peat and miscellaneous bivalves (group 5) and ascidians (part of group 6).

Discussion

The occurrence and distribution of hydroids are influenced by a complex of biotic and abiotic factors and by stochastic events (Calder 1991*b*). Emphasis here is on associations between hydroid species assemblages and substrate types in the mangal at Twin Cays.

Some invertebrate larvae are highly selective in the substrata upon which they settle and metamorphose (Williams 1964; Meadows and Campbell 1972; Chia and Rice 1978; Maki *et al.* 1990). Among Hydrozoa, substrate selection by planula larvae has been investigated by a number of researchers (e.g., see Williams 1965; Campbell 1968; Nishihira 1973; Chia and Bickell 1978; Yund and Parker 1989). Well-known hydrozoan substrate specialists include species of *Proboscidactyla*, found only on tubes of sabellid polychaetes (Hand 1954), *Eugymnanthea*, occurring in the mantle cavity of bivalve molluscs (Rees 1967; Kubota 1987), and *Hydractinia*, most frequently found on gastropod shells inhabited by pagurid crabs (Rees 1967; Yund *et al.* 1987). Several species of hydroids in the Mediterranean Sea are obligate epiphytes of the phanerogam *Posidonia oceanica* (Picard 1952; Boero 1981, 1987; Garcia 1987; Roca 1987). Hydroid assemblages on *Sargassum natans* and *S. fluitans* in the western North Atlantic (Hentschel 1922; Winge 1923; M. D. Burkenroad, in Parr 1939; Weis 1968; Morris and Mogelberg 1973; Ryland 1974; Calder 1988*a*, 1991*a*) appear distinctive, but few of the species are restricted to Sargassaceae. Elements of this fauna, part of the "displaced benthos" on pelagic gulfweed (Hedgpeth 1957), were present in this study at Twin Cays on floating *Sargassum* and *Turbinaria*. Collections from Twin Cays were inadequate to establish whether any species from the study area was actually substrate specific.

Nishihira (1965, 1973) conducted studies on hydroids and their algal substrates near Asamushi, Japan. He found hydroid abundance and diversity to be greatest on Phaeophyta (especially on Sargassaceae), least on Chlorophyta, and intermediate on

Rhodophyta. A similar pattern was observed at Twin Cays, with 17 species of hydroids colonizing Phaeophyta (Sargassaceae), 6 on Rhodophyta, and 5 on Chlorophyta. Shepherd and Watson (1970) reported that rhodophytes seemed more favourable than phaeophytes as a hydroid substrate at West Island, South Australia, and that no hydroids were found at all on chlorophytes. Differences in the suitability of algal substrates have been attributed to factors such as algal growth form, nature of the algal surface, the life-span and persistence of the alga, the presence of chemical substances produced by the algae, and the extent of bacterial and other periphyton development (Nishihira 1973). The differing vertical zonation patterns typical of green, red, and brown algae may also be important.

In physically variable environments, hydroids tend to be predominantly substrate generalist, opportunistic (*r* strategist) species (Wedler 1975; Calder 1976; Gili *et al.* 1989). Predictably, most hydroid species within the shallow and physically stressed (Rützler and Feller 1987) mangal at Twin Cays were nonspecific as to substrate. Moreover, 25% of the 48 hydroid species found in the system colonized wooden test panels exposed at Cuda Cut for 3 weeks, reflecting the rapid recruitment and early exploitation of available substrate space typical of opportunists.

Shallow-water hydroids may rapidly colonize new substrata, often forming dense monospecific assemblages, but in general they are inefficient space competitors (Gili *et al.* 1989). Many seem relegated to spatial refuges, in congruity with predictions based on the growth form of their colonies (Jackson 1979). Some species limit successful settlement of larvae of potential competitors, at least temporarily. For example, experiments by Standing (1976) indicated that *O. dichotoma* may inhibit settlement of barnacle larvae (*Balanus crenatus*) on experimental panels. One noteworthy exception to the pattern of opportunism in shallow-water hydroids is the encrusting athecate *Hydractinia echinata*, which exhibits slow rates of recruitment but is highly resistant to replacement (Sutherland and Karlson 1977).

Although generally ineffective as competitors, Boesch (1976) indicated that opportunistic species of both the high rocky intertidal zone and the low-salinity upper estuary were resistant to the stresses inherent in their particular environments and possessed attributes enhancing repopulation following perturbations. The potential for rapid recovery from natural perturbations, such as mortalities from desiccation during extremely low tides, seems likely to be high for some opportunistic hydroid species at Twin Cays. Populations of the intertidal and shallow subtidal thecate *Dynamena crisioides* either survived or rapidly recovered from an abnormally low tide in June 1983 that resulted in mass mortalities of shallow subtidal epibenthos (see Rützler and Feller 1987). *Dynamena crisioides* was abundant at Twin Cays on mangrove roots before (Spracklin 1982) and after (Calder 1991*b*) that event, and the species seems especially persistent. By comparison, the community structure of subtidal hydroid assemblages following disturbance is likely subject to a greater degree of unpredictability, if results from temperate and subtropical fouling communities apply (Sutherland and Karlson 1977). In any case, the entire mangrove ecosystem, including hydroids, is vulnerable to disturbance from human activity. The mangal, occurring in intertidal and shallow subtidal waters, seems particularly susceptible to damage from petroleum spills (Rützler and Feller 1987).

At Twin Cays, hydroids were heterogeneously distributed on a given substrate (Calder 1991*b*). They were typically diverse and well represented on mangrove roots in areas exposed to wave action or water currents. By contrast, hydroid diversity and abundance were both very low on that substrate in quiet-water areas. Moreover, hydroid species composition and relative abundances changed with water depth even over a vertical distance of only 0.5 m. So, although substratum has been emphasized in this study as a major factor in the distribution of hydroids within the mangal, other vectorial, biological, and stochastic factors (Seed and O'Connor 1981) are nonetheless important.

Among species that are obligate associates of the seagrass *P. oceanica* in the Mediterranean, those with fixed gonophores predominate, and reproduction by stolonization is prevalent (Philbert 1935; Picard 1952; Boero 1987). On phanerogams at Tulear, Madagascar, numbers of species with fixed gonophores and free medusae were nearly equal (Gravier 1970). At Twin Cays, 23 of the hydroid species are believed to produce fixed gonophores, and 25 liberate either "normal" or ephemeral medusae. Of the 13 species occurring facultatively on turtle grass (*T. testudinum*) in this study, 9 have fixed gonophores.

Are there hydroid species from Twin Cays that are endemic to mangrove systems? Just as substrate generalists predominate among local hydroids, these species appear to be relatively facultative with regard to habitat or ecological system as well. Most of the 48 species identified here have been reported elsewhere in tropical and subtropical waters of the western Atlantic (e.g., see Vervoort 1968; Spracklin 1982; Wedler and Larson 1986; Calder 1988*a*, 1991*a*). *Dynamena crisioides* is restricted to intertidal and shallow subtidal zones (Calder 1991*c*), but it occurs on a variety of substrates and in a number of different tropical marine habitats (Calder 1991*a*). *Turritopsoides brehmeri* is currently known only from Twin Cays (Calder 1988*b*, 1991*b*), but its occurrence on *Thalassia* and sponges suggests that it may colonize such substrates outside the mangal. Most if not all of the hydroids at Twin Cays appear to be species associated with a variety of shallow-water tropical marine environments, including mangrove swamps.

Acknowledgments

I thank Dr. Robert Anderson, Dr. Maria Faust, Dr. Klaus Rützler, Robert Stephens, Joseph Rosso, and Frank Ferrari for assistance in the field. I am indebted to Dr. David Barr for assistance with numerical analyses of data. The constructive comments of Dr. R. J. Larson and an anonymous reviewer improved the manuscript. Financial assistance for this study was provided by the Caribbean Coral Reef Ecosystems Program, partly supported by the EXXON Corporation, through its principal investigator, Dr. Klaus Rützler. This is Contribution No. 316 from the Caribbean Coral Reef Ecosystems (CCRE) Program, Smithsonian Institution.

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