Vertical zonation of the hydroid *Dynamena crisioides* (Hydrozoa, Sertulariidae) in a mangrove ecosystem at Twin Cays, Belize

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Received October 1, 1990


*Dynamena crisioides* is generally restricted to lower intertidal and shallow subtidal habitats along tropical and subtropical coasts. The hydroid was abundant during this study on prop roots of red mangroves (*Rhizophora mangle*) at Twin Cays, Belize, where it ranged vertically from 1.1 m below mean tide level (MTL) to 2–3 cm above MTL. The estimated percentage cover of the hydroid was maximal in the lower half of the intertidal zone (MTL and 0.1 m below MTL) and declined rapidly above and below that level. Colony height and number of branches per colony were also consistently highest in hydroids from the lower half of the intertidal zone. The percentage of colonies with gonophores was lowest at the lower and upper vertical limits of the species. Field observations and transplantation experiments suggest that the lower limits of *D. crisioides* are established by competition for space (with algae, sponges, and ascidians), smothering (by algae, sponges, ascidians, and other hydroids), and predation (by fishes). Desiccation was considered the prime factor determining the upper limits of the hydroid. Colonies transplanted to the supratidal zone were in good condition after 48 h, alive but in poor condition after 48 h, and dead after 72 and 96 h of exposure.

Introduction

Hydroids are an important faunal component of infralittoral and benthic marine epibenthos, but relatively few live as a typical part of the intertidal biota. Most of those occurring in the intertidal zone survive there only in crevices, overhangs, and tide pools (Millard 1978). One of the more noteworthy exceptions is *Dynamena crisioides* Lamouroux, 1824, frequent in tropical and subtropical waters of the Atlantic, Pacific, and Indian oceans (Millard 1975; Rees and Vervoort 1987; Calder 1991a). This species is stenobathic throughout its geographic range, usually being restricted to lower intertidal and shallow (1 m or less) subtidal zones (Millard 1975; Rees and Vervoort 1987; Calder 1991a).

*Dynamena crisioides* is common in the Caribbean region (Vervoort 1968), and Spracklin (1982) reported it as abundant in the mangrove systems of Twin Cays and Wee Wee Cay, Belize, Central America. At Twin Cays, the species is most prevalent on prop roots of red mangroves (*Rhizophora mangle*) in areas influenced by tidal currents or wave action (Calder 1991b). Its vertical range in the Twin Cays mangal, as in other coastal habitats, was reported in that paper to be very narrow; hydroids of *D. crisioides* were abundant at mean low water (MLW), somewhat less abundant at 0.1 m below MLW, and absent at a depth of 0.5 m.

This study was undertaken to investigate the vertical zonation of *D. crisioides* within the mangal at Twin Cays. Its primary objectives were (i) to document the abundance, colony size and form, and reproductive state of this hydroid over a vertical environmental gradient; (ii) to determine major factors responsible for its observed vertical zonation patterns; and (iii) to establish survivability and colony size and form of specimens transplanted to levels above, below, and within the normal vertical distribution of the species.

Materials and methods

Vertical zonation of the shallow-water hydroid *Dynamena crisioides* was studied in the mangrove system at Twin Cays, Belize, between 21 March and 4 April 1990. Tides at Twin Cays are mixed semidiurnal and resemble those described by Kjerfve et al. (1982) for nearby Carrie Bow Cay, Belize. With a mean tidal range of some 15–20 cm, the intertidal zone of the study area is especially narrow. Weather conditions have a considerable impact on tidal times and levels, and standard classifications of the intertidal zone (e.g., Stephenson and Stephenson 1972) have limited applicability to the study area.

Investigations were undertaken at three stations in the Twin Cays mangal (Fig. 1): Cuda Cut, a relatively deep (3 m) and partially exposed tidal inlet; North Bay, a shallow (0.5 m) cove with a partially exposed shoreline; and Hidden Creek, a moderately deep (1.3 m) and sheltered tidal channel. A major criterion in the selection of these stations,
Fig. 1. Location of Twin Cays, Belize, with sampling stations at Cuda Cut, North Bay, and Hidden Creek.
besides differences in depth and degree of exposure to waves and water currents, was the prevalence at all three of *D. crisioides*.

At each station, percent cover of *D. crisioides* was estimated at mean tide level (MTL), at 0.1, 0.2, 0.3, 0.4, 0.5, and (except at North Bay) 0.6 m below MTL, and at 0.1 m above MTL, using a point census method (Loya 1978). Water depth was determined using a float and metre line, following reference to a tide gauge. Fifty points were located on prop roots at each depth, and presence or absence of *D. crisioides* behind each point was recorded. To avoid bias, an effort was made to locate all census points without reference to *D. crisioides* and other biota.

Colony height, number of branches per colony, and presence or absence of gonophores were recorded from hydroids collected at various depths over the vertical range of the species at each station. Collections in Cuda Cut were acquired at MTL and at 0.1, 0.2, 0.3, and 0.4 m below MTL. In North Bay, collections were made at MTL and at 0.1 and 0.2 m below MTL. In Hidden Creek, colonies were examined from MTL and from 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, and 1.1 m below MTL. At each sampling site, 25 colonies of *D. crisioides* were examined from each depth.

Transplantation of colonies was undertaken at Cuda Cut to test the survival of hydroids at various elevations and depths. Pieces of prop root (30 cm long) from the intertidal zone at Cuda Cut, together with adhering hydroids, were transplanted horizontally to depths of 0.5, 1.5, and 2.5 m below MTL, and to elevations of 0.1 and 0.2 m above MTL, on 21 March 1990. Controls were transplanted to MTL and 0.1 m below MTL at the same locality. The experiment was replicated, and hydroids on transplanted prop roots were recovered on 4 April 1990. Thirty colonies of *D. crisioides* were examined from each level, in both experimental and control transplants, with 15 colonies sampled from each replicate. Specimens were examined from each elevation or depth to determine (i) the percentage of colonies still alive (i.e., with living coenosarc and hydranths) after 2 weeks of exposure, (ii) colony height, (iii) number of branches per colony, (iv) reproductive state, and (v) overall condition.

Survival of hydroids growing on pieces of prop roots transplanted to the supratidal zone (0.3 m above MTL) at Cuda Cut for intervals of 24, 48, 72, and 96 h (n = 10 colonies per sample) was also determined. Following microscopic examination of hydranths and coenosarc in the laboratory, colonies were placed in covered fingerbowls containing seawater and held for 2–3 days to establish their viability. Colonies removed from water were also observed in the laboratory for intervals of up to 4 h.

Other observations were made to determine (i) distribution of colonies on prop roots at the upper limits of the species in the intertidal zone; (ii) important substrate competitors, and predators, of *D. crisioides*; and (iii) the dominant species in the biota occurring with *D. crisioides* at various depths.

Hydroid anatomical terminology used here largely follows Millard (1975) and Calder (1991a).

**Results**

**Abundance and form in relation to elevation or depth**

*Dynamena crisioides* was most abundant in the lower half of the intertidal zone. Estimates of percent cover from the three stations (Fig. 2) were highest at either MTL or 0.1 m below MTL (roughly equivalent to MLW). Estimated percent cover fell to zero within a depth of 0.6 m below MTL, although a few colonies were found as deep as 1.1 m below MTL on broken-down prop roots and wood debris in Hidden Creek during qualitative sampling. Estimated percent cover also dropped to zero at 0.1 m above MTL (roughly equivalent to mean high water). In qualitative samples, no live colonies were found higher than 2–3 cm above MTL at any of the stations.

Colony form also varied along the vertical gradient (Figs. 3, 4). Mean colony height and number of branches per colony at Cuda Cut and Hidden Creek were maximal at 0.1 m below MTL. At North Bay, mean colony height was virtually identical at MTL and 0.1 m below MTL, and lower at 0.2 m below MTL. Numbers of branches per colony declined progressively from MTL to 0.2 m below MTL at North Bay.

Mean colony height of *D. crisioides* at a given elevation or depth was maximal in Hidden Creek, the most sheltered station, and minimal at North Bay, the most exposed site (Fig. 3).
Similarly, the mean number of branches per colony was highest in Hidden Creek and lowest at North Bay (Fig. 4). Subtidally (0.2 m below MTL and lower), the percentages of colonies with gonophores (Fig. 5) were consistently lowest at the lower limits of the species. Intertidally, percentages of fertile colonies were lower at MTL than at 0.1 m below MTL at all three stations.

**Competition and predation**

Mangrove roots below low tide were heavily overgrown at all three stations with an epibenthic assemblage that included sponges, ascidians, algae, hydroids, bryozoans, and anemones. The lower limits of *D. crisioides* at North Bay, the shallowest of the three stations, were established by the presence of an abundant encrusting alga. The alga largely preempted substrate space at levels more than 0.2 m below MTL, and effectively smothered colonies of the hydroid where the two overlapped. Massive sponges occupied much of the available subtidal substrate at Cuda Cut and Hidden Creek.

Mangrove prop roots were much less densely populated by the epibiota intertidally than subtidally at the three stations. Algae, as well as a few sponges, bryozoans, ascidians, and other hydroids, occurred at 0.1 m below MTL, a depth at which *D. crisioides* was also prevalent. Bare areas were common higher up at MTL. In addition to *D. crisioides*, algae (including the "bostrychaetum," or mats of algae, and an unidentified encrusting coralline species), the barnacle *Chthamalus* sp., and the oyster *Isognomon alatus* were frequent at that level. Hydroids of *D. crisioides* often grew within the bostrychaetum. Even more unoccupied space was present immediately above the range of *D. crisioides* in the intertidal zone. The sessile epibiota at that elevation included the bostrychaetum and *Chthamalus* sp.

Fouling and smothering of *D. crisioides* by other epibiota species also tended to decrease with increasing elevation. Subtidally, most hydroids were heavily overgrown or enveloped to some degree by the epibiota, including algae, sponges, other hydroids, bryozoans, corophilid amphipods, tunicates, mats of microphytes (cyanophyceans, diatoms), and detritus. Subtidal colonies of *D. crisioides* typically had branches at the distal end, but proximal branches were usually either broken off, dead, or smothered except for the tips. Hydroids in the intertidal zone frequently supported algal growth but were otherwise relatively free of epibionts.

No direct observations of predation on *D. crisioides* were made during this study other than in transplant experiments at Cuda Cut described below. However, cropped stems and branches were noted in specimens from all three stations, especially on colonies growing subtidally. In the intertidal zone, little if any predator damage was apparent on hydroids. Arrow crabs (*Stenorhynchus seticornis*) fed among intertidal colonies of *D. crisioides* during high tides at Cuda Cut, but they appeared to graze on microphytes and detritus rather than on hydroids. Colonies of *D. crisioides* offered as food to *S. seticornis* in the laboratory were rejected. Pycnogonids were collected with colonies of *D. crisioides*, but were not considered consequential in limiting the vertical distribution of *D. crisioides* at Twin Cays.

**Transplant experiments**

Colonies transplanted to depths of 1.5 and 2.5 m below MTL at Cuda Cut were subjected to predation by fishes (the blue tang, *Acanthurus coeruleus*) within 5–15 min of initial exposure. After 1 h, the hydroids were almost entirely grazed except for stolons and the extreme basal parts of stems. Predation appeared to be much less intense in Hidden Creek; no grazing was observed, and none was apparent, on colonies transplanted to a depth of 1 m for 24 h at that station.

Of those transplanted to a depth of 0.5 m below MTL at Cuda Cut, 29 of 30 colonies were alive after 14 days. Although...
predation was not directly observed in the field, most colonies had been cropped. Mean colony height and number of branches per colony (Fig. 6), both of which were significantly lower ($p < 0.001$, t-test) than for controls at MTL and 0.1 m below MTL, reflected the damage observed microscopically. Colonies at 0.5 m were also overgrown and partially smothered with a mat of microphytes by the end of the 2-week experiment.

Half of the hydroids transplanted to 0.1 m above MTL, and all of those transplanted to 0.2 m above MTL, were dead upon recovery after 2 weeks. Stems and branches of those transplanted from 0.1 m above MTL were significantly ($p < 0.001$, t-test) but sublethally cropped (apparent microscopically and from data in Fig. 6) by an undetermined predator. The dead colonies from 0.2 m above MTL showed little if any signs of predation and did not differ significantly from controls in the size and number of branches per colony (Fig. 6). Mortality of hydroids at both of these elevations was attributed to desiccation, because the coenosarc and hydranths either were absent or showed signs of drying in dead colonies.

All controls at MTL and 0.1 m below MTL were alive and in good condition at the end of the experiment. These specimens did not differ significantly either in height or in number of branches per colony from natural populations at MTL. There were virtually no signs of predator damage on these hydroids, and they were also generally free of fouling organisms.

Among transplanted colonies, only specimens from 0.1 m below MTL had live gonophores at the end of the experiment. At that level, 30% of the colonies sampled were fertile. All gonothecae on hydroids transplanted to other levels were empty.

**Exposure to air**

The upper limits of live specimens were some 2–3 cm above MTL at each station. At this elevation, colonies were most prevalent where moisture was retained longest during low tides, such as the undersides or shaded sides of prop roots, or in the crotch of root branches, or within the bostrychaetum.

Colonies of *D. crisioides* frequently clumped together as the water level receded below them during ebb tides. Some individual colonies bent over against the damp substrate, whereas others remained erect. Branches on individual colonies sometimes flexed inwards against the stem, trapping a film of water in the spaces between. However, branches often sprang outwards again once the water evaporated. When colonies were removed from water in the laboratory, each hydranth withdrew into its hydrotheca and the operculum was closed, retaining moisture in the hydrothecal cavity.

Colonies transplanted to the supratidal zone at Cuda Cut for 24 h had air bubbles inside the hydrothecae and in parts of branches and stems upon collection. However, the air bubbles disappeared and hydranths were extended for feeding within 3–4 h following immersion of these hydroids in seawater in the laboratory. Specimens out of water for 48 h were in poor condition when recovered. Many hydranths were dead and pockets of air were present inside the hydrothecae, branches, and stems. The coenosarc remained intact within the stem but was damaged on the branches, especially at the tips. After 3 days in seawater in the laboratory, active hydranths were observed in these colonies, and new growth (stolon development and branch regeneration) was noted.

None of the colonies removed from the supratidal zone after exposure to air for 72 and 96 h survived.

**Discussion**

*Dynamena crisioides* occupied a conspicuous but vertically narrow horizontal band on prop roots of *Rhizophora* at Cuda Cut, North Bay, and Hidden Creek, sites in the Twin Cays mangrove system influenced by water movement (see Calder 1991b). No living colonies were found lower than 1.1 m below MTL or higher than 2–3 cm above MTL during this study. The hydroid was most abundant, and was one of the dominant sessile species, in the lower half of the intertidal zone. No differences were apparent in the upper limits of *D. crisioides* at the three stations.

Distributions of intertidal organisms are determined by a complex of factors. On rocky shores, physical factors such as wave exposure, tides, desiccation, climate, temperature, light intensity, water currents, width of the rocky tract, proximity of sand, and substrate composition, texture, and configuration have been considered influential (e.g., see Stephenson and Stephenson 1972; Lewis 1972, 1977; Newell 1979). Some distributional phenomena, notably the vertical zonation patterns of the intertidal biota, have been attributed to a combination of biological and physical factors (Connell 1972, 1985).

Lewis (1976) described a transition from lower physical stress and higher biological diversity to higher stress and lower diversity with increasing elevation in the rocky intertidal zone. On mangrove prop roots at Twin Cays, the diversity of the sessile biota was high subtidally (e.g., see Calder 1991b). In particular, massive sponges at Cuda Cut and Hidden Creek, and a species of encrusting alga at North Bay, were more efficient competitors for space than *D. crisioides*. With increasing elevation, numbers of species competing for space decreased. The estimated percent cover of *D. crisioides* increased markedly above low tide (Fig. 2), at least partly because of reduced competition for substrate.

Observations on natural and transplanted colonies indicated that the lower limits of *D. crisioides* at Twin Cays were established by a combination of biological factors: (i) intense compe-
tion for space with the epibiota, especially sponges, algae, and ascidians; (ii) stress due to fouling and smothering of colonies by algae, sponges, ascidians, and other hydroids; and (iii) predation (e.g., by blue tangs). The upper limits of the species were established primarily by desiccation rather than by biological factors. Competition for substrate was low on prop roots at the upper boundary of *D. crisioides* in the intertidal zone. Moreover, no evidence of smothering of hydroids by algae or other epibiota species was apparent intertidally. As for predation, grazing on intertidal hydroids was apparent only on specimens transplanted to 0.1 m above MTL, where it appeared to be sublethal. The coenosarc and hydranths remained even in grazed colonies from this elevation, and regeneration of damaged parts was apparent. By contrast, dead colonies at this level showed signs of desiccation, by the lack of active or dormant living tissues. Ungrazed or little-grazed but dead colonies of *D. crisioides* were observed at 0.1 m above MTL or even higher during this study, apparently having settled and grown during unusually high tides, and subsequently having died from drying. Towards the upper limits of the species, live colonies were found where moisture was retained longest, such as the shady side or underside or crotches of prop roots. These observations also suggest that drying is a more critical limiting factor for the species at higher elevations than the restricted time available for feeding at high tide.

*Dynamena crisioides* seemed to be relegated to a spatial refuge, as might be predicted from its growth form (Jackson 1979). The species was most prevalent in the lower half of the intertidal zone, where it was alternately inundated with water and exposed to air almost every tidal cycle, where predation pressures were low, and where competition for space and smothering by sessile organisms were both reduced. On the basis of estimated percent cover, size, number of branches per colony, and percentage of colonies that were fertile, conditions appeared optimal for the species just above low water.

The conclusions about factors limiting the vertical zonation of *D. crisioides* on mangrove prop roots at Twin Cays are in accord with the hypothesis that the lower limits of intertidal species are mainly controlled by biological factors, whereas upper limits are more likely to be established by physical factors (Connell 1972). Nevertheless, studies are needed to determine settlement patterns of larvae of *D. crisioides* at Twin Cays. Recruitment of hydroids on wooden panels immersed at Cuda Cut during this study was too low to warrant the drawing of conclusions about vertical settlement patterns of planulae.

*Dynamena crisioides* is not highly modified for prolonged exposure to air, and these hydroids were ordinarily not out of water for more than one tidal cycle. Colonies transplanted to the supratidal zone for 24 h recovered with little apparent damage, but those exposed for 48 h sustained heavy mortality of hydranths and dieback of branches. None of the colonies survived intervals of 72 or 96 h out of water.

As tides receded, hydroids of *D. crisioides* in the intertidal zone avoided drying in a number of ways: (i) adjacent colonies frequently clumped together, retaining moisture; (ii) colonies sometimes bent over and adhered to the wet substrate; (iii) branches on individual colonies often flexed inwards to the stem, trapping a film of water; and (iv) hydranths withdrew into hydrothecae, and opercula were closed, holding water inside the hydrothecal cavities. The bark on prop roots, and algae on or near hydroid colonies, also helped to conserve dampness during low tides.

Although *D. crisioides* is not particularly modified morphologically for existence in the intertidal zone, its chitinous hydrothecae are operculate and deeply immersed in the stems and branches (Fig. 7). As a result, hydrothecal cavities can be capped, and a limited surface area of the hydrotheca is immediately exposed to drying. Moreover, hydrothecae are close together, and the concave area between the exposed adcauline wall of a hydrotheca extending beyond the stem or branch trapped a small amount of water in laboratory specimens. Finally, the coenosarc of branches, stems, and stolons is protected from water loss by a chitinous perisarc.

*Fig. 7. Part of a branch of Dynamena crisioides, with three pairs of hydrothecae, from MTL at Hidden Creek.*
below the intertidal zone, D. crisioides seems particularly vulnerable to pollution, especially oil spills. Alteration of mangrove habitats by activities such as filling, diking, and flooding (Odum et al. 1982) would also affect populations of this hydroid.

Acknowledgments

Financial support for this study was provided by the Caribbean Coral Reef Ecosystems (CCRE) Program, through its principal investigator, Dr. Klaus Rützler. This is Contribution No. 346 from the CCRE Program, Smithsonian Institution, partly supported by EXXON Corporation.


