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THE DISTRIBUTIONS AND GROWTH PATTERNS OF THREE EPIPHYTIC HYDROIDS ON THE CARIBBEAN SEAGRASS *THALASSIA TESTUDINUM*

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ABSTRACT

The distributions and growth patterns of *Symmetrosphyphus intermedius*, *Tridentata tumida* and *Ventromma halecioides* on leaves of the seagrass *Thalassia testudinum* from South Water Cay, Belize were examined. Colonies of *S. intermedius* and *T. tumida* smaller than 3 cm and 4 cm respectively grew up and down the leaves, but larger colonies of both species grew only downward. Downward growth has three main advantages: it maximizes the residence time on the leaves, which grow upward from a basal meristem and disintegrate or are grazed from the tip, it reduces the potential for interspecific competition with other epiphytes, and it places the hydroids in proximity to short young leaves, which may be colonized by vegetative stolons. *T. tumida* was relatively rare on the older leaf surfaces because of a progressive degeneration of the distal hydroid tissue. *V. halecioides* showed no orientation of hydrorrhizal growth and was most abundant on the older leaf surfaces, a distribution typical of facultative epiphytes. There are close similarities between the morphologies, growth patterns and distributions of *S. intermedius*, *T. tumida* and *V. halecioides* on *Thalassia*, and *Campanularia asymmetrica*, *Sertularia perpusilla* and *Aglaophenia harpago* respectively on *Posidonia oceanica* in the Mediterranean.

The seagrass *Thalassia testudinum* Banks ex Koenig (also known as turtle grass) is the most abundant of the three species of seagrasses common in the shallow particulate substrates of the Caribbean. The leaves of *Thalassia*, like those of *Posidonia oceanica* in the Mediterranean and *Zostera* spp. in temperate seas, provide important substrates for epifaunal and epifloral species (Harlin, 1980), not least because their renewal continually provides new surfaces which offer epiphytes a refuge from the interspecific competition present on more stable substrates. However, individual leaves have a short life-span and continued colonization of leaves is favored by opportunistic behavior, particularly early reproduction. In unitary organisms reproduction is usually sexual and the products of reproduction (larvae or juveniles) disperse. In modular organisms, such as hydroids, asexual reproduction may predominate and allow the colony (genet) to survive on the plant beyond the life of an individual leaf (Boero, 1987). For example, some hydroids that are seagrass epiphytes reproduce asexually, and colonize other leaves, by stolons. These are flexible vertical extensions of the hydrorrhizae (the "runners" which grow horizontally along the substrate) or the hydrocauli (the "stems" which grow vertically from the hydrorrhizae and bear the hydranths) and attach to adjacent leaves to develop into new colonies before breaking from the parent colony (Philbert, 1935; Boero, 1987).

Recent investigations of hydroid epiphytes of seagrass leaves have shown that they exhibit distinct distribution patterns on the plants which are produced by their colonization behavior and by their growth patterns (Gravier, 1970; Boero, 1981; Garcia Rubies, 1987; Hughes et al., 1991a, 1991b). In their study of three hydroids that are obligate epiphytes of *Posidonia* leaves, Hughes et al. (1991b) recorded three different growth patterns and distributions. Two species, *Campanularia asymmetrica* and *Sertularia perpusilla*, grew predominantly downward, a behavior they considered advantageous for three main reasons. Firstly, it compensates for the upward movement of the surface of the growing leaves and would

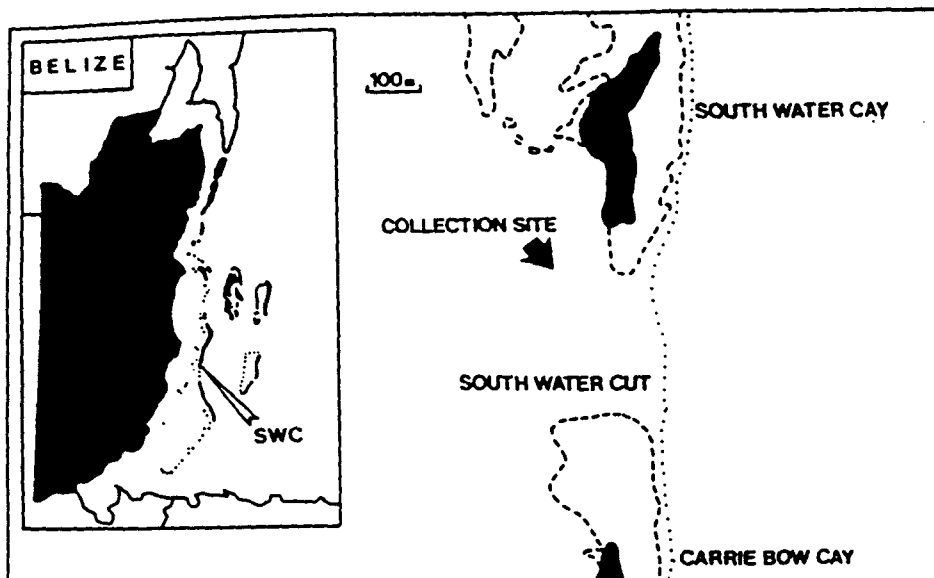


Figure 1. The location of the collection site at South Water Cay, Belize.

extend the time of survival on individual leaves, which degenerate from the tip; secondly it reduces the potential for competition with other epibiota which are most abundant on the oldest leaf surfaces; and thirdly it places the hydroid in the vicinity of the short younger leaves, which might then be colonized by stolons thereby perpetuating the colony on the plant. In addition, *Sertularia perpusilla* showed a degeneration of the distal (uppermost) tissue which, together with its downward growth, led to it being abundant on only the proximal (youngest) leaf surfaces. The third species, *Aglaophenia harpago*, showed no orientation of growth and consequently was most abundant on the distal (oldest) leaf surfaces, a distribution typical of facultative epiphytes, but where the hydroids would experience the most moving water in which to feed.

Thalassia testudinum consists of horizontal rhizomes below the sediment surface which bear leaf bundles on short erect shoots. Leaf bundles consist of up to six parallel strap-like leaves (up to 45 cm long and 1 cm wide) formed alternately on opposite sides of an enclosed meristem. Zieman (1975) recorded that 80% to 90% of all leaf growth occurs from the basal meristem at rates of up to 10 mm·d⁻¹. Therefore the leaves grow upward with the oldest leaf tissue at the tip and the youngest at the base. The continual production of new leaves creates an age gradient with the youngest leaves in the center of the leaf bundle and the oldest leaves at the periphery. The distal parts of the leaves may be grazed by, for example, small parrotfish (*Sparisoma radians*), the green turtle (*Chelonia mydas*) and the manatee *Trichechus manatus* (Randall, 1965). The older leaves do not grow and, if not grazed, degenerate progressively from the tip eventually to detach at a breakage point at the base of the blade (Tomlinson, 1972). While the leaf bundle may survive for many years, individual leaves are short lived; Zieman (1975) estimated a mean leaf life-span of 54 days. The age distribution of leaf tissue within the bundle is similar to that of *Zostera marina* (Sand-Jensen, 1975) and *Posidonia oceanica* (Ott, 1980).

This paper reports a study of the hydroids common on *Thalassia* leaves at South Water Cay, Belize. The aim was to relate their growth patterns to their



Figure 2. The hydrocaulus and

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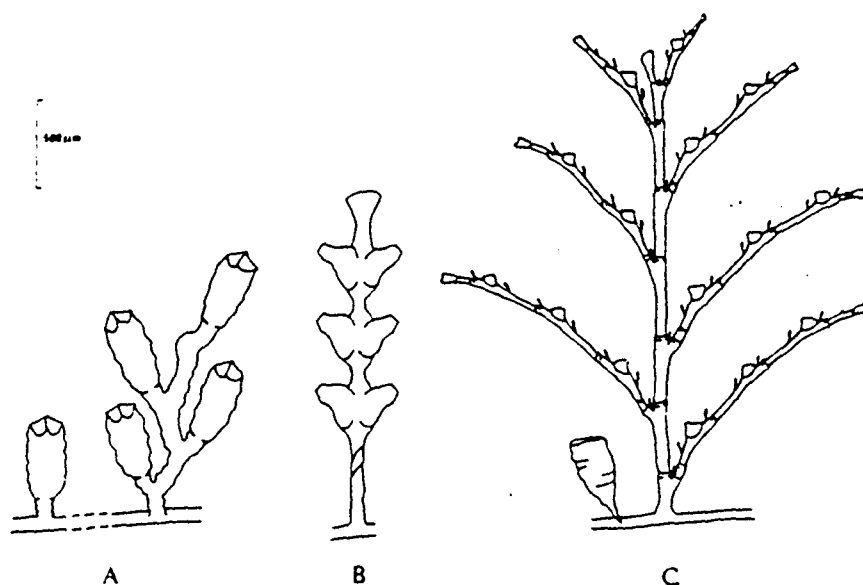


Figure 2. The morphology of A: *Symmetrosphyphus intermedius* (showing the usual short unbranched hydrocaulus and the rarer erect, branched form), B: *Tridentata tumida*, C: *Ventromma halecioides*.

distributions on the leaves and to compare the results with those of hydroids on *Posidonia* in the Mediterranean.

METHODS

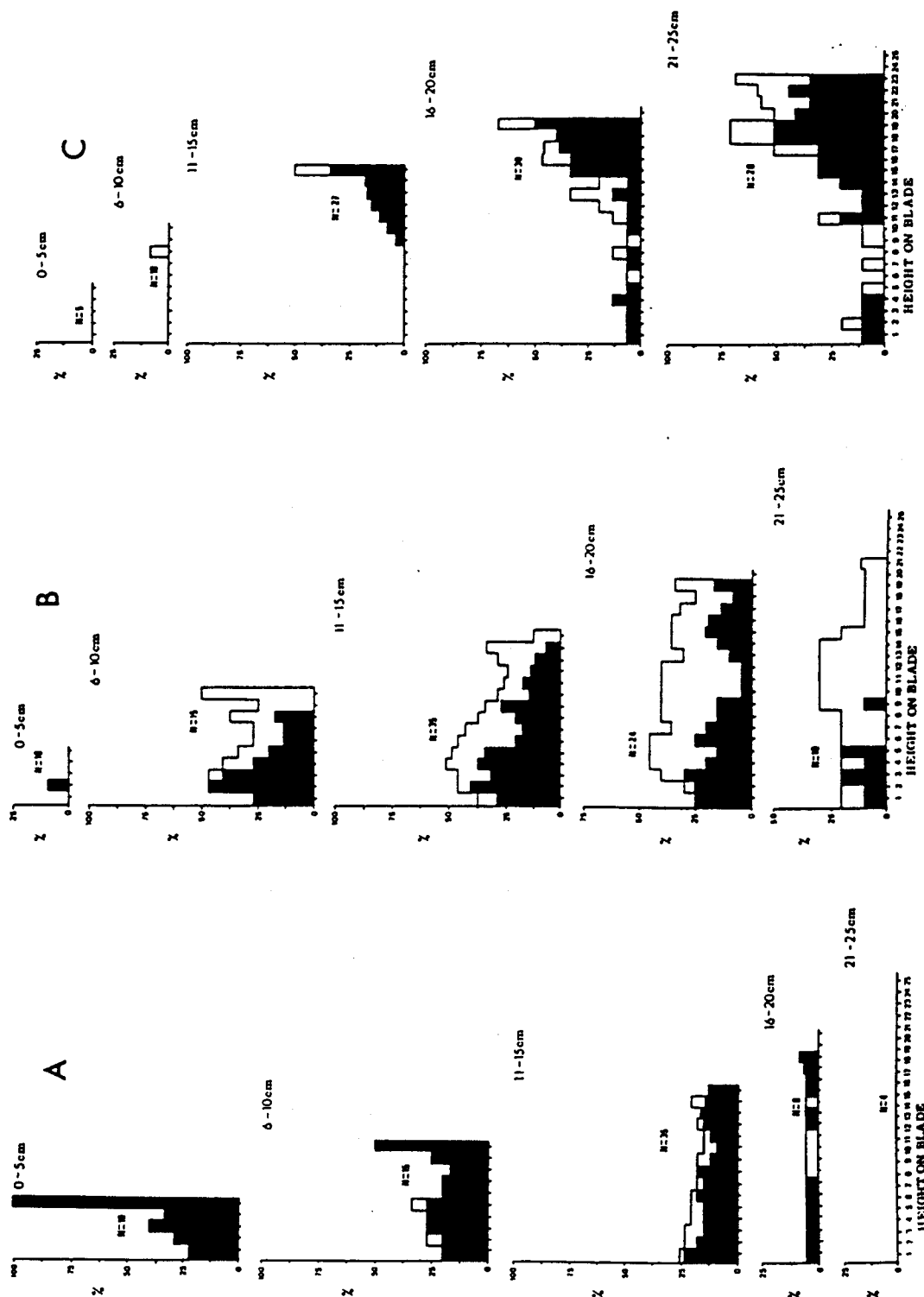
Thalassia leaf bundles were collected in South Water Cut, South Water Cay, Belize (Fig. 1), a site swept by tidal currents, at a depth of approximately 4 m, in mid August 1989 by use of SCUBA. Only leaf bundles seen to bear hydroids were collected. The leaf bundles were cut from the rhizomes, carried intact to the surface, and preserved in 5% formaldehyde in sea-water.

In the laboratory all the leaves of a bundle were detached and examined individually under a binocular microscope alongside a scale, marked at 1-cm intervals. The length of each intact leaf was measured to the nearest centimeter and leaves allocated to 1 cm size classes (for example, leaves 4.7 cm and 5.3 cm long both belong to the 5 cm class). The hydrorhizae and the positions of the hydrocauli of the hydroids on both sides of the leaf were mapped. (The differences in the abundance of hydroids on the inner and outer faces of leaves of different sizes are not examined here.) The condition of the hydroids and whether they were growing or not was also noted. The tips of growing hydrocauli were white, slightly bulbous and had developing hydrocauli immediately behind them, while the tips of hydrocauli that were not growing were identified by their dark thick perisarc and the full sized hydrocauli immediately behind them.

RESULTS

The hydroids found were, *Symmetrosphyphus intermedius* (Congdon) (Fig. 2A), *Tridentata tumida* (Allman) (Fig. 2B), *Ventromma halecioides* (Alder) (Fig. 2C), *Monothecha margareta* (Nutting), *Obelia dichotoma* (Linnaeus), *Clytia hemisphaerica* (Linnaeus), *Monostaechnas quadridens* (McCrady) and *Clytia* sp. Only the first three species were sufficiently abundant for a quantitative study. Data on their distributions on the leaves grouped into 5 cm length classes are presented in Figure 3 as the proportion (%) of 1 cm segments of leaves that were occupied by each species. Leaves which had broken tips were not used since there was no relationship between length and relative age. For each species only data from bundles bearing at least one colony of that species were used.

Symmetrosphyphus intermedius (Family Thyrosophidae) had up to seven short



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Figure 3. The dis *halecioides* on *Th* percentage of 1 cm refer to empty per

hydrocauli per centimeter of hydrorhiza, each with a single terminal hydranth, but occasional branched hydrocauli with several hydranths were observed (Fig. 2A). The hydrorhizae usually grew along the leaf parallel to the blade axis and while those of intact colonies shorter than 3 cm grew both up and down the leaves, the hydrorhizae of longer colonies showed downward growth only. The hydrorhizae were branched. The branches initially grew at 70–90° from the main hydrorhiza, and often over the edge of the leaf to the other side, but subsequently also grew down the leaf. *S. intermedius* occurred along the whole length of the leaves, but were most abundant on the shorter, younger leaves and scarce on leaves longer than 15 cm (Fig. 3A). Stolons, extensions of the hydrorhizae, were only found on the basal (youngest) 1 cm of the colonies. No gonozoids were observed.

Tridentata tumida (Family Sertulariidae) had one or two (but up to four) hydrocauli per centimeter of hydrorhiza, each with up to 25 pairs of hydranths (Fig. 2B). The hydrorhizae, like those of *S. intermedius*, usually grew parallel to the leaf axis but were only occasionally branched. Like *S. intermedius*, small intact colonies (shorter than 4 cm) were growing both up and down the leaves but all larger colonies showed evidence of downward growth only. The mean growth rate of the downward growing hydrorhizae of 20 colonies of *T. tumida* was measured by snipping the leaf edge adjacent to the growing tip and collecting the leaves 5 days later to measure the new growth. The estimated growth rate was 3.6 mm · d⁻¹. Unlike *S. intermedius*, the distal (uppermost) tips of the hydrorhizae and adjacent hydrocauli were degenerating and the distal leaf surfaces often bore only empty perisarc (Fig. 3B). Living *T. tumida* hydrocauli were found predominantly on the basal leaf surfaces (Fig. 3B). Stolons, elongations of the hydrorhizae, were observed frequently, but only on the basal 3 cm of the colonies. No gonozoids were observed.

Ventromma halecioides (Family Plumulariidae) had relatively large, delicate, feather-shaped hydrocauli with up to 24 branches, each of which bore several small hydranths (Fig. 2C). The hydrorhizae were regularly branched but with no apparent orientation of growth direction and often overgrew each other, producing a lacework effect on the leaf surface. *V. halecioides* was most abundant on the older leaf surfaces, that is on the distal parts of each leaf and on older leaves (Fig. 3C). Stolons were not observed but many colonies bore gonozoids.

DISCUSSION

There are many similarities between the results of this study and those of Hughes et al. (1991b) who examined the distributions of three species of hydroid on the Mediterranean seagrass *Posidonia oceanica*. The morphologies, growth patterns and distributions of *Symmetroscyphus intermedius*, *Tridentata tumida* and *Ventromma halecioides* on *Thalassia* were similar to those of *Campanularia asymmetrica*, *Sertularia perpusilla* and *Aglaophenia harpago* respectively on *Posidonia*.

S. intermedius and *C. asymmetrica* both have single terminal hydranths borne on short but densely packed hydrocauli, both occurred along the length of the seagrass leaves, and larger colonies of both species showed downward growth

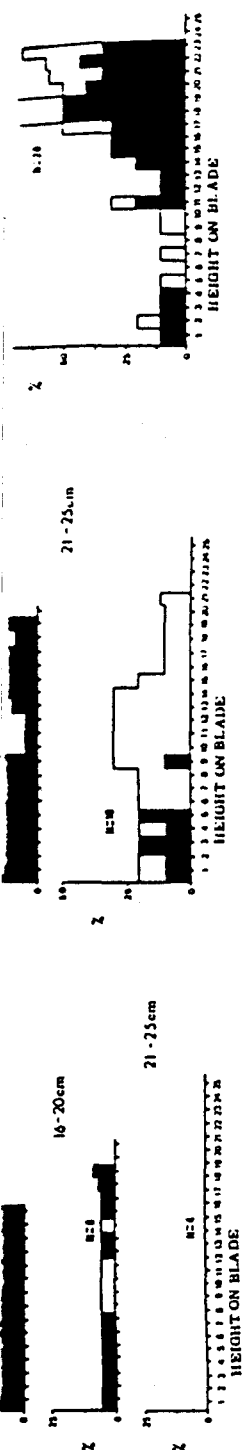


Figure 3. The distributions of A: *Symmetroscyphus intermedius*, B: *Tridentata tumida*, C: *Ventromma halecioides* on *Thalassia* leaves grouped into 5 cm length classes. The data are expressed as the percentage of 1 cm sections that were occupied. N = the number of leaves examined. The open areas refer to empty perisarc and the shaded areas refer to living tissue.

only. The hydrocauli of the confamilial *T. tumida* and *S. perpusilla* are similar morphologically. In addition, the hydrorhizae of large colonies of both species grew only downward and both showed degeneration of the most distal tissue. This results in the hydroids "moving" down the leaf, vacating the older leaf surfaces, and consequently both species were found predominantly on the basal areas of the leaves. These similarities may indicate that *S. intermedius* and *Tridentata tumida*, like their Mediterranean equivalents, are obligate seagrass epiphytes. The confamilial *V. halecioides* and *A. harpago* are also similar morphologically. Neither showed any orientation of hydrorhizal growth and both species were most abundant on the oldest leaves and on the distal, oldest, leaf surfaces.

The selective advantages and disadvantages of these different growth patterns and the resulting distributions were discussed by Hughes et al. (1991b) with respect to the *Posidonia* hydroids. Downward growth, shown by *S. intermedius* and *T. tumida* on *Thalassia*, and *C. asymmetrica* and *S. perpusilla* on *Posidonia*, extends the residence time of a hydroid on a leaf, because eventually the leaves degenerate, or are grazed, from the tip downward. Other epiphytes are usually most abundant on the older leaf surfaces, which have been available for colonization and growth for a longer period, and downward growth should reduce the potential for competition. This might be particularly significant for *S. intermedius* since their short hydrocauli may be overgrown by epiphytic algae and sessile protozoans (personal observations). This smothering probably reduces the efficiency of feeding by the hydranths and may reduce the amount of light reaching the tissues of *S. intermedius* which contain algal symbionts (Calder, 1986).

Downward growth, together with the branching of the hydrorhizae and subsequent growth to the inner surfaces of the leaves, facilitates early colonization, by stolons, of the short new leaves that develop in the center of the leaf bundle. The stolons of *S. intermedius* and *T. tumida* were all in this region, even though colonies were found higher on the leaves. No stolons were found more than 1 cm above the base of *S. intermedius* colonies and 3 cm above the base of *T. tumida* colonies. This advantageous disposition of the stolons could be achieved if they develop immediately behind the downward growing tips of the hydrorhizae and have a relatively short existence. The question of how the orientation of downward growth of *Serularia perpusilla* on *Posidonia* was achieved was addressed by Hughes et al. (1991a), but not resolved.

T. tumida, like *S. perpusilla* on *Posidonia*, was relatively scarce on the older parts of the leaves because of the progressive degeneration of their most distal tissues. Such degeneration, recognised in other hydroids (Hughes, 1986, 1987) could be a reclamation of resources from the most vulnerable parts of the colony to be used to promote the downward growth. The estimated downward growth rate of *T. tumida* hydrorhizae of $3.6 \text{ mm} \cdot \text{d}^{-1}$ is within the range of the mean upward growth rate of $2\text{--}5 \text{ mm} \cdot \text{d}^{-1}$ of *Thalassia* leaves (Zieman, 1975).

The potential disadvantages to *S. intermedius* and *T. tumida* in colonizing the proximal leaf surfaces include the reduced potential for capturing planktonic prey from the relatively slow moving water around and between the bases of the leaves. Hughes et al. (1991b) considered the possibility that hydroids in the confines of the leaf bundle may capture small epiphytes from adjacent leaf surfaces instead of feeding on planktonic prey. *S. intermedius*, with their short unbranched hydrocauli, are not adapted for efficient filter feeding. The potential for damage, by collision with adjacent leaves that converge toward the center of the leaf bundle, is reduced for both *S. intermedius* and *T. tumida* by areas of flexibility in the hard external perisarc close to the base of the hydrocauli. Annulations in the perisarc beneath the hydranth of *S. intermedius* (Fig. 2A), and an articulating

joint close to the base of the hydrocaulus of *T. tumida* (Fig. 2B), allow hydrocauli that are being compressed between two leaves to flatten against the adjacent leaf. This alleviates buckling of the tubular perisarc and may allow the hydranths to contact potential food particles on the adjacent leaves.

Ventromma halecioides, like *A. harpago* on *Posidonia*, did not exhibit orientated growth of the hydrorhizae and consequently its abundance is related to the age of the leaf surface. Only on the older leaves, which grow slowly or not at all, is downward growth sufficient to place hydrorhizae on more basal parts of the leaves (Fig. 3). This distribution is that expected of a facultative epiphyte, which *V. halecioides* is since it has been found on a variety of substrata (Boero and Fresi, 1986). Reproduction is primarily sexual and colonization of new substrata by swimming planula larvae might be highest on the peripheral parts of the plant, which are also those that have been available for colonization for the longest time. A peripheral distribution may be advantageous for *V. halecioides*, which has large, delicate, feather shaped hydrocauli suited to suspension feeding. Plumularian hydroids are often most abundant in current swept situations (Hughes, 1975) and the distal distribution of *A. harpago*, an obligate epiphyte of *Posidonia*, enhances feeding efficiency in the slow and infrequent currents of the Mediterranean (Hughes et al., 1991b).

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