

EPIPHYTES ON THE SEAGRASSES OF ZANZIBAR ISLAND (TANZANIA), FLORISTIC AND ECOLOGICAL ASPECTS

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SUMMARY. — The species composition and ecology of the seagrass epiphytes of Zanzibar Island (Tanzania) are discussed. *Thalassodendron ciliatum*, a subtidal seagrass species, had the highest epiphyte cover, followed by *Enhalus acoroides*, *Halodule uninervis*, *Cymodocea rotundata* and *Thalassia hemprichii*. A total of 49 taxa of macroalgae (5 of which are new records for the East African coast) was recorded as epiphytes on seagrasses ; the Rhodophyta form the largest fraction, exceeding the Chloro- and Phaeophyta both in species number and abundance. The preference of the epiphytes for certain host plants was mainly related to the ecological parameters of the habitat of the hosts such as tidal level, depth and relative rate of water flow. Epiphytes were most abundant in the subtidal zone where they were best developed on the perennial stems rather than on the ephemeral leaves. Differences in species composition and abundance were also observed between different parts of the stems and leaf tufts. Distinctive species compositions characterize these different habitats and plant parts. The zonation of seagrasses and their associated epiphytes along transects through a tide channel in Chwaka Bay is also described.

KEY WORDS. — Seagrass, epiphytes, seaweeds, (macro-)algae, Zanzibar.

INTRODUCTION

Sandy and muddy habitats in tropical areas are often characterized by seagrass communities (McROY & HELFFERICH 1977 ; Phillips & McRoy 1980). According to some phytosociologists, seagrass communities are the most simply structured associations of rooted plants, because they are mostly composed of a single rooting species. This often results in the monotonous appearance of seagrass meadows which can form a single zonation band from the high tide level to the subtidal (COPPEJANS *et al.* 1992). The structure of these uniform-looking seagrass beds however contains a great diversity of floral and faunal components.

Four main sub-habitats can be recognised : (1) the leaf epiphyton comprising algal microflora with associated small animals including nematodes, polychaetes and crustaceans, together with sessile fauna, such as hydrozoans, anemones, snails and echinoderms ; (2) stem and rhizome biota which include various epiphytes, polychaetes, amphipods and bivalves ; (3) species swimming among the leaves including fish and crustaceans ; and (4) sediment flora and fauna, although this may differ little from that of the surrounding benthos (McROY & HELFFERICH 1977).

Seagrass meadows are very productive ecosystems of which a large proportion is often attributed to the epiphytes (WETZEL & PENHALE

1980, SMITH & PENHALE 1980, BORUM & WIJUM-ANDERSEN 1980, HEIJN 1984, 1985, BROUNS & HEIJN 1986). Epiphytes can represent up to 50 % of the total above-sediment biomass of a seagrass meadow, although others (VERHEIJ & ERFTEMEIJER 1993) state that only 5-10 % of the total above-ground biomass of seagrass beds in reef flat environments is contributed by associated algae. Epiphytes can therefore play an important role in the functioning of seagrass ecosystems. Nevertheless epiphytes on seagrasses in tropical regions remain poorly studied. From the tropical East African coast almost nothing is known on the species composition of the seagrass epiphyton. COPPEJANS *et al.* (1992) made a first attempt to study the epiphytes on *Thalassodendron ciliatum* in Gazi Bay (Kenya). The data presented here are the results of the MSc-thesis of VANREUSEL (1998).

MATERIAL AND METHODS

General sampling. Sampling was carried out on Zanzibar Island (Tanzania) from 15/07 to 5/08/1997. A general collection of seagrasses with epiphytes was made in different intertidal and subtidal biotopes at 8 sites around the island : Nungwi, Matemwe, Kiwengwa, Pongwe, Uroa, Chwaka, Paje and Mbweni (Fig. 1). The samples were labelled and preserved in a 5% formaldehyde-seawater solution. A detailed study of the epiphytes was carried out in the laboratory. The epiphytes were removed from the host and stained with aniline blue or fast green, for the purpose of identification. All specimens are deposited in the Herbarium of the University of Ghent (GENT).

Vegetation survey. For the phytosociological study, seagrasses were sampled along two transects in the western tide channel of Chwaka Bay mangrove system (Fig. 2). Both transects were situated parallel to each other over the whole width of the channel. Transect A, situated close to the mouth of the channel, contained 14 sampling plots ; Transect B, situated more inland, contained 6 plots. In each plot 1-6 specimens of each seagrass species were collected. The following environmental variables were measured : depth ; substrate ; slope angle ; seagrass species composition, density and height ; and surrounding macroalgal vegetation were noted. Fig. 2C shows the relative depth of the sampling plots, the mean high and low water mark, the

extreme low water mark, and the occurring seagrass species.

For each epiphytic species the abundance on the seagrasses was quantified by cover estimates using % values. If several layers of epiphytes were present, the sum of the cover estimates was calculated ; this explains % values of more than 100%. Distinction was made between the leaves and stems (if present) of the seagrass. In order to enable us to study the differences in epiphytic species composition along a stem, the length of each stem was first measured and cut into pieces of 7 cm (starting from the stem apex). Epiphyte cover was then estimated for each portion. For the investigation of the differences in species composition between different leaves of the same plant, each leaf was studied separately. Also, differences between the inner and outer surface of the leaves were investigated. Each stem-portion and each leaf-side will hence forth be referred to as a relevé. The numbers of the leaf relevés are as follows : "sample_number.seagrass_number.L.I/O" ("I" for inside, "O" for outside) ; the numbers for the stem relevés are indicated as "sample_number.seagrass_number.(subnumber for side branch if present). A/B/C/etc. (A for the upper, youngest stem part, etc.). The numbers of the seagrass specimens with corresponding species can be found in Table 1. Next to the cover estimates per leaf relevé, the distribution of the epiphytes in each relevé was drawn schematically.

TABLE 1

Seagrass species and corresponding numbers of the seagrass specimens. The numbers consist of two subnumbers, the first one refers to the sample number, the second one to the seagrass number in the specific sample.

Species	Seagrass numbers
<i>Cymodocea rotundata</i>	8.1 ; 8.2 ; 8.3 ; 25.2 ; 25.3
<i>Enhalus acoroides</i>	1.2 ; 13.1 ; 13.3 ; 17.2 ; 25.1
<i>Halodule uninervis</i>	1.1 ; 1.3 ; 9.1 ; 9.2 ; 9.3 ; 10.6 ; 10.7 ; 11.2 ; 13.2 ; 13.4 ; 13.5
<i>Halodule wrightii</i>	21.4 ; 21.5 ; 21.6 ; 35.1
<i>Thalassia hemprichii</i>	3.1 ; 3.2 ; 3.3 ; 4.1 ; 4.2 ; 5.1 ; 5.2 ; 5.3 ; 5.4 ; 6.2 ; 25.4 ; 34.1 ; 34.2 ; 34.3 ; 34.4
<i>Thalassodendron ciliatum</i>	10.1 ; 10.2 ; 10.3 ; 11.1 ; 12.1 ; 15.1 ; 16.1 ; 16.2 ; 18.1 ; 18.2 ; 18.3 ; 19.1 ; 21.1 ; 21.2 ; 21.3 ; 23.1

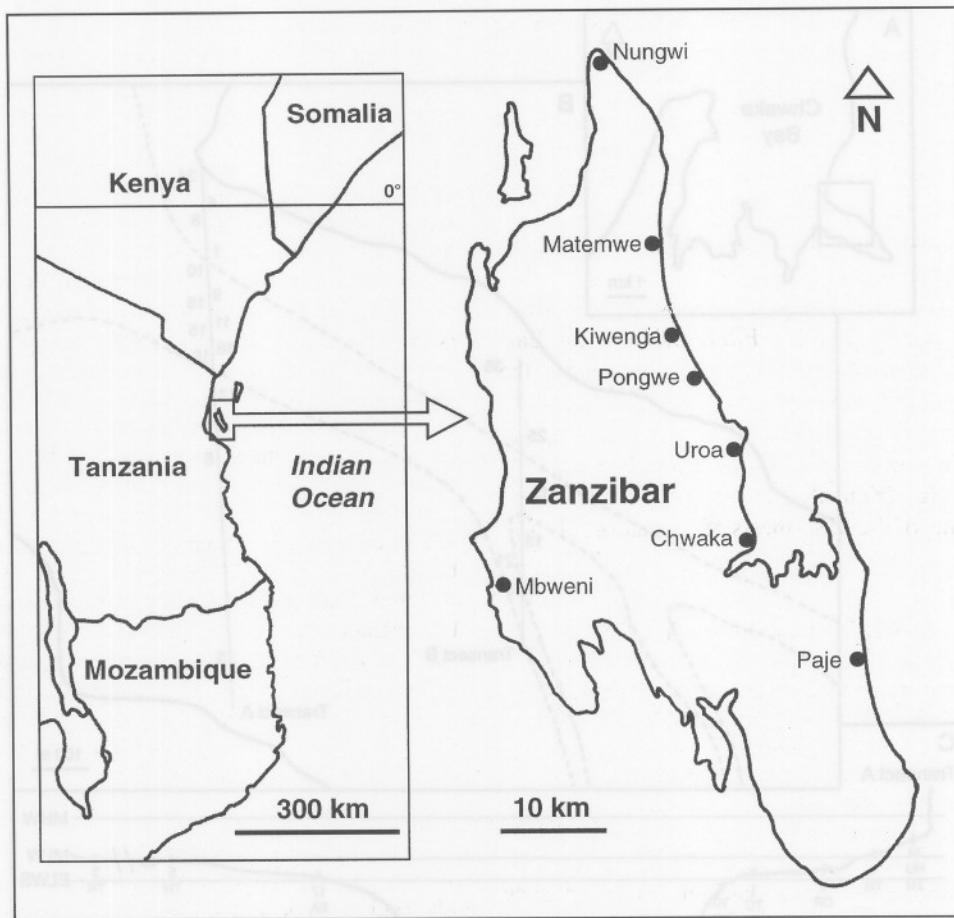


Fig. 1.—Location of Zanzibar Island off the coast of Tanzania, and location of the 8 sample sites around Zanzibar.

Data analysis. The cover estimates are expressed in % values. The data set consists of 520 relevés (365 from leaves and 155 from stem portions) from 64 seagrass specimens. A two way indicator species analysis (TWINSPAN) (HILL 1979) was chosen as classification method.

RESULTS

FLORISTIC ASPECTS

DEN HARTOG (1984) mentions 10 seagrass species for Zanzibar Island : *Cymodocea rotundata* Ehrenberg et Hemprich ex Ascherson, *C. serrulata* (Brown) Ascherson et Magnus, *Enhalus*

acroides (Linnaeus f.) Royle, *Halophila ovalis* (Brown) Hooker f., *H. stipulacea* (Forsskål) Ascherson, *Halodule uninervis* (Forsskål) Ascherson, *H. wrightii* Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, *Thalassia hemprichii* (Ehrenberg) Ascherson, *Thalassodendron ciliatum* (Forsskål) den Hartog.

All 10 species were collected during our survey but *Cymodocea serrulata*, *Halophila stipulacea* and *Syringodium isoetifolium* did not occur in our transects in Chwaka Bay. We therefore have no detailed data on epiphytic growth on these species. *Halophila ovalis* and *H. stipulacea* are fast growing pioneer species with short living

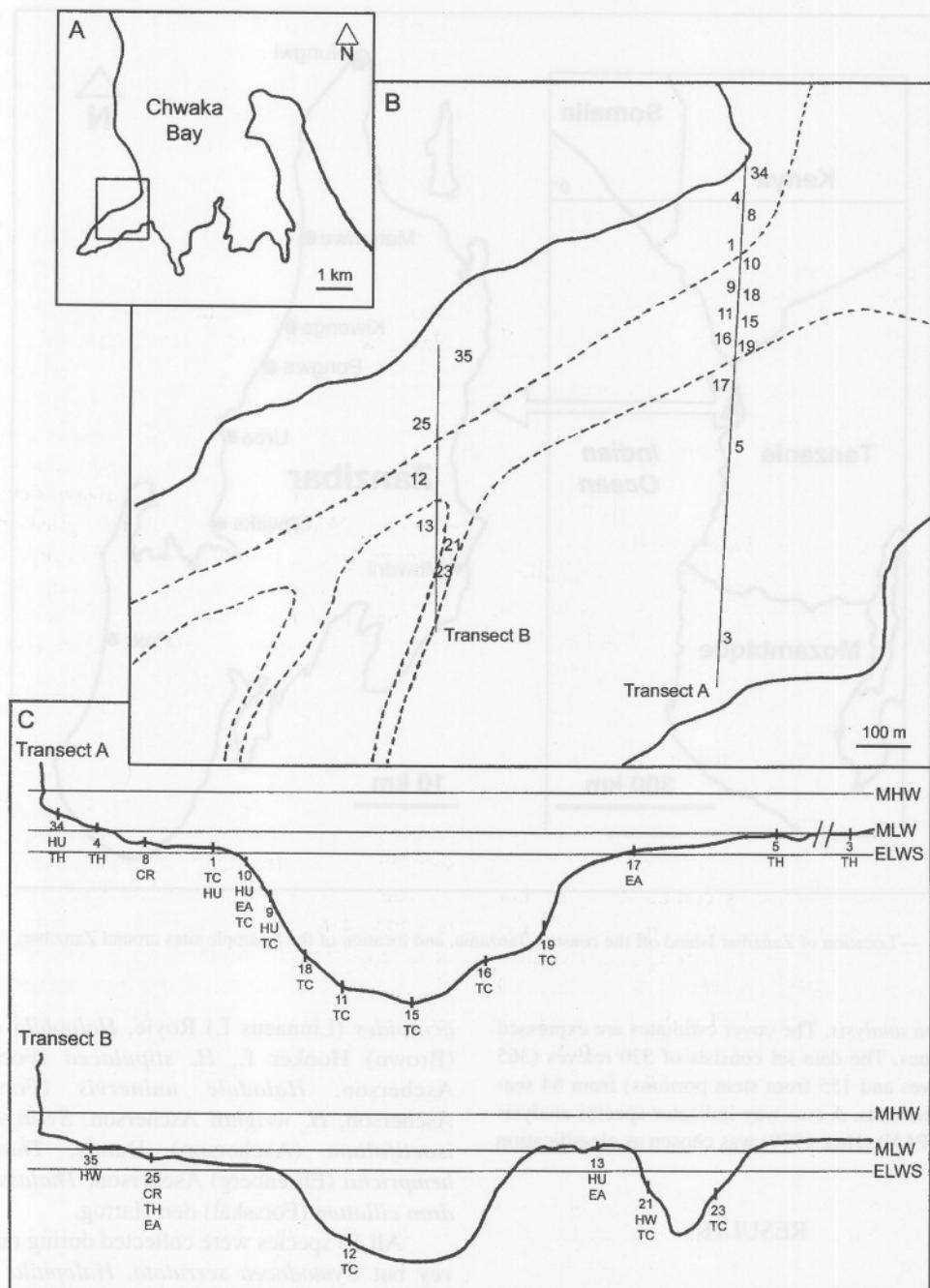


Fig. 2. — A. Chwaka Bay with indication of the western tide channel. B. Detail of the western tide channel, with the situation of the two transects; the dotted lines represent the extreme low water mark, numbers represent the sample plots. C. Cross section through the two transects showing the relative depths of the sampling plots. Tide levels: MHW: mean high water mark, MLW: mean low water mark, ELWS: extreme low water mark. Composing species: CR: *Cymodocea rotundata*, EA: *Enhalus acoroides*, HU: *Halodule uninervis*, HW: *Halodule wrightii*, TC: *Thalassodendron ciliatum*, TH: *Thalassia hemprichii*.

leaves and no lignified stem. They are therefore not suitable for epiphyte growth ; only a few epiphytes have been found on the old decaying leaves. *Halodule uninervis* is a pioneer species characterized by narrow strap-like leaves (up to 3.5 mm). This species was found in a wide range of habitats with an epiphytic cover related to its position in the intertidal and varying from 0 to 50 %. The leaves of *Halodule wrightii* are even narrower and were almost devoid of epiphytes. *Thalassodendron ciliatum* is a subtidal species, growing from just below low water mark down to -10 m. It is characterized by a lignified stem up to 70 cm long and terminal tufts of 3-10 distichously placed, recurved, strap-like leaves. The stems were densely covered by diverse epiphytes ; the leaves form a good substrate for crustose corallines but were less suitable for other epiphytes. *Enhalus acoroides* usually grows in monospecific stands in shallow subtidal habitats down to 4 m deep. The leaves are broad and tough, up to 1 m long, and are a suitable substrate for numerous epiphytes. *Thalassia hemprichii* prefers mid to high intertidal habitats and in general had a very low epiphyte cover. *Cymodocea rotundata* is common in the infralittoral fringe and therefore is submerged almost continuously ; the leaves were sometimes fully covered by *Ceramium flaccidum*.

The epiphytic species composition did not differ markedly between the 8 sites around the island. All epiphytic species found at these sites, were also collected at Chwaka Bay. In total 49 algal species were found on the different seagrass species : 27 Rhodophyta, 14 Chlorophyta, 6 Phaeophyta and 2 Cyanophyta. The Rhodophyta also exceeded the other groups in total cover (83%) ; Phaeophyta (14%), Chlorophyta (1%) and Cyanophyta (2%). The species with the acronyms used in the TWINSPAN classification are listed in Table 2 ; also mentioned are the ecological preferences, notes on morphology and distribution, and references to representative illustrations. Neither the Cyanophyta, nor the encrusting Corallinales were identified to species level. Two entities or growth forms of Cyanophyta were recognised : isolated filaments and tuft forming

specimens. Filamentous Cyanophyta were found to be common epiphytes on leaves, but they never occurred in large quantities. In contrast to macroalgal leaf epiphytes which were found to be more dominant on the older leaf apices, the filamentous blue-greens were more common at the leaf basis.

ECOLOGICAL AND PHYTOSOCIOLOGICAL ASPECTS

From the 520 leaf and stem relevés, 80 were devoid or almost devoid of epiphytes. These relevés were not used in the TWINSPAN. Most 'empty' relevés were from plants growing in the mid or high intertidal, a zone where epiphytic growth is less developed. As discussed previously, the leaves of the two *Halophila* species and *Halodule wrightii* were almost always devoid of epiphytes. Young leaves of other seagrass species are equally epiphyte-poor, partly because of the short colonisation time, partly because they are protected by the older leaves of the same shoot. Other relevés with very few epiphytes were from habitats with a very high water flow rate which might hamper the settlement of epiphyte spores.

The total cover of the epiphytes on subtidal seagrasses was much higher than on intertidal specimens (Fig. 3) ; plants from the infralittoral fringe (between mean and spring low tide) showed an intermediate epiphytic cover. This indicates that permanent submersion, creating a far more stable habitat, is a very important factor in determining epiphytic growth. The total epiphyte cover on stems (if present) exceeded the cover on the leaves. In habitats with a high water flow rate the cover on the leaves was very low whereas the cover on stems did not seem to be affected by this factor (at least in the upper parts). Leaf sheaths were devoid of epiphytes and therefore were excluded from this study.

The differences in total cover on the leaves varied significantly between the different species, but this was mainly a consequence of the different habitats in which they occurred. In similar ecological conditions no host preference could be observed between the different seagrass species (except for *Halodule wrightii*). The subtidal species *Thalassodendron ciliatum* had the highest

TABLE 2

Epiphytic species on the seagrasses of the 8 sites around Zanzibar Island ; acronyms used in TWINSPLAN ; ecological preference [(1a) species restricted to the intertidal zone, (1b) species with a distinct preference for intertidal habitats, (1c) species with a scattered distribution but with higher abundance values in intertidal habitats, (2a) species restricted to subtidal zones, (2b) species with a marked preference for subtidal habitats, (3) species without preference for a specific tidal zone, (L) species found exclusively on leaves, (L') species with a distinctive preference for leaves, (S) species growing exclusively on stems, (S') species with a marked preference for stems] ; notes on morphology and distribution ; and references to representative descriptions and illustrations.

Species	Acronym	Ecological preference	Notes on morphology and distribution	References
RHODOPHYTA				
<i>Acrochaetium caespitiforme</i> Børgesen	Acr cae	2a S' - entangled with <i>Asteronema rhodochortonoides</i>	upright, rarely branched filaments, diameter ~ 6 µm	Stegenga et Kemperman 1983 : 68, fig. 2-3
<i>Amphiroa rigida</i> Lamouroux	Amp rig	2a S'	often forming large dense masses	Jaasund 1976 : 79, fig. 159
<i>Anotrichium tenue</i> (C. Agardh) Nægeli	Ano ten	2a L' - uncommon	tetrasporophyte ; upright axes occasionally branched, creeping axes attached by rhizoids	Jaasund 1976 : 113, fig. 229 ; Price & Scott 1992 : 67-69, fig. 19
<i>Caulacanthus ustulatus</i> (Turner) Kützing	Cau ust	2b S'	cylindrical axes, attached by multicellular disks	Jaasund 1976 : 89, fig. 180 ; Wynne 1995 : 277-280, fig. 13-15
<i>Centroceras clavulatum</i> (C. Agardh) Montagne	Cen cla	1b - locally common	tetrasporophyte	Jaasund 1976 : 109, fig. 222 ; Price & Scott 1992 : 81-82, fig. 25
<i>Ceramium camouii</i> Dawson	Cer cam	2b		Jaasund 1976 : 107, fig. 218 ; Cribb 1983 : 78-79, pl. 27, figs. 5-6, pl. 28, figs. 1-4
<i>Ceramium codii</i> (Richards) Feldmann-Mazoyer	Cer cod	1a - a single specimen		Jaasund 1976 : 107, fig. 216 ; Cribb 1983 : 78-79, pl. 27, figs. 1-4
<i>Ceramium flaccidum</i> (Kützing) Ardisson	Cer flac	1c - warm pools, common		Cribb 1983 : 82, pl. 31, fig. 2 ; pl. 59, fig. 1-4 ; Price & Scott 1992 : 89 fig. 27A-E ; Wynne 1995 : 292-294, fig. 36
<i>Ceramium mazatlanense</i> Dawson	Cer maz	3 - common		Jaasund 1976 : 107 ; Wynne 1995 : 294-296, fig. 42
<i>Chondria pygmaea</i> Garbary et Vandermeulen	Cho pyg	3	Previously only recorded from the Red Sea and the Seychelles	Garbary & Vandermeulen 1990 : 312, fig. 2-16 ; Wynne 1995 : 303, fig. 52-55
crustose corallines	cru cor	2b - very common	Belonging to different genera and species.	
<i>Falkenbergia hillebrandii</i> (Bornet) Falkenberg [=Asparagopsis taxiformis (Delile) Trevisan]	Fal hil	2a S' - entangled with other epiphytes	tetrasporophyte	Jaasund, 1976 : 69, fig. 140 ; Norris, 1992 : 2

Species	Acronym	Ecological preference	Notes on morphology and distribution	References
<i>Gelidiella lubrica</i> (Kützing) Feldmann et Hamel	Gel lub	2a S - also growing on crustose corallines, very common	tetrasporophyte ; upright axes and creeping stolons, firmly attached by rhizoids	Hatta & Prud'homme van Reine 1991 : 353-354, fig. 3a-f ; Wynne 1995 : 268, fig. 6
<i>Gelidiopsis intricata</i> (C. Agardh) Vickers	Gel int	2a S' - very common	tetrasporophyte ; upright axes and creeping stolons, firmly attached by rhizoids	Jaasund 1976 : 87, fig. 177 ; Cribb 1983 : 56, pl. 13, fig. 1-2 ; Price & Scott 1992 51-54, fig. 13A-F
<i>Gracilaria corticata</i> J. Agardh	Gra cor	2a S' - common	tiny specimens, often grazed or affected by <i>Gracilaricolax</i> sp., a typical parasite for <i>Gracilaria</i> spp.	Jaasund 1976 : 83, fig. 168, pl. 7
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	Her sec	1c	creeping axes with alternating determinate and indeterminate upright axes.	Schneider & Searles, 1997 : 196-198, fig. 11
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn f. <i>tenella</i> (C. Agardh) Wynne	Her sft	2a L' - common		Wynne 1995 : 307-308, figs. 57-58
<i>Heterosiphonia crispella</i> (C. Agardh) Wynne	Het cri	2a		Wynne, 1985 : 85-87 ; Jaasund 1976 : 121, fig. 246 (as <i>Heterosiphonia wurdemanii</i> (Bailey) Falkenberg)
<i>Hypoglossum simulans</i> Wynne, Price et Ballantine	Hyp sim	2a	tetrasporophyte	Wynne & De Clerck (2000)
<i>Jania adhaerens</i> Lamouroux	Jan adh	2a S - also epiphytic on other seagrass epiphytes		Jaasund 1976 : 77, fig. 154 ; Price & Scott 1992 : 48-50, fig. 12A-C
<i>Jania pumila</i> Lamouroux	Jan pum	2a S' - uncommon		Jaasund 1976 : 77, fig. 156 ; Wynne 1995 : 270
<i>Laurencia minuta</i> Vandermeulen, Garbarek et Guiry	Lau min	1c	Described from Israel, in the Indian Ocean only recorded in the Seychelles	Vandermeulen et al. 1990 : 239-240, fig. 1-13 ; Wynne 1995 : 312, fig. 66-70
<i>Laurencia papillosa</i> (C. Agardh) Greville	Lau pap	2a S - uncommon		Jaasund 1976 : 139, fig. 281, pl. 10
<i>Leveillea jungermannioides</i> (Hering et Martens) Harvey	Lev jun	2a S - locally common	creeping thallus with alternating leaf-like branchlets	Jaasund 1976 : 131, fig. 265 ; Cribb 1983 : 127-128, pl. 32, fig. 4 ; Wynne 1995 : 315, fig. 71
<i>Polysiphonia scopulorum</i> Harvey var. <i>villum</i> (J. Agardh) Hollenberg	Pol sco	2a S		Hollenberg 1968 : 81, 83, fig. 7A-C Cribb 1983 : 133 ; Price & Scott 1992 : 212
<i>Spyridia filamentosa</i> (Wulfen) Harvey	Spy fil	2a S' - also epiphytic on other seagrass epiphytes		Jaasund 1976 : 111, fig. 224 ; Cribb 1983 : 94, pl. 26, fig. 2-4 ; Price & Scott 1992 : 131, fig. 45A-E
<i>Stylonema alsidii</i> (Zanardini) K. Drew	Sty als	2a L - uncommon	irregularly branched filaments, diameter : 15-20 µm	Stegenga et. al., 1997 : 210, pl. 61 : fig. 4-5

TABLE 2 — continued

Species	Acronym	Ecological preference	Notes on morphology and distribution	References
PHAEOPHYTA				
<i>Asteronema rhodochortonoides</i> (Børgesen) Müller et Parodi	Ast rho	2a S' - uncommon	creeping axes and branched upright axes, diameter 8-11 µm	Müller & Parodi 1994 : 471-474, figs. 1-7, 9-11 ; Jaasund 1976 : 37, fig. 74 (as <i>Ectocarpus rhodochortonoides</i>)
<i>Dictyota humifusa</i> Hörnig, Schnetter et Coppejans	Dic hum	2b	well developed subtidally, poorly developed intertidally	Hörnig <i>et al.</i> 1992 : 57, fig. 6
<i>Feldmannia irregularis</i> (Kützing) Hamel	Fel irr		plurilocular sporangia 80-110 µm long, 25-40 µm wide	Kuckuck, 1963 : 371, fig. 6
<i>Hincksia rallsiae</i> (Vickers) Silva	Hin ral	2a - a single well-developed specimen		Jaasund 1976 : 37, fig. 73 (as <i>Giffordia rallsiae</i>)
<i>Sphacelaria novae-hollandiae</i> Sonder	Sph nov	2a S'	filaments (diameter 40-45 µm) forming dense tufts, propagules 70-100 µm long, 50-80 µm wide	Jaasund 1976 : 37, fig. 77
<i>Sphacelaria rigidula</i> Kützing	Sph rig	2a S' - often together with <i>Sphacelaria novae-hollandiae</i> but more abundant	filaments, diameter 20-30 µm, propagules 150-300 µm long	Jaasund 1976 : 37, fig. 75 (as <i>Sphacelaria furcigera</i> Kützing)
CHLOROPHYTA				
<i>Boergesenia forbesii</i> (Harvey) Feldmann	Boe for			Jaasund 1976 : 15, fig. 31
<i>Boedlea composita</i> (Harvey) Brand	Boo com	2a S	small specimens, anastomosis by means of tenacula	Jaasund 1976 : 11 fig. 23
<i>Bryopsis pennata</i> var. <i>secunda</i> (Harvey) Collins et Hervey	Bry pen	2a S'	main axis diameter 200-300 µm, ramuli diameter 100-130 µm	Jaasund 1976 : 17 fig. 36
<i>Caulerpa verticillata</i> J. Agardh	Cau ver	2a S' - a single specimen	stolons ~250 µm diameter	Coppejans & Preud'homme van Reine 1992 : 705, fig. 21, B
<i>Chaetomorpha</i> sp.	Cha spe	1b - high intertidal	minute specimens	
<i>Chlorodesmis hildebrandtii</i> A. Gepp et E. Gepp	Chl hil	2a S' - a single specimen	minute specimen	Jaasund 1976 : 27, fig. 55
<i>Cladophora vagabunda</i> (L.) van den Hoek	Cla vag	1b		Egerod 1974 : 136-137, fig. 13-16 ; Jaasund 1976 : 7, fig. 15, pl. 1 [as <i>Cladophora fascicularis</i> (Mertens) Kützing]
<i>Derbesia</i> sp.	Der spe		Upright filaments, diameter ~50 µm, unbranched, zoïdocysts ~130 µm long, ~75 µm wide First record of this genus along the East African coast	

Species	Acronym	Ecological preference	Notes on morphology and distribution	References
<i>Enteromorpha</i> sp.	Ent kyl	1b - high intertidal		Jaasund 1976 : 1, fig. 1
<i>Halimeda macroloba</i> Decaisne	Hal mac	2a S' - on basal stem portions, uncommon		Jaasund 1976 : 31, fig. 63
<i>Microdictyon</i> sp.	Mic spe	uncommon	anastomosis by means of smooth annular outgrowths of the apical cells, branching flabellate, basal attachment of thallus : section <i>Calodictyon</i> .	Setchell 1929 : 502
<i>Phyllocladion anastomosans</i> (Harvey) Kraft & Wynne	Phy ana	uncommon	minute specimens, stipitate reticulate monostromatic blade, anastomosis by means of tenacula	Kraft & Wynne 1996 : 131-140, figs. 16-25
<i>Ulva reticulata</i> Forsskål	Ulv ret	1a - high intertidal, uncommon	lamina ~50 µm thick	Jaasund 1976 : 3, fig. 5
<i>Valoniopsis pachynema</i> (Martens) Børgesen	Val pac	- a single specimen		Jaasund 1976 : 13, fig. 26
CYANOPHYTA				
isolated filamentous specimens	Cya fil	3 L - on the leaf base		
tuft forming specimens	Cya tuf	3		

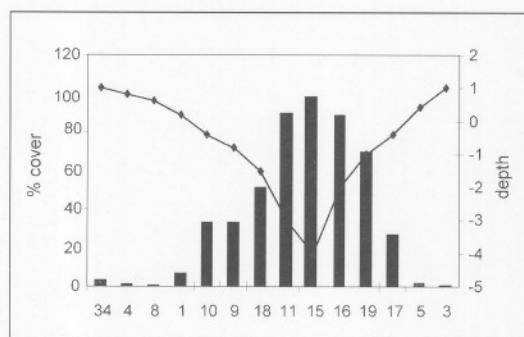


Fig. 3. — Average epiphyte cover on the seagrasses of the sample plots of transect A. Bars indicate the average epiphyte cover (%) per relevé of the seagrass specimens in a sample. The line indicates the depths (m) of the sample plots.

epiphyte cover, followed by *Enhalus acoroides*, *Halodule uninervis*, *Cymodocea rotundata* and *Thalassia hemprichii* with intermediate cover, and *Halodule wrightii* with extreme low cover (Table 3). The leaves of *Thalassodendron ciliatum* were mainly covered by crustose corallines and despite their permanent submersion they were poorly covered by other macroalgal epiphytes. The high cover values on *Cymodocea rotundata* and *Enhalus acoroides*, which were growing in high intertidal, warm pools, are a result of high covers of *Ceramium flaccidum*.

Differences in total epiphyte cover were observed between leaves of the same plant as well as between leaf-sides of the same leaf. Older leaves had a higher cover than younger ones : fig. 4 shows a linear correlation between leaf age and epiphytic cover in *Thalassodendron ciliatum*. This is easily explained by the fact that the colonising time of older leaves is longer. It should be stressed that the meristem of the leaves of seagrasses is basal. Therefore apical parts are older and frequently more epiphytised ; basal parts are younger and epiphyte-poor. Differences in total cover on the inner ("upper") and outer ("lower") surface of the leaves was tested using a Wilcoxon signed rank test (Clarke 1994 : 99-100). No significant differences were found for the leaves of *Thalassia hemprichii* and *Halodule uninervis*. On the leaves of *Thalassodendron ciliatum* the epiphyte cover was significantly higher on the inner

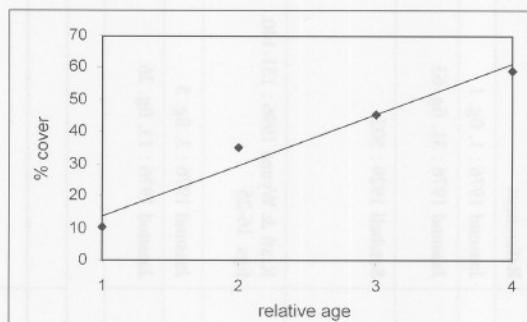


Fig. 4. — Epiphyte cover related to the relative age of the 4 oldest leaves of *Thalassodendron*. The cover values represent the average epiphyte cover (%) per leaf relevé. 1-4 : relative age of the 4 oldest leaves (4 : oldest, 1 : youngest).

surface. This difference was caused by crustose corallines which were the dominant group and preferred the upper side (exposed to the sunlight) of the leaves. The cover of other algae was similar on both sides. Here too, the epiphyte cover was higher at the leaf apex than at the base ; filamentous Cyanophyta were more abundant at the protected leaf base.

Stems form an ideal substrate for epiphytes as a result of their hard texture and long life span. Total cover of the 155 stem portions studied here was found to be mostly high, varying from 0-196 % with an average of 80 %. Only two seagrass species from the study area possess upright stems : *Halodule uninervis* occasionally, and *Thalassodendron ciliatum* which always forms a well developed stem of variable length. Epiphyte cover on *Thalassodendron* stems varied from 0 to 196 % with an average of 83 %. This was higher than the cover on *Halodule* which ranges from 1 to 110 % and an average of 48 %. The total cover on stems did not differ significantly between the various sites along the transects, and does not seem to be influenced by the water flow rate or the substrate type on which they grow.

Within the stem of the same plant (both of *Thalassodendron* and *Halodule*) differences in epiphyte cover could be observed between the different portions. The growing point of the stem is located just under the leaf sheath ; the youngest stem portions therefore are situated at the apex.

TABLE 3

Differences in epiphyte cover on the leaves of six seagrass species. Average cover (%) per leaf relevé of all epiphytes, encrusting corallines, and non-encrusting epiphytes ; number of relevés examined, number of relevés devoid of epiphytes, and the % value of these empty relevés.

Species	Average cover of all epiphytes (%)	Average cover of encr. corr. (%)	Average cover of non-encr. corr. (%)	# relevés	# empty relevés	% empty relevés
<i>Thalassodendron ciliatum</i>	29.6	28.3	1.3	160	22	13.7
<i>Enhalus acoroides</i>	12.2	6.0	6.2	34	7	20.5
<i>Halodule uninervis</i>	11.3	7.6	3.7	48	11	22.9
<i>Cymodocea rotundata</i>	6.5	0	6.5	26	13	50
<i>Thalassia hemprichii</i>	1.9	0.3	1.6	79	27	34.2
<i>Halodule wrightii</i>	0.3	0	0.3	10	6	60

Here the epiphytic cover was low, increasing downwards, remaining constant over the middle portion, and decreasing towards the base (Fig. 5).

CORRELATIONS BETWEEN EPIPHYTE COMPOSITION, HABITAT AND SEAGRASS PORTION

For the TWINSPLAN analysis average cover values of the stems and blades per plant were used. The TWINSPLAN classification of plots is shown in Figure 6. Indicator species (marked by *) as well as preferential species are indicated at each division. Acronyms of the species names are listed in Table 2. At the first division the seagrasses of intertidal habitats are separated from the subtidal ones. Some relevés with aberrant species composition do not follow this division (indicated in italic in Fig. 6). The intertidal group (IT) is mainly characterized by *Ceramium flaccidum*. The subtidal group (ST) is mainly characterized by crustose corallines, *Gracilaria corticata*, *Dictyota humifusa* and *Herposiphonia secunda* f. *tenella*. The intertidal plots are divided into a group with seagrasses of plot 13 and some epiphyte poor seagrasses (IT-1), characterized by *Laurencia minuta* and *Centroceras clavulatum*, and all other intertidal samples (IT-2), characterized by filamentous Cyanophyta and *Enteromorpha* sp. Plot 13 (IT-1.1) is situated in a shallow pool and is the only plot where seagrasses were growing on a substrate of low intertidal rhodoliths

instead of coral rubble or sand. Samples 10.6, 13.4 and 35.1 (IT-1.2) are characterized by a species poor epiphyton. The IT-2 group is divided into a group from shallow, sandy, warm pools which remain submerged at all times (IT-2.1), and a group with similar pools which emerge regularly (IT-2.2).

The subtidal group is divided into a group with all leaf samples (ST-L) and a group with all stem samples (ST-S). The 'subtidal-stem' group is mainly characterized by the indicator species *Dictyota humifusa*, *Gracilaria corticata*, *Gelidopsis intricata* and *Jania pumila*. The ST-S group is divided into samples from the shallow channel face (ST-S.1) and samples from the deeper part of the channel (ST-S.2). The subtidal-leaf group is not characterized by common species but rather by the absence of the ST-S indicator species. The *Halodule wrightii* samples (ST-L.1) form an exception in the ST group since this seagrass species grows normally in the intertidal zone ; this group is characterized by a low and species poor epiphyton. The ST-L.2 group is divided into a subtidal leaf group of *Thalassodendron ciliatum*, *Halodule uninervis* and *Enhalus acoroides* (ST-L.2.1), all characterized by a high cover of encrusting corallines, and a leaf group from the infralittoral fringe (ST-L.2.2), characterized by filamentous Cyanophyta. Further division of this last group is mainly based on the ecological parameters depth and rate of water flow.

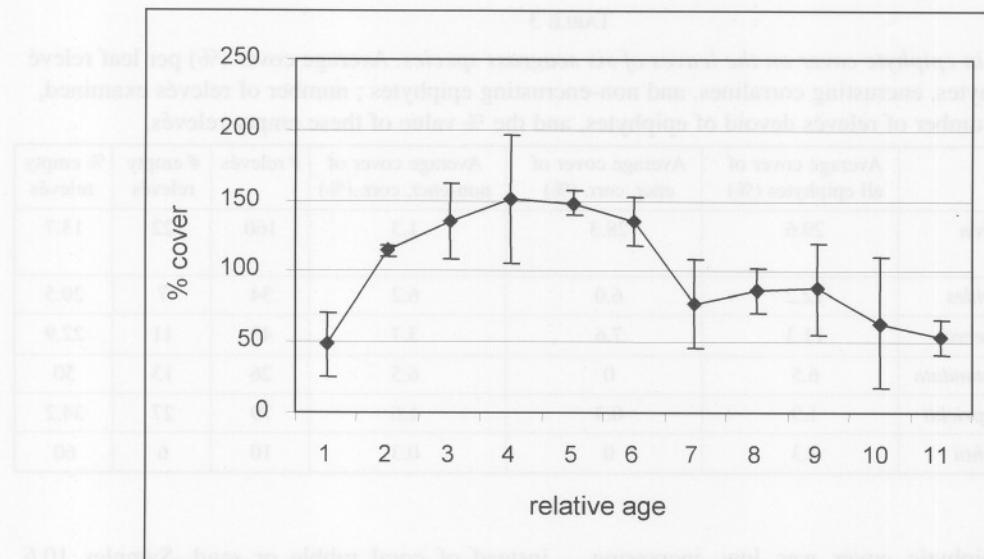


Fig. 5. — Average epiphyte cover per stem portion of all *Thalassodendron* and *Halodule* (with stems) specimens. 1-11 : relative age of the portion (1 : youngest, most apical portion, etc.).

On the basis of distribution data, TWINSPLAN results, and ordinations (Principal Component Analysis), the epiphytes can be classified according to their ecological preference as summarised in Table 2 : (1a) species restricted to the intertidal zone, (1b) species with a distinct preference for intertidal habitats, (1c) species with a scattered distribution but with higher abundance values in intertidal habitats, (2a) species restricted to subtidal zones, (2b) species with a marked preference for subtidal habitats, and (3) species without preference for a specific tidal zone. Class (2a) and (2b) can be divided into subclasses according to their substrate preference : (L) species found exclusively on leaves, (L') species with a distinctive preference for leaves, (S) species growing exclusively on stems, (S') species with a marked preference for stems.

ZONATION ALONG THE TRANSECTS

On hard substrate (fossil coral, sometimes with a very thin layer of sand) the *Thalassia hemprichii* meadows of the mid intertidal were characterized by a very poor epiphytic composition : *Cladophora vagabunda*, *Chondria pygmaea*

and a sporadic *Ceramium mazatlanense* were the only epiphytes. *Laurencia papillosa* and *Cystoseira myrica* (S. Gmelin) C. Agardh were the main accompanying epilithic macroalgae. In the infralittoral fringe the epiphytic flora became slightly richer, including next to the above mentioned species, the first crustose corallines, blue-greens, *Enteromorpha* sp., *Centroceras clavulatum* and *Ceramium flaccidum*. Their cover remained low. Accompanying epilithic species were : *Gelidiella acerosa* (Forsskål) J. Feldmann & G. Hamel, *Dictyosphaeria cavernosa* (Forsskål) Børgesen and *Turbinaria tanzaniensis* Jaasund.

On sandy substrate the seagrass vegetation was more varied. In the upper intertidal *Halophila ovalis* formed open stands sometimes combined with *Halodule wrightii*; both species were almost devoid of epiphytes. The mid intertidal zone was characterized by patches of *Thalassia hemprichii*, *Halodule uninervis* and *H. wrightii*. Locally these species grew in mixed stands. The epiphytes were rare : blue-greens, *Ceramium mazatlanense*, scarce and small *Caulacanthus ustulatus* and *Dictyota humifusa*. In the infralittoral fringe and

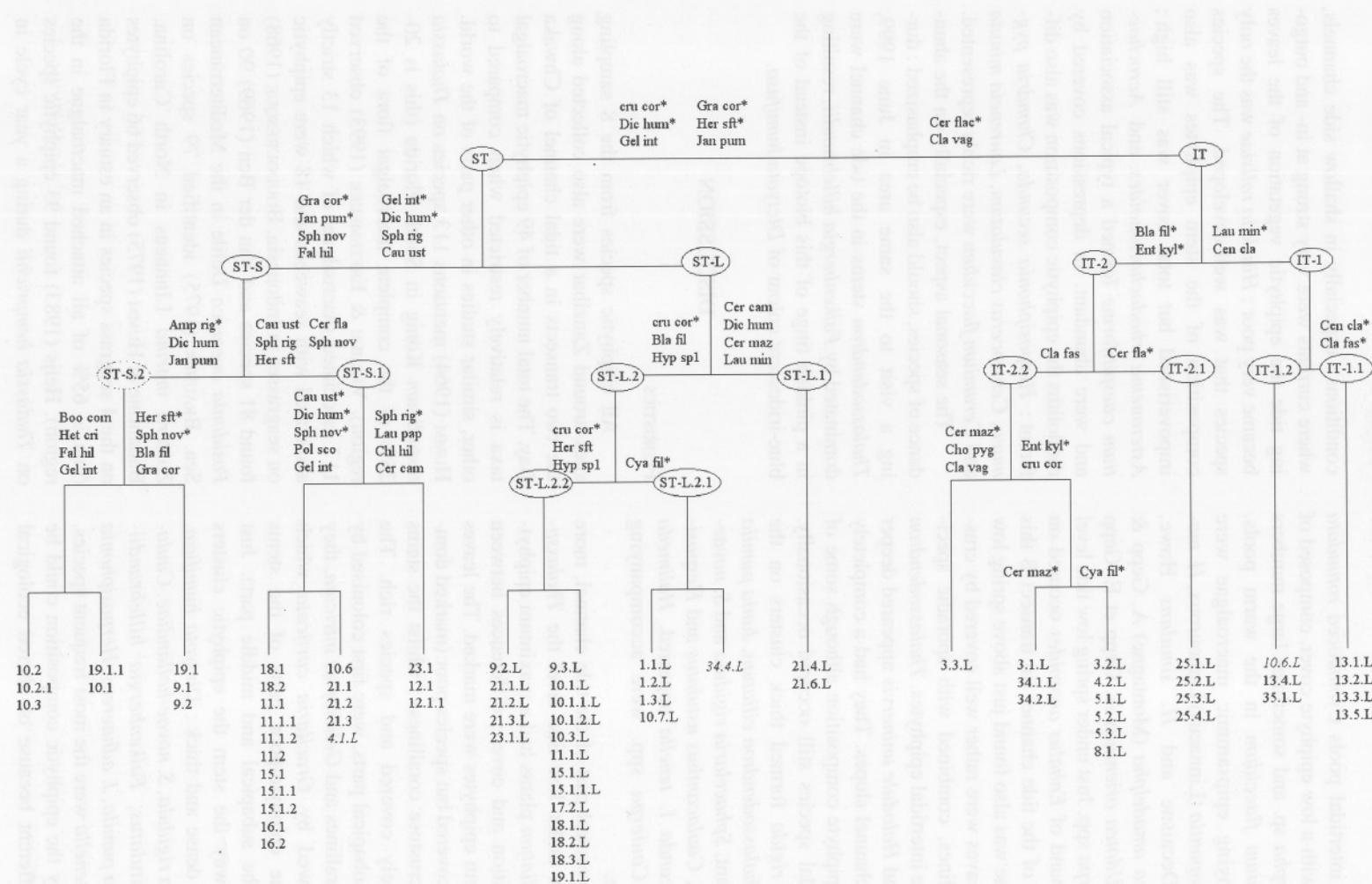


Fig. 6. — TWINSPLAN classification of plots. Indicator species at each division are marked by a (*) and preferential species are listed below them. The relevés with aberrant species composition are indicated in italic. See text for further explanation.

in deeper intertidal pools *Cymodocea rotundata* appeared with a low epiphyte cover, composed of *Enteromorpha* sp. and sometimes large numbers of *Ceramium flaccidum* in the warm pools. Accompanying epipsammic macroalgae were *Halimeda opuntia* (Linnaeus) Lamouroux, *H. macroloba* Decaisne and *H. simulans* Howe, *Avrainvillea amadelpha* (Montagne) A. Gepp & E. Gepp, *Udotea orientalis* A. Gepp et E. Gepp and *Caulerpa* spp. Just under spring low tide level a narrow band of *Enhalus acoroides* occurred on both sides of the tide channel (in transect B this narrow zone was also found just above spring low tide). Its leaves were rather well covered by crustose corallines, combined with sporadic specimens of the intertidal epiphytes. *Thalassodendron ciliatum* and *Halodule uninervis* appeared deeper along the channel slopes. They had a completely different epiphyte composition although some of the intertidal species still occurred occasionally. *Amphiroa rigida* formed thick clusters on the stems of *Thalassodendron ciliatum*, *Jania pumila* was abundant, *Sphaerelaria rigidula* and *S. novae-hollandiae*, *Caulacanthus ustulatus* and *Herposiphonia secunda* f. *tenella* appeared. *Halimeda* spp. and *Caulerpa* spp. were accompanying macroalgae.

In the central part of the tide channel, more than 1.5 m under low tide level the *Thalassodendron ciliatum* plants had a maximum epiphytic composition and cover; differences between leaf and stem epiphytes were marked. The leaves were well-covered but species poor (marked dominance of crustose corallines); whilst the stems were densely covered and species rich. The youngest, subapical parts, were first colonised by crustose corallines and *Gelidiopsis intricata*, they were followed by *Gracilaria corticata* which preferred the epiphyte-poor parts of the stems (between the subapical and middle part). Just above halfway the stem the epiphytic clusters were most dense and thick: *Dictyota humifusa*, *Sphaerelaria rigidula*, *S. novae-hollandiae*, *Caulacanthus ustulatus*, *Falkenbergia hillebrandii*-phase, *Jania pumila*, *J. adhaerens*, *Herposiphonia secunda* f. *tenella* were the most frequent species.

Locally the epiphytic composition could be strongly different because of altered ecological

conditions: especially in shallow side channels, where currents were very strong at in- and outgoing tide the epiphytic vegetation of the leaves became very poor: *Hincksia rallsiae* was the only species that was well-developed. The species composition of the stem epiphytes was also impoverished but total cover was still high; *Asteronema rhodochortonoides* and *Acrochaetium caespitiforme* formed a typical association and were abundant. In depressions covered by rhodoliths the epiphytic composition was also different: *Herposiphonia secunda*, *Chondria pygmaea*, *Centroceras clavulatum*, *Laurencia minuta* and *Ceramium flaccidum* were richly represented.

The seasonal aspect, especially on the abundance of species, should also be emphasized: during a visit to the same area in June 1999, *Thalassodendron* stems in the tide channel were dominated by *Falkenbergia hillebrandii*, resulting in a pinkish tinge of this biotope instead of the blue-iridescent colour of *Dictyota humifusa*.

DISCUSSION

FLORISTICS

All epiphytic species from the 8 sampling sites around Zanzibar were also collected along the two transects in a tidal channel of Chwaka Bay. The total number of 49 epiphytic macroalgal taxa is relatively restricted when compared to other, similar studies in other parts of the world. HUMM (1964) mentions 113 species on *Thalassia testudinum* König in South Florida (this is 20-25% of the complete macroalgal flora of the region). VERHEIJ & ERFTEMEIJER (1993) observed 117 associated macroalgae, of which 13 strictly associated with seaweeds and 18 were epiphytic on seagrasses in Indonesia. BOUDOURESQUE (1968) found 81 species and Van der Ben (1969) 90 on *Posidonia oceanica* Delile in the Mediterranean Sea. BRAUNER (1975) identified 79 species on *Zostera marina* Linnaeus in North Carolina. Ballantine & HUMM (1975) observed 66 epiphytes on the 4 seagrass species in an estuary in Florida (this is 65% of all attached macroalgae in the region). Heijns (1983) found 93 epiphytic species on *Thalassia hemprichii* during a year cycle in

Papua New Guinea. The data presented in these papers are generally the result of rather extensive research projects over several seasons. VERHEIJ & ERFTEMEIJER (1993) and REYES & Sansón (1997) studied the temporal distribution of epiphytes on seagrasses and found seasonal variation in the number of some species. Reasons for the limited number of epiphytes in this study are : (1) probably some species are missing because of their seasonality (this study was carried out during one month in the dry season) ; (2) some taxonomic groups were not identified (not even to genus level), e.g. the crustose Corallinaceae. WALKER and WOELKERLING (1988) identified 3 genera in their study in Shark Bay, Western Australia. Here they are regarded as a single taxon. (3) Some species such as *Hypnea* spp. and *Tolyptiocladia calodictyon* were previously observed as epiphytes on seagrasses but are not included as such in this study ; (4) as the main purpose of this study was an ecological approach (distribution of epiphytes along a transect and on individual plants) smaller species have probably been overlooked. Although the number of macroalgal epiphytes is limited, they contain 4 species (*Chondria pygmaea*, *Laurencia minuta*, *Acrochaetium caespitiforme* and *Hypoglossum simulans*) and one genus (*Derbesia* sp.) new for the East African coast. They were recently reported for the East African coast by COPPEJANS *et al.* (2000). *Hypoglossum simulans* is discussed in WYNNE & DE CLERCK (2000).

The Rhodophyceae represented by 27 species, are dominant in species number and contribute for 83% of the epiphyte cover. This is mainly due to the cover by crustose corallines, but also the frequent presence of *Gelidiella lubrica*, *Gelidiopsis intricata*, *Ceramium flaccidum*, *C. camouii*, *Jania pumila* and *Gracilaria corticata*. According to Heijns (1985) and BROUNS & Heijns (1986) crustose Corallinaceae also are the dominant epiphytic species on seagrasses in Papua New Guinea throughout the year, with a mean cover of 18% per plant. Research in Australia (WALKER & WOELKERLING 1988) shows that 40% of the dry weight of the leaves of *Amphibolis antartica* (Labillardière) Sonder et Aschers is composed of CaCO₃ from the epiphytic Corallina-

ceae (*Fosliella*, *Pneophyllum*, *Melobesia*). These Corallinaceae considerably contribute to the sediment composition (up to 15-30%). In Chwaka Bay they are present in 65% of the relevés presenting epiphytes. On the leaves they have a mean cover of 14%, on the stems of 41%. The cover on the leaves of the different seagrass species is strongly divergent : 28% on *Thalassodendron ciliatum*, 7.5% on *Halodule uninervis*, 6% on *Enhalus acoroides* and 0.3% on *Thalassia hemprichii*. *Cymodocea rotundata* and *Halodule wrightii* were devoid of corallines. This distribution does not reflect a preference for a specific seagrass, but rather the biotope where it occurs : corallines thrive best under continuous submerged conditions and therefore are best developed on *Thalassodendron ciliatum*. As the surface area of the leaves is many times larger than that of the stems the total biomass of epiphytic corallines on the leaves is much higher than on the stems. WALKER & WOELKERLING (1988) found 60% more coralline biomass on the leaves of *Amphibolis* (a morphologically similar seagrass to *Thalassodendron ciliatum*) than on the stems.

The Phaeophyceae epiphytes are only represented by 6 species, but they contribute for 14% of the epiphytic cover. The large quantities of *Sphaerelaria rigidula* and *S. novae-hollandiae*, as well as of *Dictyota humifusa* on *Thalassodendron* stems, are mainly responsible for this relatively high cover. The green algal epiphytes, represented by 14 species contribute for only 1% of the epiphytic cover. They are mainly small and rarely occurring species. The blue-greens, which were not identified, represent 2% of the total cover.

GENERAL ECOLOGICAL ASPECTS

Species number, as well as cover, of seagrass epiphytes are highest in the subtidal zone, especially on *Thalassodendron ciliatum*. Permanent submersion resulting in more constant temperature, salinity and pH, and the presence of perennial substrates (the stems) are the main factors optimising their development. Even in this subtidal biotope, leaves are a less suitable substrate for epiphytic growth than stems. Possible reasons could be : (1) the smooth surface of the leaves

prevent spore attachment, (2) the motion of the leaves in currents or waves (shear stress) detach spores or germlings, (3) the densely packed leaves partly cover each other, prevent colonisation, (4) the scouring effect of the leaves among themselves eliminating developing epiphytes, (5) the presence of the leaves to the water surface resulting in a (too) strong irradiation for most species (except for corallines which are partly protected against strong light by the CaCO_3 impregnation), (6) the relatively short life span of leaves not allowing the development of numerous epiphytic species. The greatest number of epiphytes and the densest cover are found on the oldest parts (apices) of the upper surface of the oldest leaves (the lowermost ones). Only blue-greens are more abundant on younger (basal) leaf parts. This may be due to the fact that Cyanophyta frequently are early colonizers which are easily outcompeted by the crustose corallines. Under some conditions (nutrient rich environment) they can remain abundant.

Seagrass stems are an optimal substrate for epiphyte growth because of (1) the rough surface (leaf scars), optimising spore fixation, (2) less subject to continuous motion, (3) more spaced, allowing water currents, optimising the supply of spores, (4) less strong irradiation (shaded by the leaf cover), (5) the perennial nature of the stem allowing the development of slow growing species. The subapical (youngest) part of the stem has a low epiphytic cover due to the short colonisation time. The maximum density of epiphytes is generally situated above halfway the stem. Then the cover decreases towards the stem base, possibly as a result of the decrease in light intensity and the increasing scouring effect of bottom sediments.

Sublittoral populations of *Halodule uninervis* generally have a high epiphytic cover on the leaves. When stems are formed, epiphytic cover is variable but in general smaller than on similar *Thalassodendron ciliatum* stems. A possible explanation is that the stems of *Thalassodendron* have a harder texture and make them more suitable for epiphyte growth. *Enhalus acoroides* also is a subtidal seagrass species, but

the long (up to 1 m), tough, perennial, vertically placed, strap-like leaves are not highly epiphytized, even when growing mixed with *Thalassodendron ciliatum* with dense epiphytic growth on the stems and leaves. No explanation was found, but the production of exudates preventing spore germination may be a hypothesis.

In the intertidal, some seagrasses are (almost) devoid of epiphytes : *Halophila ovalis* has small, very short-lived leaves and grows in high intertidal, shallow, warm pools, an environment which is not suitable for macroalgal development. *Halodule wrightii* is growing in similar pools and also has short-lived, narrow leaves ; it rarely has any epiphytic growth. In some cases (not in Chwaka Bay) populations have been formed in pools with a pinkish red fringe at the leaf margins composed by *Ceramium* sp. The other intertidal species *Thalassia hemprichii*, *Cymodocea rotundata* and *Halodule uninervis* have a similar, rather poor, epiphytic flora, the composition of which greatly depends on the habitat in which they grow (level above low tide, intertidal pools or emerged tidal flats).

The list with ecological preferences of epiphytic species should be considered with caution : it is exclusively based on observations in a single area, in one season ; data from other tidal channels (possibly with freshwater influence), lagoons, open-sea areas should be added. Moreover, some species were only observed occasionally, obfuscating clear conclusions.

The zonation scheme of seagrasses and associated epiphytic flora described here is based on two transects only. Rough observations and comparisons with other sites around Zanzibar seem to confirm that it can be generalized for the island. Along open sea coasts of Tanzania (south of Dar es Salaam) *Thalassodendron ciliatum* stems are characterized by large quantities of *Dictyota* species (of which the newly described *D. rigida* DE CLERCK et COPPEJANS). Similar studies in other East African areas would therefore be of great importance to test the conclusions and hypotheses formulated here. As stated previously, these are preliminary results for the East African coast.

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