P.S.Z.N. I: Marine Ecology, 16 (2): 165–179 (1995)

ISSN 0173-9565

Accepted: April 14, 1995

Low-Tide Exposure of Sponges in a Caribbean Mangrove Community

K. RÜTZLER

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA.

With 5 figures and 2 tables

Key words: Intertidal *Porifera*, red-mangrove roots, fouling community, temperature-salinity stress, desiccation.

Abstract. Sponges on subtidal red-mangrove prop roots may become exposed to air many times per year during very low tides. Full exposure is stressful and potentially fatal, particularly if occurring in full sun. Large root sponges show distinct species zonation between mean low water and −0.5 m. *Haliclona implexiformis* and *Lissodendoryx isodictyalis* are near the top while *Scopalina ruetzleri* are near the lower end of the range. Temporary experimental desiccation resulted in 100% recovery of all three species after they had been exposed to either sun or shade for up to 2 h. *Scopalina* is the least resistant and lost over 90% tissue within 3 days after the 4-h and 6-h experiments; the remaining cell mass succumbed to infestation by microbes. *Haliclona* and *Lissodendoryx* recovered from as much as 6 h in full sun but lost 85% and 80% of the original tissue volume, respectively. In *Lissodendoryx*, clusters of larvae developed in the regenerating fragments. Water loss tolerated by the three species is estimated as 66% of wet weight in *Haliclona*, 54% in *Lissodendoryx* and 38% in *Scopalina*. Salinity of interstitial seawater (pore water) extracted from exposed sponges rose from ambient 3.5% to 4.3–4.8% after 1 h, to 5.1–5.9% after 6 h. Most endobionts died or left their host during this last phase. Natural vertical zonation in these sponges reflects their resistance to tidal exposure.

Problem

Mangroves are the predominant tropical shallow-water community worldwide and have a distribution parallel to that of coral reefs. For several years we have studied an example of this ecosystem in Belize in the Central American Caribbean (RÜTZLER & FELLER, 1987, 1995). We distinguish between two types: mainland-fringing mangrove forests with predominately estuarine character and nutrient and sediment input from land runoff; and island-mangrove swamps that are characterized by near-oceanic salinity and local nutrient cycling and sediment production. An important attribute that distinguishes Caribbean mangroves from most others is a tidal range of less than 0.5 m. Island mangroves are the predominant type in the extensive lagoon behind the barrier reef of Belize and indeed throughout the West Indies.

In our study area at Twin Cays, just inside the barrier reef of southern Belize (RÜTZLER & MACINTYRE, 1982), red mangrove (*Rhizophora mangle*) lines the perimeter, interior lakes, and tidal canals and is anchored in the mud-covered peat

bottom by long, arched prop roots. These roots provide most of the solid (non-sedimentary) substrate in this environment and support a rich sessile-benthos community that extends well into the subtidal zone. The main components are algae, sponges, and tunicates, with many associated invertebrates and a few fishes that find shelter among the fouling community, particularly inside the sponges.

Sponges are generally not considered resistant to environmental extremes such as exposure to air during low tide because they are unable to move or close their aquiferous system, have no protective shells or cuticular structures, and generally have only one reproductive period per year (only few species are reported as r-strategists). The present study was prompted by the observations that there is a vertical zonation of sponge species on mangrove roots and that large subtidal portions of roots with sponges had become exposed to air during a series of exceptionally low mid-day tides in the wake of a major El Niño event in 1983. These low tides, almost 40 cm below 0 (mean low water) arrived during periods of full sunlight and left large, massive sponges air-exposed for periods of 1–4 h or more. The objectives of this study were to determine for selected species the natural frequency, duration and tolerance of exposure to air, find possible protective mechanisms against water loss or aiding recovery from desiccation, and clarify whether sponge zonation on the roots reflect the degree of their resistance to tidal exposure.

Material and Methods

Surveys of mangrove-root species zonation were made by snorkeling through Hidden Creek, Twin Cays (16°49.95'N, 88°06.34'W; maps in DE WEERDT *et al.*, 1991; RÜTZLER, 1993) for 0.5 h and measuring the distance from the water line to the center point of each specimen recorded to the nearest centimeter. Depth data were corrected against a tidal tracing obtained at the same location and related to mean low water (0 m). Other tidal information was taken from data published by the National Oceanic and Atmospheric Administration (NOAA, US Department of Commerce), Tidal Analysis Branch, for Key West (time correction for Belize: +14 min for high water, +47 min for low water). NOAA tables were supplemented by time-series measurements (30-min intervals) from the National Museum of Natural History's coral reef field station on Carrie Bow Cay (ca. 3 km from Twin Cays) using either a capacitive or an ultrasonic sensor. The Carrie Bow Cay records are complete for 9 months, January to June, September, November, and December 1993, partial for rest of that year (the tide gauge was inoperative during 1994). All records were used to calculate mean lower low water which is the datum (0 cm) for the NOAA tables.

Sponges chosen for the experiments belong to different families and orders of the class *Demospongea* (recent descriptions in parentheses): *Haliclona implexiformis* (HECHTEL), *Chalinidae*, *Haplosclerida* (DE WEERDT *et al.*, 1991:202); *Lissodendoryx isodictyalis* (CARTER), *Myxillidae*, *Poecilosclerida* (VAN SOEST, 1984:54); and *Scopalina ruetzleri* (WIEDENMAYER), *Axinellidae*, *Axinellida* (WIEDENMAYER, 1977:145, as *Ulosa*). To determine resistance to desiccation, specimens of all three species were cut under water into uniform pieces (ca. 20 × 25 mm ectosomal area, 15 mm thick; 8 ml volume) and tied to acrylic grid frames (light-diffuser panels) using 40 lb (18 kg)-test monofilament fishing line and brass crimps. Each fragment was kept at least 20 mm apart from the next and, once returned to its habitat, healed and attached to the new substrate over night. After 6 days (4–10 May 1994) *in situ* (but well below low-tide level) recovery was complete as indicated by new tissue growth. At that point, replicates (4 for each species and treatment) were exposed to air in sun and shade, for 1, 2, 4, and 6 h (10 May 1994) and immediately resubmerged and returned to the habitat. The condition of all experimental sponges was monitored daily for 6 days after the treatment. Quantitative estimates of tissue health were made on days 3 and 6 and compared with controls that were never exposed to air.

Identical but separate treatments were used for histological observations by light and transmission electron microscopy and for determining water loss rates. Microscopy samples were fixed in 1.5%

glutaraldehyde buffered in 0.2 M cacodylate with 0.1 M sodium chloride and 0.4 M sucrose (pH 7.2). For light microscopy, epoxy-resin embedded sections were ground, polished, and stained in safranin-crystal violet according to RÜTZLER (1978); semithin (0.5 μm) TEM sections stained in methylene blue were also used. TEM subsamples were post-fixed in 2% osmium tetroxide in the same buffer mix. Results of more detailed electron microscopy will be reported separately (RÜTZLER, in press).

An extra set of samples consisting of one small (ca. 30 ml volume) but entire specimen of each of the experimental species was sacrificed to determine water loss over time during exposure to air. It was suspended in the open shade (air flow, 0–1 $m \cdot s^{-1}$; relative humidity, 68%) and weighed fresh (wet weight to 0.01 g after quick external blot with tissue paper) and after 1 h, 3 h and 6 h between 10:00 h and 16:00 h. Ash-less dry weight was calculated after weighing (to 0.1 mg) aliquots dried to constant weight at 70 °C and ashed in a muffle furnace at 510 °C.

During the period of preparation, experiment, and recovery (28 April to 16 May, 1994), the tidal regime at Twin Cays was recorded by a float sensor in a still well (4:1 gear ratio to recording stylus) located on a dock in the island's main channel. A self-contained thermistor temperature recorder (24 min time series, 0.1 °C resolution) was installed at the Hidden Creek sponge habitat site just below lowest expected tide level for this period. Salinity measurements were taken with a refractometer to the nearest part per thousand.

Results

1. Physical parameters and zonation

Hidden Creek is typical for tidal channels at Twin Cays. It connects an open bay (Boston Bay) and a swamp-enclosed lake (Hidden Lake) and allows tidal water flow between the two. The creek is about 150 m long, 2–4 m wide, and 0.5–2 m deep. Starting from Boston Bay, it meanders roughly due southwest for two thirds of its way, then turns north toward the lake. The present study was conducted in the initial 30 m portion of the channel.

Boston Bay is an expansion of the main channel that separates Twin Cays; it is in direct connection with the barrier-reef lagoon and has water of similar quantity. In contrast, Hidden Lake is an isolated, shallow (less than 50 cm) lake with mud and peat bottom that is subject to extreme fluctuations of temperature and salinity. During each tidal cycle, the water from one of these two very different environments flows through the long, narrow channel, reaching at times considerable speed, and mixes with that of the other. During the sunny experimental period (8–16 May, 1994), temperature cycled with the tides between 28.1 °C and 35.9 °C, salinity between 3.3% and 3.9%. Previous measurements at the same location peaked at 16 °C/39 °C and 2.8%/4.1%.

The tides in the Carrie Bow Cay area are microtidal and of the mixed semidiurnal type (KJERFVE *et al.*, 1982). Records taken during 1993 show a monthly range of 22–48 cm (average 35.4 cm). Tidal range at Twin Cays during 29 April to 16 May 1994 was 34 cm (the gauge at Carrie Bow Bay was inoperative at that time). Tidal predictions for the past 3 years (1992–1994) were also consulted to determine frequency of ebb-tide exposures to 0 cm (mean lower low water) or below. These may occur at a peak frequency of 9–14 times a month between April to June (Table 1).

The bottom of Hidden Creek is made up of peat covered by mud, decaying mangrove leaves, bacterial and algal mats, and occasional strands of turtle grass (*Thalassia testudinum*). The sides are vertical or undercut, exposing peak banks behind a phalanx of red mangrove prop roots arching down from the trees that

Table 1. Frequency of ebb tides exposing MLLW (0 m) or lower occurring during full daylight hours (10:00 h–16:00 h) in a 3-year period (Key West predictions corrected for Belize time).

	frequency				
month	1992	1993	1994	range	average
January	2	0	0	0–2	0.7
February	5	7	8	5–8	6.7
March	9	8	4	4–9	7.0
April	10	9	12	9–12	10.3
May	13	12	12	12–13	12.3
June	14	14	11	11–14	13.0
July	14	14	13	13–14	13.7
August	1	6	4	1–6	3.7
September–December	0	0	0	0	0

line the channel. Where the mangroves (*Rhizophora mangle*) are tall and dense the channel banks are in deep shade. In other places, where the trees are small or there are gaps in the canopy, the creek may be radiated by full sun.

Vertical or overhanging peat banks and prop roots are the only solid substrates along these creeks that have moderate sediment exposure and allow sessile filter feeders, such as sponges and ascidians, to develop species-rich communities. Limiting for vertical distribution (other than substrate availability) are the fine mud sediments on the bottom and the water level at the top. The calcified green alga *Halimeda opuntia* is a strong competitor for space. A census of the most common and quantitatively important invertebrates fouling the mangrove roots at the entrance of Hidden Creek revealed 12 species, 10 of them sponges (Fig. 1).

Tide tables and graphs allow estimates of frequency of annual low-tide exposure (in % of tides) for each position, assuming that it is occupied by an average-sized specimen (or cluster, in case of the non-sponges) of which one half falls dry for at least 1 h. Starting at high tide level, the mangrove oyster, *Isognomon alatus* (*Isognomidae*, not a true oyster), the only obligatory intertidal species of the group, occupies the range of +24 to −2 cm (0 = mean lower low water, MLLW); exposure frequency of an animal in the center is 84% of low tides. Below follow *Haliclona implexiformis* (*Chalinidae*, *Haplosclerida*) starting at +13 cm (73%); the pale anemone *Aiptasia pallida* (*Aiptasiidae*) and *H. tubifera* (*Chalinidae*, *Haplosclerida*), +8 cm (44%); *Lissodendoryx isodictyalis* (*Myxillidae*, *Poecilosclerida*), *Spongia tubulifera* (*Spongiidae*, *Dictyoceratida*), and *Geodia papyracea* (*Geodiidae*, *Choristida*; studied in this location by RÜTZLER, 1988), +3 cm (15%); *H. curaçaoensis* (*Chalinidae*, *Haplosclerida*), −2 cm (13%); *Scopalina ruetzleri* (*Axinellidae*, *Axinellida*), *Tedania ignis* (*Myxillidae*, *Poecilosclerida*), *?Dictyodendrilla* sp. (*Dictyodendrillidae*, *Dendroceratida*), *Biemna caribea* (*Biemnidae*, *Poecilosclerida*), −12 cm (0.2%).

2. Effects of exposure to air

The effects of different exposures, indicated by the success rate of recovery after return to the habitat, are summarized in Table 2. In all, three replicates were lost

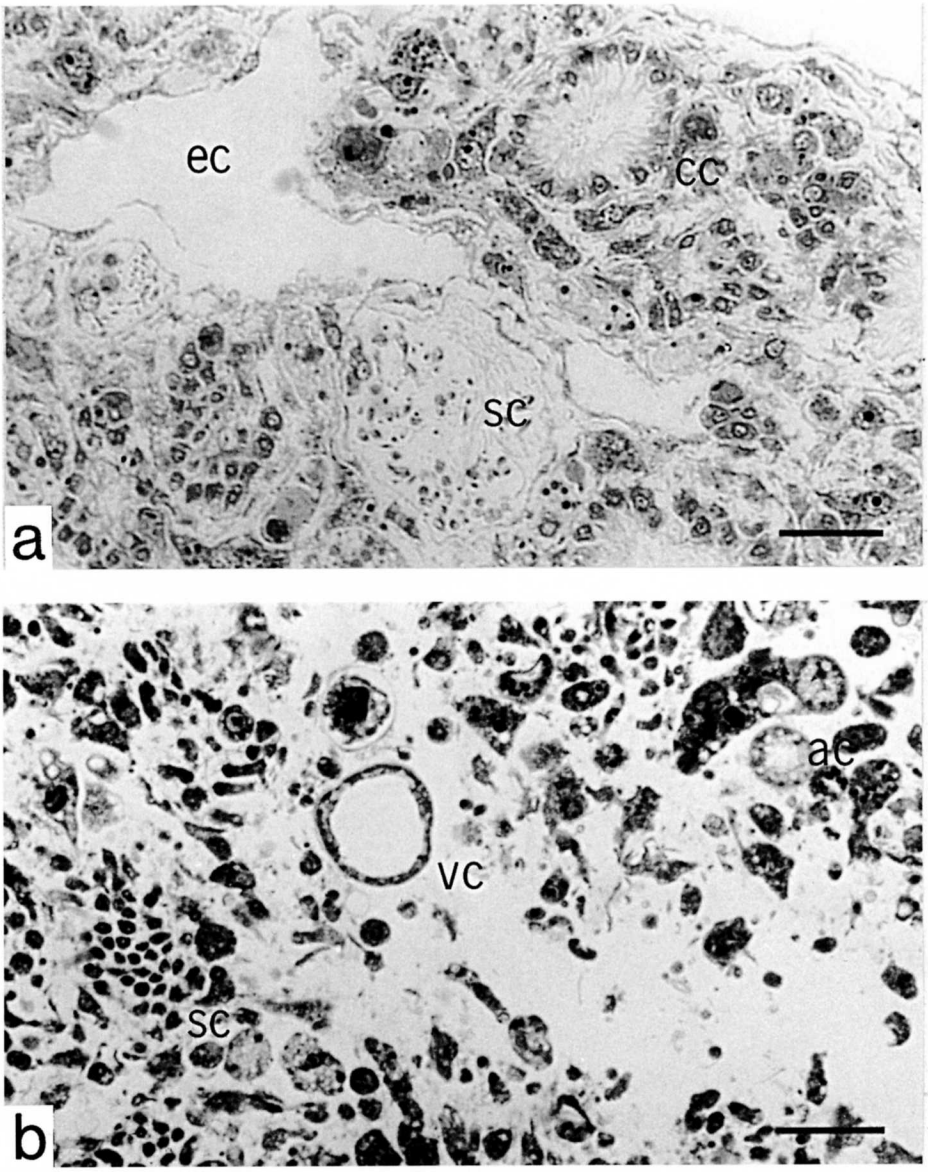

Fig. 2. *Scopalina ruetzleri*, light micrographs. a: healthy sponge showing choanocyte chambers, exhalant canal, and spermatogenic cysts. b: similar area after 6 h exposure to air, with choanocytes in confusion and vacuolated archeocytes. (ac = archeocyte, cc = choanocyte chamber, ec = exhalant canal, sc = spermatogenic cysts; vc = vacuolated cell; scales: 20 μm).

Choanocyte chambers are ovoid, 23×29 μm, with 10–12 cells per central cross section. Archeocytes measure 10–13 μm, some large, elongated cells reach 18×18 μm. Globiferous cells, 8×14 μm, spermatogenic cysts (50 μm) in various stages of development, and embryonic larvae (350 μm) are common. Air-exposed specimens lose their organized chambers, as seen in the above species, and have a few enlarged

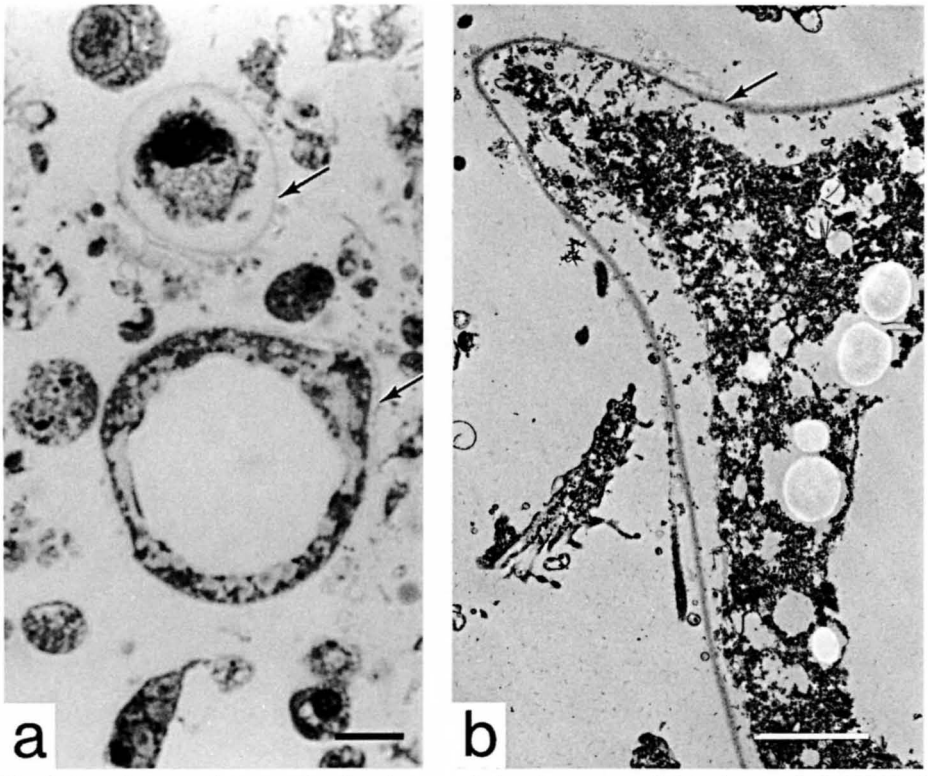

Fig. 3. *Scopalina ruetzleri*, vacuolated and encapsuled archeocytes. a: light micrograph. b: TEM of detail (arrows point to spongin-like capsules; scales: a = 50 μm, b = 2 μm).

archeocytes with single vacuoles. TEM examination of some of the stressed spermatogenic cysts reveal disintegrating spermatozoa (Fig. 4c, d). Fragments regenerating from severely damaged specimens were found to contain healthy early stages of larvae.

Scopalina ruetzleri is a brilliant orange species with conulous surface skin over extended, large (2–6 mm and more) choanosomal lacunae. Its consistency is very soft and fleshy. The ectosomal zone is 100 μm thick and the densest of the three species, packed with cells and spongin. The histology is complex, with great diversity of cell types (Fig. 2a; still under study). Chambers are ovoid to baggy irregular in outline, 32×34–50×27 μm, lined by 21–23 cells per central cross section; chambers are tightly crowded together. Archeocytes are large (15×7–18×8 μm) but less common than more rounded cells, 16–23 μm, that are filled with characteristic angular, highly refractile inclusions of less than 1 μm. Spermatogenic cysts are about 22–40 μm in diameter. Air-exposed specimens show disorganized choanocytes and enlarged vacuolated archeocytes (Fig. 2b), with either a single large or a group of small vacuoles. Some cells are encapsuled by a thin layer of spongin-like material (Fig. 3), others are disintegrating (Fig. 4a, b). Presence of non-symbiotic bacteria indicate the start of decay processes that lead to the death of the entire specimen (Fig. 5).

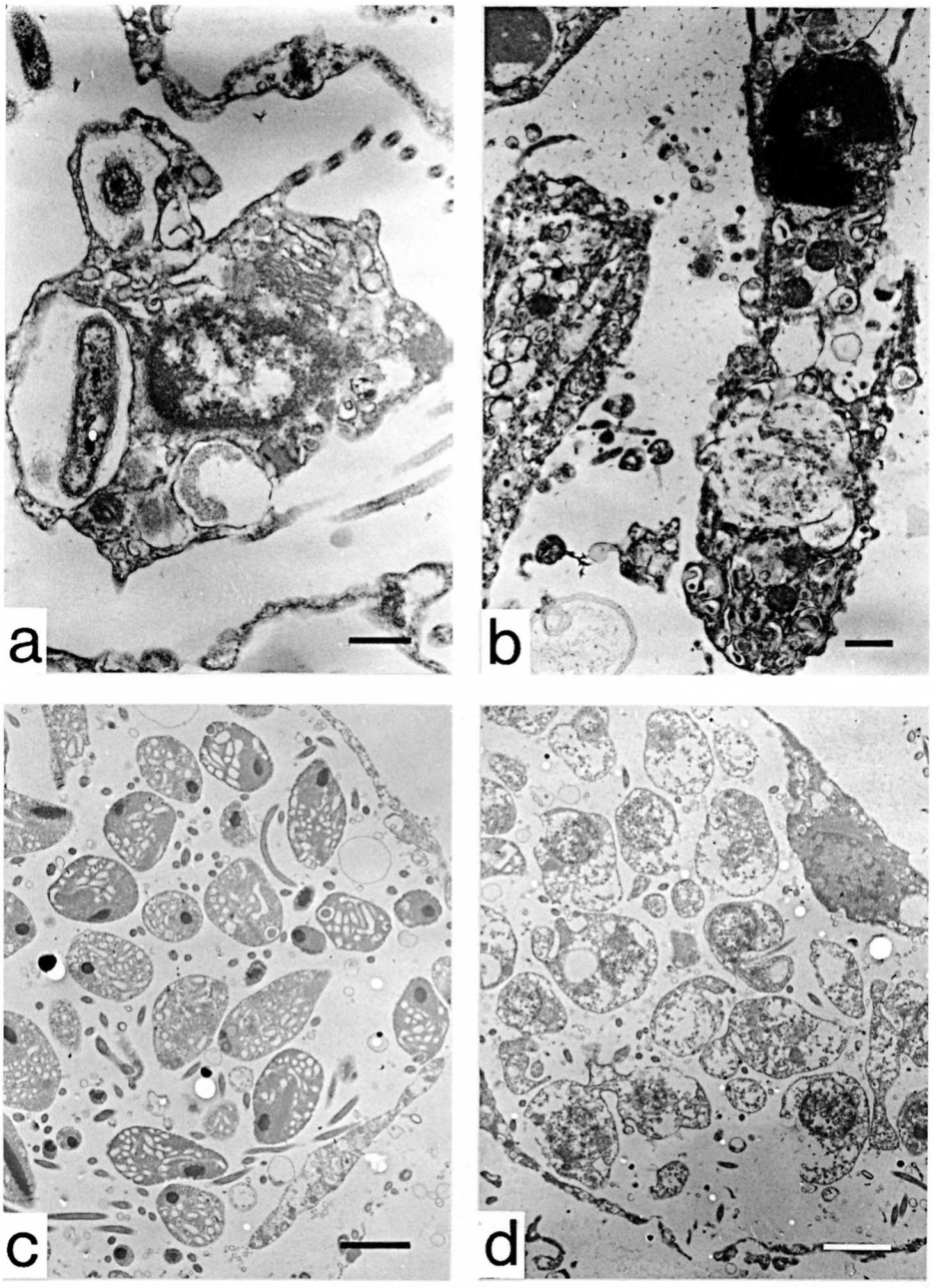

Fig. 4. TEM of sponge-cell details before and after exposure to air. a: *Scopalina ruetzleri*, healthy choanocyte with bacteria in digestive vacuoles. b: similar cell undergoing cytolysis. c: *Lissodendoryx isodictyalis*, healthy spermatogenic cyst. d: similar cyst with cytolysis of spermatozoa in progress. (scales: a, b = 500 nm, c, d = 2 μm).

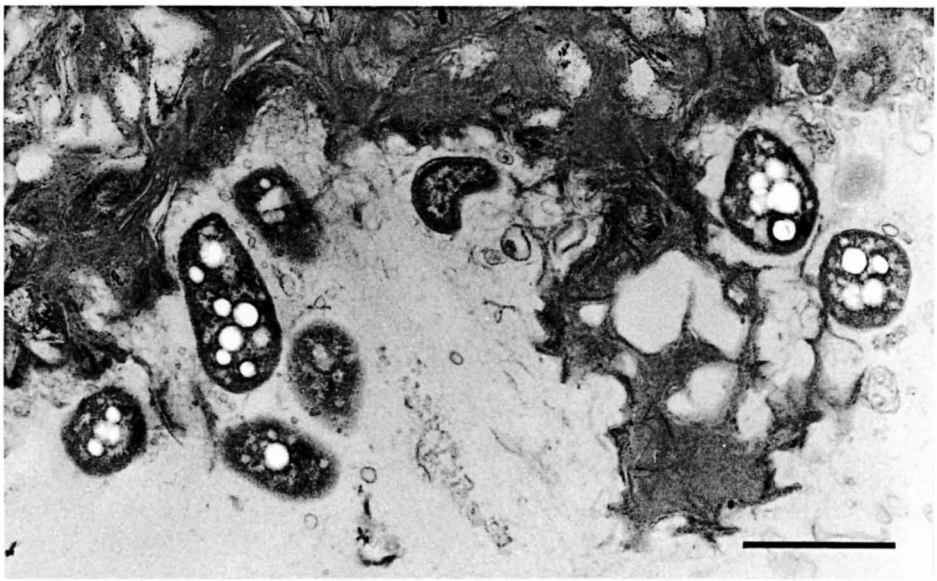

Fig. 5. *Scopalina ruetzleri*, TEM of disintegrating inclusion cell with decay-associated bacteria (scale = 1 μm).

Discussion

The rich fouling community on prop roots of mangroves like Twin Cays expresses a distinctive intertidal zonation despite a mean tide of only 15 cm. The effect of water level changes can be enhanced by certain combinations of astronomical and meteorological conditions and cause substantial physical disturbance. Such stochastic processes, also including strong tidal currents, waves, and the effects of predation, may be at least partly responsible for the conspicuous instability of these communities (BINGHAM & YOUNG, 1995). On the other hand, species adapted to resist these disturbances contribute toward community structure and predictability. The present observations show that *Haliclona implexiformis* and *Lissodendoryx isodictyalis* occupy a higher and more stressful level in the space hierarchy of the limited mangrove prop-root habitat than *Scopalina ruetzleri* and confirm the original hypothesis that both have substantially higher resistance to desiccation than the latter species.

Reports on truly intertidal sponges are uncommon and mostly restricted to cool (boreal) climatic zones. The animals are primarily found close to low-tide level and in damp, sun-protected habitats, such as the lower surfaces of rocks and boulders, shaded crevices, and areas overgrown by seaweed (DE LAUBENFELS, 1947; BURTON, 1949; ELVIN, 1976). Specially adapted species may survive direct sun exposure by growing buried in mud that holds water for hours, as was observed in a Malaysian mangrove channel (RÜTZLER, 1964). In the tropics, sponges subject to drying during low tide become exposed to four major adverse conditions: loss of oxygen and food supply provided by circulation of fresh seawater, increase in salinity by evaporation of interstitial water retained by the animal, increase of exposure to ambient radiant energy, including temperature and ultraviolet radiation, and,

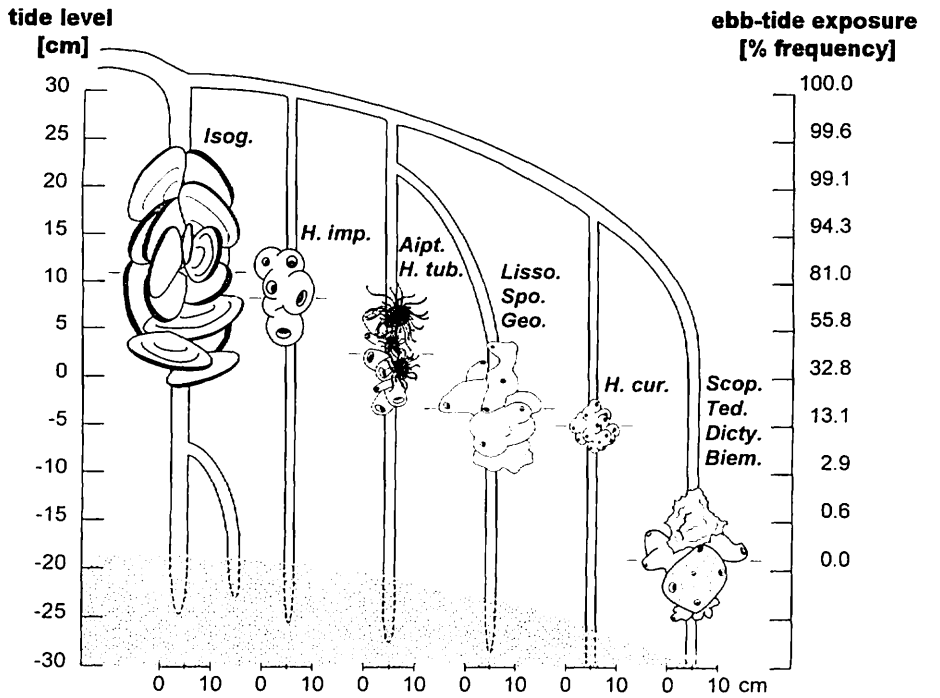

Fig. 1. Schematic presentation of ebb-tide frequencies and vertical distribution (mean ranges) of the most common large invertebrates fouling red-mangrove prop roots at the Boston Bay entrance of Hidden Creek, Twin Cays. (*Aipt.* = *Aiptasis pallida*; *Biem.* = *Biemna caribea*; *Dicty.* = *?Dictyodendrilla* sp.; *Geo.* = *Geodia papyracea*; *H. cur.* = *Haliclona curaçaoensis*; *H. imp.* = *H. implexiformis*; *H. tub.* = *H. tubifera*; *Isog.* = *Isognomon alatus*; *Lisso.* = *Lissodendoryx isodictyalis*; *Scop.* = *Scopalina ruetzleri*; *Spo.* = *Spongia tubulifera*; *Ted.* = *Tedania ignis*).

from their support frame but not more than one per series of four replicates; controls remained unchanged.

Exposure of 1 h in shade or sun had only negligible effects. Development of an initial, slight bacterial infection (whitish filaments of the multicellular, sulfur-fixing *Beggiatoa*) on *Scopalina ruetzleri* disappeared by day 3. Exposure of 2 h was tolerated well, in shade and sun, by both *Haliclona implexiformis* and *Lissodendoryx isodictyalis* but not by *Scopalina*. Those replicates of *Scopalina* exposed to the sun entered a dormant stage, indicated by permanent body contraction with skeleton fibres left exposed, preservation of live colour, and lack of decay-associated microbe community. Recovery after extensive tissue reorganization is considered possible but could not be confirmed during the observation period. Exposure of 4 h resulted in some tissue loss in *Haliclona* from the shaded series but only two replicates were affected. Eventually, both specimens regenerated fully, sloughed the dead cell and skeleton mass and by recovery day 6 replaced the loss with new growth. *Lissodendoryx* showed no signs of stress from air exposure in either shade or sun. *Scopalina* on the other hand, suffered extensive cell death as indicated by discoloration and *Beggiatoa* infection over most of the body surface of all replicate specimens. All experimental sponges of this species had become macerated by day

Table 2. Results of desiccation experiments in shade (L−) and in full sunlight (L+) described in the text. Quantitative dead-tissue estimates (% of sponge volume) are averaged for all replicates, unless otherwise stated. Health status was compared to non-exposed controls and judged from colour change (live *vs.* dead tissue), turgor, new tissue growth, and presence of *Beggiatoa* (*Begg.*, a group of sulfur-fixing, multicellular bacteria).

	recovery time			
experiment	1 day	3 days	6 days	comments
L−, 1 h				
Haliclona	A	A	A	[1]*Begg.* at base of explants
Lissodendoryx	A	A	A	
Scopalina	B[1]	A	A	
L−, 2 h				
Haliclona	A[1]	A	A	[1]1 replicate lost from support frame
Lissodendoryx	A	A	A	
Scopalina	A	A	A	
L−, 4 h				
Haliclona	C[1]: 5% dead	B[2]	A[3]	[1]dead tissue in 2 replicates only [2]regenerating, dead tissue sloughed
Lissodendoryx	A	A	A	[3]fully recovered
Scopalina	D: 90% dead	D: 95% dead	E[4]	[4]macerated except for spongin filters; disease community with feeding ciliates
L−, 1 h				
Haliclona	C: 35% dead	C: 42% dead	A[1]	[1]fully regenerated, dead tissue sloughed
Lissodendoryx	C: 46% dead	C: 10% dead	A[2]	[2]replicates filled with mature larvae
Scopalina	C: 48% dead	D: 91% dead	E	
L+, 1 h				
Haliclona	A	A[1]	A	[1]1 replicate lost
Lissodendoryx	A	A	A	
Scopalina	A	A	A	
L+, 2 h				
Haliclona	A[1]	A	A	[1]*Begg.* at base of explants
Lissodendoryx	A	A	A	
Scopalina	B[1]	B	B	
L+, 4 h				
Haliclona	A[1]	A	A	[1]1 replicate lost
Lissodendoryx	A	A	A	[2]*Begg.* infested
Scopalina	C[2]	D[2]: 91% dead	E	
L+, 6 h				
Haliclona	C[1]: 78% dead	C[2]: 85% dead	A, E[3]	[1]*Begg.* infested
Lissodendoryx	C: 79% dead	C[1]: 80% dead	A, E[3]	[2]live cells in 2 replicates
Scopalina	E	E	E	[3]1 replicate fully recovered, 3 dead

(A = excellent: full turgor, new growth; B = good: somewhat contracted but no signs of decay, no new growth; C = passable: stressed, contacted, signs of infection, tissue loss < 50% of volume; D = bad: infection and tissue loss > 50%; E = dead.)

6 and only the skeleton and a predatory microbial and ciliate community remained. Exposure of 6 h in the shade caused immediate and substantial (almost half) tissue loss in all three species. The condition in *Haliclona* and *Scopalina* deteriorated further over the next 3 days but while all replicates of *Scopalina* had died by day 6, *Haliclona* recovered and replaced all dead material with new growth. *Lissodendoryx* from the same experiment recovered steadily and fully and by day 6 showed new

growth in all replicates and developing and mature larvae in three of the specimens (only early stages of embryos were noted in the controls and were barely noticeable without use of a microscope). Exposure of 6 h in the sun resulted in the immediate death of *Scopalina* and in the demise of two replicates in *Haliclona*, three in *Lissodendoryx*. Surprisingly, parts of the remaining specimens (amounting to 20% of the original sponge volume) survived and, ultimately (day 6) one replicate of each of the two species regenerated into a healthy specimen.

Weight determinations of water loss during suspension in air show that *Lissodendoryx* holds the most water (37.1 $g \cdot g^{-1}$ ash-less dry weight), followed by *Haliclona* (31.7 $g \cdot g^{-1}$ ADW), and *Scopalina* (16.0 $g \cdot g^{-1}$ ADW). *Lissodendoryx* benefits from the slowest water loss (by drip and evaporation combined): 5.2% after 1 h, 21% after 3 h, 54% after 6 h. *Haliclona* loses at the rate of: 6.9% (1 h), 26% (3 h), 66% (6 h); *Scopalina*: 8.9% (1 h), 38% (3 h), 82% (6 h). This simulates the water retention of the three species at their estimated exposure tolerance thresholds during the recovery experiments, that is about 3 h for *Scopalina* and 6 h for the other two species. Salinity of interstitial water retained by these sponges was measured in different replicates after 1 h and 6 h (3 h not taken). It rose to 4.3% (1 h) and 5.4% (6 h) in *Lissodendoryx*, to 4.5% (1 h) and 5.9% (6 h) in *Haliclona*, and to 4.8% (1 h) and 5.1% (6 h) in *Scopalina*. These data indicate that loss by drip (suggested by the 1-h value) is lowest in *Lissodendoryx*, highest in *Scopalina*, loss by evaporation (6-h value) is lowest in *Scopalina*, highest in *Haliclona*. Because gravity drives water to the lower portions of the air-exposed sponge, associated species of endofauna such as polychaetes, crustaceans, and ophiuroids first migrate there, later leave the sponge or die.

3. Histological expression of stress

The histology of specimens fixed immediately after 6 h exposure to air and sun was examined and compared with untreated controls (Figs 2–5). Processes of possible cell repair or replacement over time could not be observed by this method.

Haliclona impexiformis is a pinkish violet, soft but elastic-compressible cushion-shaped sponge. The surface is punctate, the interior has a dense, bread-like porosity. Most aquiferous canals are under 0.5 mm in diameter; canals near the oscula may reach 2 mm in diameter. The ectosome is about 500 μm thick, primarily a loose reticulation of spicules supporting strands of cellular tissue. Choanocyte chambers are more or less spherical, 25×27 μm in diameter, with 12–15 choanocytes per central cross section. Numerous large archeocytes (7–8 μm) and spermatogenic cysts (16–20 μm) in different developmental stages (some with spermatids and spermatozoa) are the most conspicuous elements in the healthy choanosome. In air-exposed samples, most choanocyte chambers are disorganized, with many choanocytes dispersed at random throughout the mesohyle. Some archeocytes appear inflated (9–13 μm) and enclose large (3–4 μm) vacuoles.

Lissodendoryx isodictyalis is pale grayish green (experimental specimen) to blue, firm and tough in consistency. The surface is skin-like smooth, the interior coarsely porous from aquiferous canals measuring 0.5–2.0 mm (average, 0.8 mm) in diameter; 5 mm or larger canals are near the oscula. The ectosomal zone is dense with cells and reinforced by tangentially placed spicules; it measures 60–100 μm.

eventually, loss of cellular water upon draining and drying of the internal cavity and aquiferous system. These conditions may be enhanced, accelerated, or complicated by unusually long-lasting low tides and adverse weather conditions during exposure, such as unobstructed mid-day sun, strong wind, and heavy rain storms.

Sponges circulate water by means of choanocyte-lined chambers that connect a complex inhalant and exhalant canal system. When undisturbed, they pump water — steadily or with cyclic activity — at a great rate. *In situ* measurements of three common reef sponges in Jamaica showed water transport rates ranging from 0.2 l to almost 1 l per cm^3 sponge per h and a transport efficiency of 20–23 l water per ml oxygen consumed (REISWIG, 1974). Temporary shut-down of water flow (for hours or a few days) occurs in the field (REISWIG, 1971) and under unfavourable aquarium conditions (RÜTZLER, unpublished), but this state lacks other stress factors associated with exposure to air.

There are no obvious protective features in intertidal sponge species, such as shells that reduce evaporation. Unlike some other invertebrates studied in the same mangrove swamp (FERRARIS *et al.*, 1994) they are unable to move from unfavourable habitats and lack organs that control ionic gradients between environment and cell. The sponge body between the interior aquiferous system and the exterior surrounding seawater is enveloped by pinacoderm and choanocyte cell layers and is composed of mesohyle (an intercellular matrix) in which cells and skeleton (spongin, spicules) are embedded. Because sponges tolerate a considerable range of salinity but lack proper body fluids, it has long been suggested that they use an intracellular mechanism of osmoregulation comparable to protozoans (HARTMAN, 1985). Indeed, contractile vacuoles have been demonstrated in pinacocytes (and in several other cell types) of the freshwater family *Spongillidae*. The vacuoles surround the nucleus and are connected to a system of nephridial tubules and lacunae radiating through the cytoplasm (WEISSENFELS, 1974; BRAUER, 1975). To date, no comparable structures are known in marine sponges. The vacuolization of some archeocytes observed in the present study (Figs 2b, 3) are interpreted as stress related, not an indication of osmoregulation. Based on ionic comparisons of marine sponges and habitat water (PROSSER, 1967), the necessity of contractile vacuoles (at least under normal conditions) has been questioned because osmotic water loss rather than gain is to be expected (SIMPSON, 1984). However, several ecologic and experimental studies show that marine sponges readily invade brackish-water environments, particularly the euryhaline clionids ('oyster pests') that can live and function normally in 1.5–2.0% salinity and can recovered from several days of exposure to salinities as low as 1.0% (HOPKINS, 1956; HARTMAN, 1958). Unusually harsh conditions for sponges have been described from brackish Chilka Lake (India, connected to the Sea of Bengal) where spongillids coexist with several species of marine demosponges (ANNANDALE, 1915). Although long-term measurements of habitat conditions are not known, the spongillids were found in salinities of 0–1.0%, the marine species under conditions ranging from 0 (or 'quite fresh') to 2.0%, some even to full salinity (3.6%).

Few studies are available describing the response of marine sponges to hypersaline environments. In the laboratory, dissociated cells of *Microciona prolifera* re-aggregated at salinities ranging from 1.2 to 4.3% (GALTSOFF, 1925), similar experiments with *Iotrochota birotulata* resulted in re-aggregates between 2.4 and

3.8% (DE LAUBENFELS, 1932). These observations, however, do not clarify regulatory mechanisms and are not good indicators of salinity resistance in whole sponges.

It appears that for a sponge the most important initial defense during air exposure is to prevent or resist water loss. *Scopalina* starts out with a water content that is lower than that of the other species, which is unimportant as long as the water is retained. However, *Scopalina*, also initially (1–3 h), loses a greater proportion of its water than the other two sponges and by 6 h has lost a dramatic 82%, probably by run-off from the large internal lacunae. The effect of this loss is reflected by tissue deterioration after 2–4 h in sun or shade (Table 2). Subsequent to initial water loss by drainage, water is lost by evaporation. Thus, sponge cells are bathed in hypersaline water, a condition to which they may be able to adapt. Typically, cells of invertebrates exposed to hypersalinity initially accumulate inorganic ions intracellularly but water follows to restore cell volume. This has the effect that most intracellular components are restored to near their original concentrations while inorganic ion concentrations remain high. Subsequently, if the stress persists, long-term adaptation involves replacement of elevated intracellular inorganic ions. This is necessary because elevated cellular sodium (Na), potassium (K), and chlorine (Cl) will eventually disrupt macromolecular function. Inorganic ions are typically replaced with non-perturbing osmolytes, such as amino acids, trimethylamines, and polyols (FERRARIS, 1993, and reference therein). Whether sponge cells utilize these mechanisms is as yet unknown. During earlier experiments with *Lissodendoryx isodictyalis* and *Tedania ignis* at Twin Cays (FERRARIS & RÜTZLER, unpublished, 1987) we found that these sponges do not undergo predicted cell shrinkage when exposed to desiccation. This may indicate the existence of a limiting phase of cell-volume regulation via accumulation of inorganic ions, as outlined above. That sponge cells process volume-regulatory ability as well may be indicated by the response of the species in the current study. Interstitial salinity clearly increases in all three species and two of them, *Haliclona* and *Lissodendoryx*, recover completely implying some mechanism of adaptation. It will be of interest to pursue a comparison of the cell-volume regulatory abilities of these sponges.

It is also important to distinguish between tolerance of short-term extremes and capability to adapt to long-lasting or repeated conditions that cause physiological stress. Periods of adverse conditions can be bridged by closing pores and ceasing pumping activity (HARTMAN, 1958; REISWIG, 1971) and by the formation of gemmules which are best known from spongillids but are also common in some marine species (SIMPSON & FELL, 1974). It has been shown, however, that although gemmules protect cells from salinity extremes — indeed their formation and germination are influenced by osmotic pressure changes — they do not provide increased resistance to desiccation (FELL, 1975).

Even less well understood than osmoregulation are the effects of solar radiation on sponges, particularly if the cooling and spectral-filter action of the water is lacking. Tissue temperature in tide- and sun-exposed sponges can rise rapidly ($13\,^{\circ}C \cdot h^{-1}$ in tempered climate; ELVIN 1976) but this effect may be offset by cooling from evaporation. More severe effects can be expected from ultraviolet radiation that is known to damage and kill even submerged sponges in 1–2 days (JOKIEL, 1980).

Extended full exposure eventually leads to drainage of interstitial seawater from

large lacunae which in certain species are presumed to be adaptations allowing conservation of a water reserve (ANNANDALE, 1918). Among the species used in the present experiments, however, *Scopalina ruetzleri* has the largest internal lacunae which were shown to drain faster than the smaller and more complex interstitial space system of the other two species where friction and other hydraulic forces help to retain pore water. Evaporation, on the other hand, is controlled by the presence of an external barrier, such as a dense ectosome, which is well developed in *S. ruetzleri* and *Lissodendoryx isodictyalis* but missing in *Haliclona implexiformis*. It may well be the combination of anatomical advantages with physiological disposition that makes *L. isodictyalis* the most resistant to low-tide exposure in the group.

Summary

Twin Cays, Belize, as most mangrove islands in the Caribbean, have a small tidal amplitude. Hidden Creek, one of the deeper drainage channels, is subjected to a mean tidal range of 35 cm and supports a rich fouling community that covers peat banks and prop roots of red mangrove (*Rhizophora mangle*) below the high-water line. Tidal currents bring about extreme and abrupt changes in temperature and salinity and astronomical and meteorological factors may cause as many as 14 ebb tides below mean lower low water per month. Sessile organisms occur in vertical zonation that reflects their degree of adaptation to intertidal exposure. In this habitat, sponges that are typically subtidal in distribution can also be found in the lower intertidal where they are subject to air exposure and desiccation.

Field experiments involving controlled exposures of three sponge species to air in shade and sun show that *Haliclona implexiformis* and *Lissodendoryx isodictyalis* recover from a treatment of 4 h out of water and in full sunlight. In these species, portions of specimens may survive 6 h in full sun and regenerate into healthy sponges after a few days. Morphological adaptations help to slow water loss by drip and evaporation. *Scopalina ruetzleri* survives only 2 h of exposure to air and has poor morphological water retention quality.

Histological and cytological examination of air-exposed specimens shows stress primarily in the form of disorganized choanocyte chambers, enlarged vacuolated archeocytes, and disintegrating spermatozoa. Evidence, such as the absence of cell shrinkage, suggests that a cellular volume-regulatory mechanism exists in these sponges.

Acknowledgements

The author is grateful to JOAN D. FERRARIS, National Institutes of Health, Bethesda, Maryland, for valuable contributions to the discussion. She and HENRY M. REISWIG, McGill University, Montreal, Quebec, provided expert reviews of the manuscript. Thanks also to KATHLEEN SMITH for laboratory assistance, particularly the preparation of Fig. 1. MOLLY RYAN and MIKE CARPENTER aided in field work and with the preparation of illustrations. ANDREA BLAKE sectioned and took electron micrographs; HILARY SMITH helped with photographic printing. GEORGE HAGERMANN, SeaSun Power Systems, Alexandria, Virginia and JIM HUBBARD, NOAA's Tidal Analysis Branch, Silver Spring, Maryland, provided tidal data. This is contribution number 443, Caribbean Coral Reef Ecosystems Program (CCRE), National Museum of Natural History, Washington, D.C.

References

ANNANDALE, N., 1915: Fauna of the Chilka Lake, Sponges. Mem. Ind. Mus. Calcutta, **5:** 21–54.

––, 1918: Zoological results of a tour in the Far East. Mem. Asiat. Soc. Bengal, **6:** 193–216.

BINGHAM, B. L. & C. M. YOUNG, 1995: Stochastic events and dynamics of a mangrove root epifaunal community. P.S.Z.N. I: Marine Ecology, **16:** 145–163.

BRAUER, E. B., 1975: Osmoregulation in the fresh water sponge, *Spongilla lacustris*. J. Exp. Zool., **192:** 181–192.

BURTON, M., 1949: Notes on the ecology of sponges. Br. Sci. News, **2:** 83–85.

ELVIN, D. W., 1976: Seasonal growth and reproduction of an intertidal sponge, *Haliclona permollis* (BOWERBANK). Biol. Bull., **151:** 108–125.

FELL, P., 1975: Salinity tolerance and desiccation resistance of the gemmules of the brackish-water sponge, *Haliclona loosanoffi*. J. Exp. Zool., **194:** 409–412.

FERRARIS, J. D., 1993: Molecular approaches to the study of evolution and phylogeny of the Nemertina. In: R. GIBSON, J. MOORE & P. SUNDBERG (Eds.), Advances in Nemertean Biology. Hydrobiologia, **266:** 255–265.

––, K. FAUCHALD & B. KENSLEY, 1994: Physiological responses to fluctuation in temperature or salinity in invertebrates. Adaptations of *Alpheus viridari* (Decapoda, Crustacea), *Terebellides parva* (Polychaeta) and *Golfingia cylindrata* (Sipunculida) to the mangrove habitat. Mar. Biol., **120:** 397–406.

GALTSOFF, P. S., 1925: Regeneration after dissociation (an experimental study on sponges). I. Behaviour of dissociated cells of *Microciona prolifera* under normal and altered conditions. J. Exp. Zool., **42:** 183–221.

HARTMAN, W. D., 1958: Natural history of the marine sponges of southern New England. Bull. Peabody Mus. Nat. Hist., **12:** 1–155.

HOPKINS, S. H., 1956: Notes on the boring sponges in Gulf Coast estuaries and their relation to salinity. Bull. Mar. Sci. Gulf Caribb., **6:** 44–58.

JOKIEL, P. L., 1980: Solar ultraviolet radiation and coral reef epifauna. Science, **207:** 1069–1071.

KJERFVE, B. K., RÜTZLER & G. H. KIERSPE, 1982: Tides at Carrie Bow Cay, Belize. In: K. RÜTZLER & I. G. MACINTYRE (Eds.), The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I, Structure and Communities. Smithsonian Institution Press, Washington, D.C.: 47–51.

LAUBENFELS, M. W. DE, 1932: Physiology and morphology of Porifera exemplified by *Iotrochota birotulata* HIGGIN. Publ. Carnegie Inst. Washington, **435:** 37–66.

––, 1947: Ecology of the Sponges of a brackish water environment, at Beaufort, N.C. Ecol. Monogr., **17:** 31–46.

PROSSER, C. L., 1967: Ionic analyses and effects of ions on contractions of sponge tissue. Z. vgl. Physiol., **6:** 69–74.

REISWIG, H. M., 1971: In situ pumping activity of tropical Demospongiae. Mar. Biol., **9:** 38–50.

––, 1974: Water transport, respiration and energetics of three tropical marine sponges. J. Exp. Mar. Biol. Ecol., **14:** 231–249.

RÜTZLER, K., 1964: Aspects of littoral life in the Indian Ocean. Atti Sem. Stud. Biol. Bari, **1:** 1–17.

––, 1978: Sponges in coral reefs. In: D. R. STODDART & R. E. JOHANNES (Eds.), Coral Reefs: Research Methods. Monographs on Oceanographic Methodology, 5. Unesco, Paris: 299–313.

––, 1988: Mangrove sponge disease induced by cyanobacterial symbionts: failure of a primitive immune system? Dis. Aquat. Org., **5:** 143–149.

––, 1993: Caribbean Coral Reef Ecosystems program, progress report 1991–1993. National Museum of Natural History, Smithsonian Institution, Washington, D.C.; 20 pp.

––, C. FELLER, 1987: Mangrove swamp communities. Oceanus (Woods Hole Oceanographic Institution), **30**(4): 16–24.

––, 1995: Caribbean mangrove swamps. Scientific American (in press).

–– & I. G. MACINTYRE, 1982: The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. Smithson. Contrib. Mar. Sci., **12:** 9–45.

SIMPSON, T. L., 1984: The biology of sponges. Springer-Verlag, New York, Berlin, Heidelberg, Tokyo; 662 pp.

–– & P. E. FELL, 1974; Dormancy among the Porifera: Gemmule formation and germination in freshwater and marine species. Trans. Am. Microsc. Soc., **93:** 544–577.

SOEST, R. W. M. VAN, 1984: Marine sponges from Curaçao and other Caribbean localities. Part III. Poecilosclerida. Studies on the Fauna of Curaçao and other Caribbean Islands, **66**(112): 167 pp.

WEERDT, W. H., K. RÜTZLER & K. P. SMITH, 1991: The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters. Proc. Biol. Soc. Wash., **104:** 189–205.

WEISSENFELS, N., 1974: Bau und Funktion des Süßwasserschwamms *Ephydatia fluviatilis* L. (Porifera). I. Das Nephridialsystem der Pinacocyten. Cytobiologie, **8:** 269–288.

WIEDENMAYER, F., 1977: Shallow-water sponges of the western Bahamas. Exp. Suppl. 28, Birkhäuser Verlag, Basel & Stuttgart; 278 pp.

P.S.Z.N. I: Marine Ecology, 16 (2): 180 (1995)

ISSN 0173-9565

Book Review

HAYWARD, P.J., J.S. RYLAND & P.D. TAYLOR (Eds.): **Biology and Palaeobiology of Bryozoans**. Proceedings of the 9th International Bryozoology Conference, School of Biological Sciences, University of Wales, Swansea, 1992. Olsen & Olsen (Fredensborg), 1994. 240 pp., ISBN 87-85215-23-6

This volume is currently the last one in a long series published by the 'International Bryozoology Association', which organizes conferences of high scientific standard at triennial intervals: the first was held in Milan in 1968, the last one in Wellington, New Zealand in 1995. From the very beginning these Bryozoology Conferences had been intended to offer an opportunity for both zoologists *and* palaeontologists to present results of their studies on *Bryozoa*. Bryozoology in the broadest sense of the word has always been the goal of these meetings and, therefore, the wide range of topics involved include: taxomony, biogeography, ecology, biochemistry, pollution problems, *etc.*

Following this fundamental framework, the 45 publications (out of 58 papers presented at the conference) included in this volume concern an impressive variety of studies within bryozoology: larval release and settlement, larval morphology, astogenetic and ontogenetic development, distribution patterns, growth and survival strategies, food sources, feeding efficiency and rates, a bryozoan-sponge symbiosis, taxonomy, zoogeography, freshwater bryozoans, *etc.* With respect to palaeontology, papers concern bioimmuration, taphonomy, budding patterns, evolution, palaeoecology, and palaeobiogeography, including faunas from the Ordovician (Ireland, Australia) through the Devonian, Carboniferous, Permian, Triassic, and Cretaceous up to the Tertiary (Austria, Egypt, Spain). Using this approach, this volume offers an excellent survey of progress and activities in the field of bryozoan research. Author, keyword and systematic indexes are valuable and useful extras.

A referee system was applied, guaranteeing a high scientific standard; excellent quality of printing and illustrations and a rather moderate price (ca. US $120) are an additional recommendation for this book. The purchase of this volume is therefore an utmost necessity for all those biological and palaeontological institutes, museums, *etc.* concerned with the study of ecology and biodiversity in invertebrates in general.

NORBERT VAVRA, Vienna/Austria