THE CHEMICAL AND COMMUNITY ECOLOGY OF TIDEPOOL MACROALGAE OF MOUNT DESERT ISLAND, MAINE, U.S.A.

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Johnson and Skutch (Ecology 9:192-196, 1928) noted that Mount Desert Island tidepool macroalgal communities were correlated with height; low pools were dominated by red and brown in contrast to high pools dominated by green algae, a point also noted by Femino and Mathieson (Bot.Mar.23:319-332, 1980). Sze (J. Wash.Acad.Sci. 73:121-127, 1983) found that pools of southern Maine also showed this same pattern. Factors reported to account for this distributional pattern are temperature, salinity and pH (Femino and Mathieson, Bot.Mar.23:319-332, 1980) and times of submergence and emergence (Johnson and Skutch, Ecology 9:192-196, 1928); Sze, Bot.Mar.25:269-276, 1982). Grazing by littorines is also reported as an important factor in the structure of tidepool macroalgal communities (Lubchenco, Amer.Nat.112:23-39, 1978; Wolfe and Harlin, Bot.Mar.31:537-546, 1988). Lubchenco reported that species diversity for eight Massachusetts pools was highest with intermediate littorine densities. Wolfe and Harlin conversely found that species diversity and littorine density were inversely correlated for eight pools in Rhode Island, although pool types were also associated with pool height, volume, and surface area. Community analysis of macroalgal communities from pools from Rhode Island, Massachusetts, southern Maine, and the west coast of Ireland indicated three types of pools: 1) high green algal pools, 2) mid to low red-brown pools with high littorine densities, and 3) mid to low red-brown algal pools with low densities of littorines. In addition, Wolfe, Harlin and Albert (unpublished) report that algal allelopathy may be another factor influencing the composition of tidepool macroalgal communities. In this study, we examined macroalgal communities of 36 pools on Mount Desert Island and attempted to determine in situ rates of exudation of Folin-Ciocalteau reactive compounds (FCRC's) for selected macroalgae. Wolfe, Harlin, and Albert suggest that based on field and culture studies FCRC's may affect algal growth.

After examination of possible sites on Mount Desert Island for tidepool study, 36 pools, ranging in height, size, and macroalgal communities, were chosen for study during June 1 through July 7, 1992. Five pools were located at Thunderhole, seventeen at Otter Point, and fourteen at Wonderland. All pools were located within the boundaries of Acadia National Park. Height above mean low water (MLW) was determined by triangulation using a line level and a pole calibrated against the predicted low water level (U.S.Department of Commerce Tide Tables, 1992). Mean depth for each pool was calculated from the average of depth measurements (n=27-262). Littorine (primarily Littorina littorea) densities per square meter were calculated using 10 cm by 10 cm or 25 cm by 25 cm quadrats (n>10 for each pool). To record the occurrence and abundance of each macroalgal species in each of the 36 pools, macroalgal percentage cover was recorded. Cover was determined by overall pool visual estimates and quadrat (10 cm by 10 cm or 25 cm by 25 cm) estimates. All macroalgal species were ranked for percentage cover on a scale of 1, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100. Species were determined according to Taylor (University of Michigan Press, 1957), lists compiled by the Acadia National Park headquarters and by local surveys (Van Hemert, M.S. thesis, University of Maine, 1966). Two genera, Ralfsia and Phymatolithon, were not determined to species level. For each pool, the number of total species was calculated, as well as the percentage of species as Chlorophyta, Phaeophyta, and Rhodophyta. Species diversity (H') was calculated for each pool. A computer program was used to calculate Horn's index of similarity (R_o). Average linkage cluster analysis (Legendre and Legendre, Elsevier Scientific Publishing Company, 1983) was used to draw similarity dendograms.

To determine the rate of in situ exudation of FCRC's, an attached blade of Laminaria digitata, Alaria esculenta, or Laminaria saccharina in Otter Point Pool 15 was placed in a 1 liter flask and flooded with tidepool seawater. Each flask was made buoyant by the insertion of one clear plastic balloon, which was slightly inflated. Initial samples of seawater were withdrawn from each flask using a 50 ml syringe, placed in plastic bottles, and refrigerated until analyzed for FCRC's. At the end of six hours during tidepool emergence, samples were again withdrawn from each flask. Analysis was performed using 10 ml of sample, to which 0.5 ml of FC reagent was added, followed by 1.5 ml of sodium carbonate (2N). After centrifugation for 3 min., absorbance was read on a Beckman (Model DU-40) double-beam spectrophotometer. A standard curve ranging from 0 to 2000 μg/L in artificial seawater was prepared using phloroglucinol as the standard.

A total of 51 taxa were found in the pools which ranged in height from 92 to 803 cm above mlw (Table 1). Species were Chlorophyta: Chaetomorpha linum (Müll.) Kütz., Chaetomorpha melagonium (Webnn. et Mohr) Kütz, Cladophora glaucescens (Griffiths ex Harvey) Harvey, Cladophora gracilis (Griffiths ex Harvey) Kütz., Cladophora rudolphiana (C. Agardh) Harvey, Enteromorpha compressa (Linnaeus) Greville, Enteromorpha intestinalis (L.) Link, Monostroma oxyspermum Kützing) Doty, Rhizoclonium erectum Collins, Rhizoclonium kerneri Stockmayer, Rhizoclonium tortuosum, Spongomorpha arcta (Dillwyn) Kützing, Spongomorpha spinescens Kützing, Ulva lactuca L., Phaeophyta: Alaria esculenta (Linnaeus) Greville, Ascophyllum nodosum (L.) LeJol., Chordaria flagelliformis (Müller) C. Agardh, Dictyosiphon foeniculaceus (Hudson) Greville, Ectocarpus tomentosus (Hudson) Lyngbye, Elachistea fucicola (Velley) Areschoug, Fucus distichus L., Fucus edentatus De la Pylaie, Fucus spiralis L., Fucus vesiculosus L., Laminaria digitata (Huds.) Lamour., Laminaria saccharina (L.) Lamour., Petalonia fascia (Müll.) Kuntze, Ralfsia sp., Scytosiphon lomentaria (Lyngb.) Link, Rhodophyta: Ahnfeltia plicata (Huds.) Fries, Ceramium hooperi (Harvey) Taylor, Ceramium rubriforme (Kylin), Ceramium rubrum (Huds.) C.Ag., Chondrus crispus Stackh., Carollina officinalis L., Cystoclonium purpureum (Huds.) Batt., Dumontia contorta (Gmel.) Rupr., Hildenbrandia rubra (Sõmmerf.) Menegh., Mastocarpus stellatus (Stackh.) Guiry, Palmeria palmata (L.) Greville, Phymatolithon sp. Foslie, Polysiphonia elongata (Hudson) Harvey, Polysiphonia fibrillosa Greville, Polysiphonia flexicaulis (Harvey) Collins, Polysiphonia lanosa (L.) Tandy, Polysiphonia urceolata (Lightfoot) Greville, Porphyra miniata (Lyngbye) C. Agardh, Porphyra umbilicalis (L.) J. Agardh, Spermothamnion turneri (Mertens) Areschoug. Of the total number of species, most (21) were red algae, with the green algae having the smallest number (14) of the total. Pools ranged in total number of species from 4 (Pool 8 at Wonderland) to 26 (Pool 18 at Otter Point). The mean number of species per pool was 14. High pools tended to have lower numbers of species. Littorine densities ranged from 0 to 680 m^{-2}. Several pools did not contain littorine snails.

For the 36 pools the percentage of total species as Chlorophyta was significantly ($p < 0.01$) positively correlated with tidepool height (Fig. 1). The percentage of total species as Rhodophyta and percentage of total species as Phaeophyta were significantly ($p < 0.05$) positively correlated with littorine density. A dendrogram of the 36 pools showed the presence of four groups (Fig. 2). One group, consisting of Otter Point pools 8,9,10,11,12, and 17, was characterized as high pools with low littorine densities. These pools were dominated by green algae including Enteromorpha spp. and Cladophora spp. A second group of pools, consisting of Thunderhole pools A-E, and Otter Point pools 1-5, were low to mid pools with low littorine densities. Most of these pools had a high cover of Spongomorpha spp. A third group of pools, including Otter Point pools 10,14, and 15 and Wonderland pools 1,2,3,4,6,7,9,12,13,14 were either pools of high tidepool height or littorine density. Exudation of FCRC's for Laminaria digitata was 11.0 $\pm$ 4.2 (SD) $\mu g\ hr^{-1}\ gm\ dry\ wt.^{-1}$, for Alaria esculenta = 34.6 $\pm$ 15.7 (SD), and for Laminaria saccharina = 5.9 $\pm$ 5.3 (SD).

Characterization of tidepools as shown here bears resemblance to that found for pools from Rhode Island, Massachusetts, southern Maine, and Ireland (Wolfe and Harlin, Bot.Mar.31:525-546, 1988). Harlin and Wolfe also found that for eight Rhode Island pools the percentage of total species as Chlorophyta was positively correlated with pool height whereas the percentage as Rhodophyta was negatively correlated with pool height. They also reported that the percentage of total cover as Rhodophyta was positively correlated with littorine density but the percentage contributed by Chlorophyta was negatively correlated with littorine density and showed that community dissimilarity was significantly associated with pool height, littorine density, and volume. They proposed the existence of three types of pools: a) high green algal pools, b) mid to low red-brown algal pools with high densities of littorines, and c) mid to low red-brown algal pools with low densities of littorines. The existence of a fourth group of pools on Mount Desert Island, namely those with low littorine densities and a large cover of Spongomorpha spp. may be result of niche broadening in an intertidal zone with a large tidal amplitude (nearly 5 meters). The importance of tidal height and littorine density in the determination of tidepool macroalgal communities has been shown in the studies mentioned previously. The influence of exuded FCRC's by macroalgae on tidepool macroalgal communities is still unclear. Wolfe, Harlin, and Albert (unpublished) suggest that based on work of macroalgal cultures and measurements of FCRC's in eight Rhode Island pools, allelochemical interactions may play a role in tidepool communities. The range of rates of exudation as found by Wolfe et al. bracket the range found for exudation as reported here. These in situ experiments of exudation of FCRC's by three species of Phaeophyta suggest that accumulation of FCRC's may occur during tidepool emergence. There is potential that FCRC's and other exuded chemicals may play a role, in addition to tidepool height and littorine density, in the determination of the structure of tidepool macroalgal communities.

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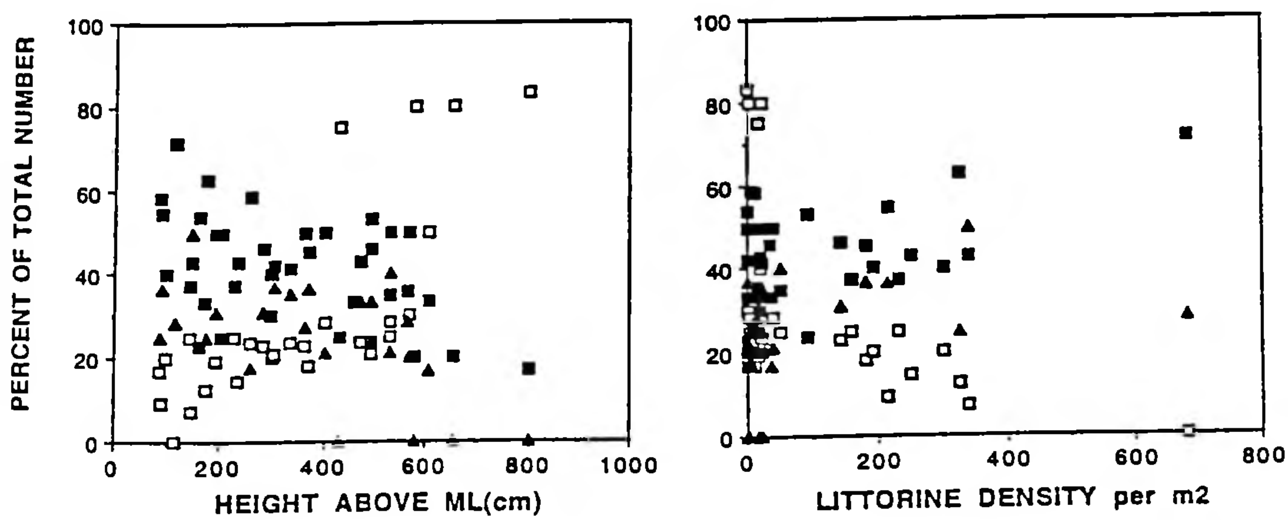

Figure 1. Left panel: The relationship of height above mean low water with the percentage of total macroalgal species for 36 tidepools on Mount Desert Island, Maine, U.S.A. r for Chlorophyta (open squares) = 0.71, r for Phaeophyta (solid triangles) = 0.58, r for Rhodophyta (solid squares) = 0.58. Right panel: The relationship of littorine density (per square meter) with the percentage of total macroalgal species for 36 tidepools on Mount Desert Island, U.S.A. r for Chlorophyta (open squares) = 0.46, r for Phaeophyta (solid triangles) = 0.40, r for Rhodophyta (solid squares) = 0.36.

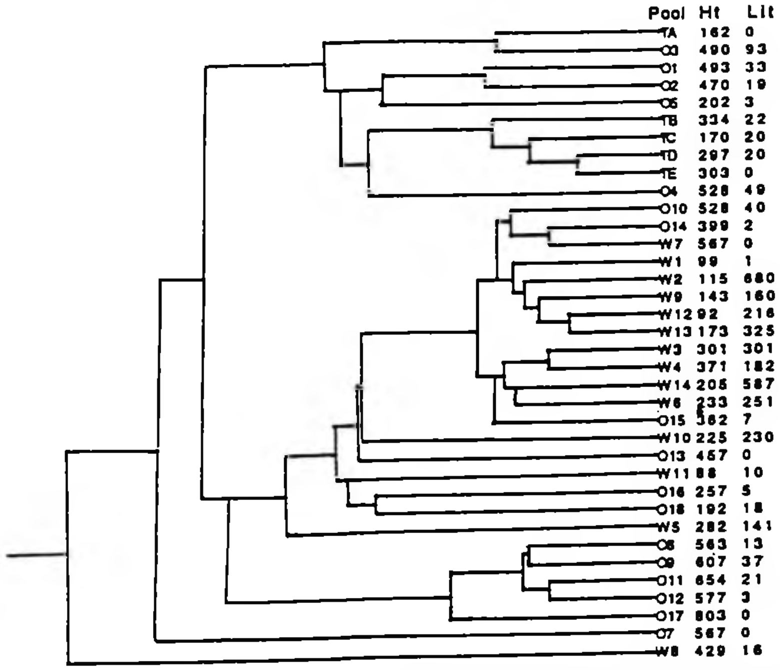

Figure 2. A dendrogram of the similarity of macroalgal communities for 36 tidepools on Mount Desert Island, Maine, U.S.A. Pool height is measured as cm above mean low water, littorine density as the number of littorine snails per square meter.

Table 1. Biological and physical characteristics of 36 tidepools on Mount Desert Island, Maine, U.S.A

Pool	Location	Height above mlw	Ave. Depth (cm)	No. of Macroalgal Species	Species Diversity (H')	Littorine Density per m^{-2}
A	Thunderhole	162	15	13	1.45	0
B	Thunderhole	334	21	17	1.92	22
C	Thunderhole	170	5	9	1.20	20
D	Thunderhole	297	18	10	1.21	20
E	Thunderhole	303	15	19	1.97	0
1	Otter Point	493	22	24	2.66	33
2	Otter Point	470	42	21	2.49	19
3	Otter Point	490	10	17	2.11	93
4	Otter Point	528	23	20	1.97	49
5	Otter Point	202	31	16	1.99	3
7	Otter Point	567	16	10	1.42	0
8	Otter Point	563	24	14	1.62	13
9	Otter Point	607	22	6	1.26	37
10	Otter Point	528	22	14	1.74	40
11	Otter Point	654	15	5	1.15	21
12	Otter Point	577	17	5	0.91	3
13	Otter Point	457	1	12	1.84	0
14	Otter Point	399	18	14	1.34	2
15	Otter Point	362	47	22	2.38	7
16	Otter Point	257	40	17	2.12	5
17	Otter Point	803	33	6	1.45	0
18	Otter Point	192	35	26	2.90	18
1	Wonderland	99	12	20	2.30	193
2	Wonderland	115	11	7	1.57	680
3	Wonderland	301	13	10	1.98	301
4	Wonderland	371	9	11	1.94	182
5	Wonderland	282	17	13	2.13	141
6	Wonderland	233	22	14	2.36	251
7	Wonderland	148	16	14	1.11	340
8	Wonderland	429	11	4	0.68	16
9	Wonderland	143	29	16	1.71	160
10	Wonderland	225	10	8	1.34	230
11	Wonderland	88	7	12	1.75	10
12	Wonderland	92	10	11	1.57	216
13	Wonderland	173	11	8	1.20	325
14	Wonderland	205	17	13	–	587