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J. Exp. Mar. Biol. Ecol. 177 (1994) 37–71

JOURNAL OF
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

The ecology of intertidal algal crusts: variation within a functional group

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(Received 12 January 1993; revision received 9 September 1993; accepted 9 November 1993)

Abstract

Encrusting marine algae are found at all depths in the photic zone from polar to tropical seas worldwide, yet little is known about their ecology. Crusts (including red, brown, and green algae as well as lichens and Cyanobacteria) tend to predominate in areas of high disturbance (e.g. from herbivores or sand scour) or high stress (= low potential productivity, e.g. high on the shore). Patterns of crust and herbivore distribution and abundance were quantified in the intertidal zone in Washington state, and then the two environmental parameters predicted to be critical to among-crust variation in survival were manipulated: disturbance potential by varying abundances of herbivores, or by eliminating herbivores and artificially disturbing crusts with nylon and steel brushes; productivity potential by transplanting crusts along an environmental gradient from the high to the low intertidal zone and onto a submerged raft. Within-functional-group variation among crusts was studied by transplanting eight species (varying in calcification, thickness, tightness of construction, and other characters), and measuring their survival and growth over 2–3 yr in the different environments. Crusts varied widely in their responses to both disturbance and productivity potential. In general, thick, calcified, or very tightly constructed crusts withstood being steel-brushed at regular intervals. Nylon brushing sometimes actually benefitted these crusts relative to the controls (unbrushed but cleaned monthly), probably because of the reduction in fouling. In contrast, thinner or more loosely-constructed species showed poor survival when steel-brushed and often suffered significant losses even when nylon-brushed. Most crusts tended to do best in habitats having higher productivity potential (lower intertidal zone), showing mortality or reduced growth when transplanted into more stressful areas, although two species were healthiest under “stressful” conditions, i.e. desiccated or submerged in high pools. Experiments in the laboratory with herbivores (littorinid snails, limpets, and a chiton) demonstrated that they did not always consume the species that are mechanically easiest to remove (as indicated by the steel brushing experiments). Three species were avoided, including a brown known to contain high concentrations of phenolics, a blue-green crust, and a lichen with a blue-green phycobiont. All crusts grew very slowly, even in their optimal habitats; the fastest species grew

laterally at <20 mm/yr, and the slowest measurable at <0.5 mm/yr. Some species showed no lateral growth over 2 yr. This low ability to sequester space, and their two-dimensional growth form, means that crusts often rely on grazers or other disturbance to keep from being overgrown. In other cases, they grow in areas where desiccation or low light levels apparently eliminate other algal forms. Crusts survive disturbance by either resisting it (through calcification or toughness), tolerating it (by being thick or regenerating rapidly), or avoiding it (by having an opportunistic life history, living in refugia such as crevices or high tidepools, or being unpalatable). Their life histories are highly variable, allowing them to exploit habitats in different ways. For example, in the mid intertidal zone in Washington the three dominant crust species include: (1) a fast-growing, frequently-recruiting brown (*Ralfsia pacifica* Hollenberg) that senesces after several years and sloughs away; (2) a fast-growing but rarely-recruiting red ("Petrocelis") that lives for decades; and (3) a very slow-growing and rarely-recruiting red [*Hildenbrandia rubra* (Sommerfelt) Meneghini] that persists even when overgrown, and regenerates following disturbance. These diverse morphologies and life history strategies help make this morphology an ecological success.

Key words: Crustose algae; Disturbance; Functional group; Herbivory; Morphology; Stress

1. Introduction

The relationship between form and environment has been explored in diverse organisms, e.g. terrestrial plants in general (Grime, 1977, 1981; Harper, 1977), marsh grasses (Bertness & Ellison, 1987), corals and bryozoans (Hughes & Jackson, 1985; Jackson & Hughes, 1985), infaunal animals and sessile colonial animals (Woodin & Jackson, 1979), and marine algae (Littler & Littler, 1980). Due to their relative simplicity of construction, there is a clear link between form and function (e.g. growth rates, resistance to herbivory) in marine macroalgae; this leads to predictable patterns of dominance of certain growth forms associated with certain levels of environmental stresses and disturbance (Norton et al., 1982; Steneck & Watling, 1982; Littler & Littler, 1984a; Steneck & Dethier, 1994).

The encrusting growth form (or functional group, *sensu* Steneck and Watling, 1982) is widespread and abundant in the marine realm and includes many unrelated taxa, including red, brown, and green algae, as well as marine lichens and Cyanobacteria (blue-green algae). These share the morphological features of growing prostrate along the substratum and being composed primarily of upright filaments of cells appressed together laterally. Within this basic form, however, there is broad variation: in degree of calcification of the cell walls (heavy to none), surface rugosity and texture, thickness, adherence of the filaments to each other and to the substratum, cell size, and degree of cell-cell connection (e.g. secondary pits, fusions).

Encrusting algae are probably the least well understood but most widespread functional group. Crusts have been overlooked because they are often hidden beneath larger algal forms or difficult to distinguish from the rock substratum, and because differentiating species is difficult. Floral surveys frequently omit them or lump them as "encrusting algae" without further identification. Yet surveys show that they can be found

on virtually any hard substratum in the photic zone, and in some environments are the most abundant algal form. They are found from polar to tropical seas (e.g. Stephenson & Stephenson, 1972), and from the upper intertidal zone down to lower in the photic zone than any other plants (Wilce, 1967; Littler et al., 1986; Vadas & Steneck, 1988). In addition, they are described as being a dominant floral element in a peculiar variety of habitats: polar and tropical intertidal zones (e.g. Ellis & Wilce, 1961; Menge & Lubchenco, 1981; Gaines & Lubchenco, 1982), high intertidal pools (Sze, 1980; Dethier, 1981, 1984), marine caves (Lami, 1939; Dellow & Cassie, 1955), sand-scoured areas (Daly & Mathieson, 1977; Kendrick, 1991), unstable cobbles (e.g. Bertness et al., 1983; Davis & Wilce, 1987; Scheibling & Raymond, 1990), the deep sublittoral (Lüning, 1970; Sears & Cooper, 1978; Littler et al., 1986), and heavily grazed areas (e.g. Kitting, 1980; Underwood, 1980; Menge & Lubchenco, 1981; Levings & Garrity, 1983; Littler & Littler, 1984b; Steneck, 1986; and many others).

Ecological differences among algal functional groups have been comparatively well studied. Steneck & Dethier (1994) reviewed the literature on functional groups and found that while crusts are broadly distributed, the environments where they dominate the flora occur at the extremes of two independent gradients. These habitats are characterized as potentially productive (non-stressful) but highly disturbed (by herbivores or physical disruption), or undisturbed but highly stressful (e.g. due to low light or intense desiccation). Most of the environments named above (caves, high intertidal, etc.) clearly fall into one of these categories. While it is often thought that all crusts are indicators of intense herbivory, this is not the case. Here I consider both crusts that are resistant to herbivory (and other forms of disturbance) and those that are not, in an attempt to understand the range within this growth form.

Ecological differences among algal species *within* a functional group have not been examined. In this study I investigate the ecology of encrusting algae, in particular how crusts of different construction fare under different natural and manipulated environments. This is the first study to examine the ecological variation within this diverse and abundant group. My approach was to quantify local patterns of crust distribution and abundance, manipulate processes hypothesized to be responsible for these patterns, and examine the crust characters that appear to contribute to the success of particular species. I worked in the intertidal zone of Washington state, which has a rich crustose flora showing a wide range of morphological and life history characters. Manipulated ecological processes (those which strongly determine *among* functional group patterns in the marine realm) were disturbance and stress (or its inverse, productivity potential, *sensu* Steneck & Dethier, 1994). Previous studies have shown that calcification and perhaps cell size are correlated with grazer-resistance in crusts (see Discussion); I hypothesized that in general, these characteristics plus thickness, adherence to the substratum, and tightness of adjoining of filaments should allow crusts possessing these features to withstand biomass removal (by grazers, sand scour, or other sources of disturbance) better than can crusts lacking these characters. I had no a priori hypotheses about morphological features of crusts that can withstand stress.

2. Methods and definitions

2.1. Study sites

Observations and experiments were carried out in the northwest corner of Washington state. Most studies were in the San Juan Islands, including sites at Yellow Island (YI) and Pile Point (PP). Additional observations were made on Tatoosh Island, on the outer coast.

2.2. Definitions

Critical extrinsic conditions for any alga are the potential for disturbance, such as from herbivores, and those aspects of the physical environment that control growth. Steneck & Dethier (1994) define productivity potential as an integrated measure of the extrinsic variables that affect algal growth, especially light, water motion, nutrients, and desiccation. The literature and algal growth data (reviewed in Steneck & Dethier, 1994) suggest that in general, productivity potential for marine algae is highest just below mean low water (in the shallow subtidal zone), and decreases both up into the intertidal zone (because of desiccation and other stresses) and down into the lower photic zone (because of light attenuation). Stated another way, stress (factors that reduce growth: Grime, 1977) increases from low to high intertidal zones. The other critical extrinsic variable considered was the level of potential herbivore-induced disturbance. Such disturbance has two components: the frequency of grazing (estimated here by the density or biomass of a given grazer) and the intensity, or abilities of the different grazer species to bite deeply into algae. For the quadrat data (below), I distinguished shallow-grazing molluscs (littorinid snails and pulmonates), deep-grazing molluscs (limpets and chitons), and urchins, which graze more deeply into algal tissue than any of the molluscs (based on literature reviewed in Steneck & Watling, 1982; Steneck, 1983, 1990).

2.3. Quantitative survey

To quantify patterns of crust distribution and abundance, a total of 166 random 100 cm² quadrats, stratified by tidal height (4–5 levels) were censused in the San Juan Islands and on Tatoosh Island ($N = 5–26$ quadrats/level: see Fig. 1). Tidepools and sediment-impacted areas were not surveyed quantitatively, as these represent very different physical environments. Percent covers of crusts and other sessile organisms were estimated visually with the aid of squares marked off within the quadrat (for justifications of this technique, see Dethier et al., 1993). Herbivores were counted and their lengths (molluscs) or test diameters (urchins) recorded. These measurements were used to estimate herbivore biomass, using equations of size to dry mass (Menge, 1972; Dethier & Duggins, 1988). Samples of crusts were collected from each quadrat by chipping out a bit of substratum with a hammer and chisel, and returned to the laboratory for taxonomic verification. Additional samples (Table 1) were collected from various habitats for measurements of thickness and cell sizes. Fleishy crusts were hand

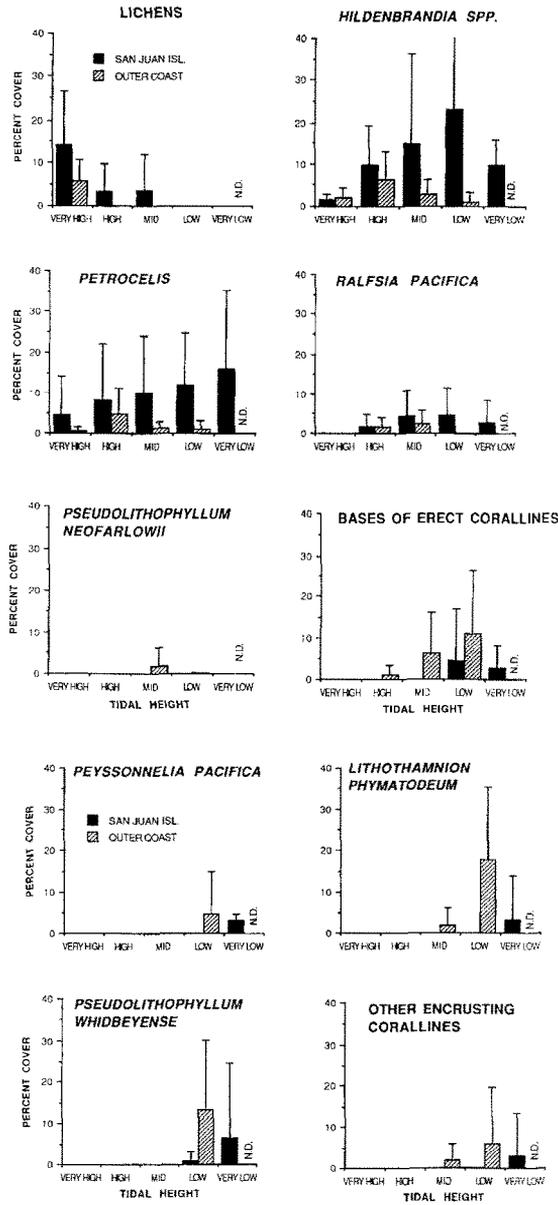


Fig. 1. Abundances of crusts at different tidal heights in the intertidal zone at two sites in Washington, arranged in approximate order of zonation patterns. Values are means and 1 SD. For the San Juans, number of quadrats from the Very High to the Very Low zone are 10, 18, 23, 31, and 27, respectively; tidal heights are $\sim > 2, 1.3, 0.6, 0,$ and -0.6 m. For the coast, N's from the Very High to the Low zone are 5, 14, 13, and 26; tidal heights are $\sim > 3, 2, 1,$ and 0 m, respectively. Very low sites were not censused at Tatoosh Island (N.D. = no data). "Lichens" = *Arthopyrenia orustensis* and *Verrucaria* spp. (wide variety of taxonomically difficult forms). "Other Encrusting Corallines" include *Lithophyllum impressum*, *Pseudolithophyllum muricatum*, and *Mesophyllum vancouveriense*, all uncommon outside of pools except in the low zone at Tatoosh.

Table 1
Morphological and anatomical characters of common Washington crusts

Species	Abbr.	Div.	San Juan Island			Tatoosh			Cell area	CALC.	ADH	TIGHT
			THK	SD	N	THK	SD	N				
<i>Lithophyllum impressum</i>	LIMP	R	383	146	152	567	218	5	60	X	X	X
<i>Lithothamnion phymatodeum</i>	LPHY	R	340	197	3	480	437	18	41	X	X	X
<i>Pseudolithophyllum whidbeyense</i>	PWHID	R	468	313	28	295	128	17	77	X	X	X
<i>Pseudolithophyllum neofarlowii</i>	PNEO	R	293	72	4	324	90	5	25	X		X
Articulated coralline bases		R	222	80	27	260	121	27	ND	X	X	X
<i>Ralfsia fungiformis</i>		P	474	228	6	440	243	5	ND			X
"Petrocelis"	PETR	P	451	201	167	362	130	23	20		X	(X)
<i>Peyssonnelia pacifica</i>	PEYS	R	325	166	23	258	223	17	90	(X)	X	X
<i>Ralfsia pacifica</i>	RALF	P	394	196	71	332	151	12	37			X
<i>Hildenbrandia occidentalis</i>	HOCC	R	421	197	29	ND			11		X	X
<i>Hildenbrandia rubra</i>	HRUB	R	124	55	75	ND			9		X	X
<i>Isactis plana</i>	ISAC	CY	246	80	19	ND			13		X	
<i>Arthopyrenia orustensis</i>	ARTH	L	216	51	45	ND			112			
<i>Verrucaria mucosa</i>	VERR	L	199	86	20	ND			24		X	X
" <i>Ralfsia californica</i> "		P	120	43	21	ND			39		X	X
<i>Rhodophyseta elegans</i>	RHOD	R	110	51	20	ND			20		X	X
<i>Pseudovella consociata</i>	PSEU	C	46	15	7	ND			23		X	(X)

Abbreviations are given for experimentally manipulated species. Division R = Rhodophyta, P = Phaeophyta, C = Chlorophyta, CY = Cyanobacteria, L = lichens. Crust thicknesses (THK: mean and 1 SD) are given from the two sites surveyed. ND no data were collected for that species at that site. Calcified crust thicknesses from Tatoosh Island are mostly less than those listed in Steneck & Paine (1986), perhaps because they sampled non-randomly for the healthiest specimens. Cell areas are calculated from the upper 1/3 of the crust ($N = 5$ specimens), listed in μm^2 . An X indicates the presence of the listed character in each species, while (X) indicates weak development of that character. CALC = calcified, ADH = adherent (to the substratum), TIGHT = filaments tightly adjoined.

sectioned and examined under $100\times$, while calcified crusts were broken and measured with a dissecting scope. Voucher specimens of all species are in the collection of the author. Basic anatomical and morphological characters of the crusts from each region are summarized in Table 1. The species are listed roughly in order of hypothesized resistance to disturbance based on the presence of the listed characters. Taxonomic authorities for the crust species in this study are listed in Steneck & Paine (1986) and Dethier (1987), along with a discussion of the taxonomic problems with some of these entities.

2.4. Manipulating environmental parameters

Inasmuch as a number of co-acting parameters (intertidal stresses, herbivory, competition with other algae) could result in observed patterns of crust distribution and abundance, a series of experimental manipulations were conducted to investigate controlling processes. I was particularly interested in whether manipulating environmental stress and disturbance would affect the growth or survival rates of the common crust species, and how crust morphology affects crust response.

A variety of species were transplanted into experimental areas along a gradient hypothesized to differ in productivity potential, then the disturbance regime was artificially varied. Productivity potential was assumed to be determined by tidal height (see Definitions, above), with production increasing with decreasing height on the shore. Thus, I manipulated productivity potential via choice of habitats, and disturbance potential directly (see below). Crusts were transplanted by collecting them on a chip of their rock substratum and imbedding multiple chips into a patty of marine putty, Kopper's Splash Zone Compound. Each chip was placed with the crust as flush as possible with the putty surface. Crust edges in direct contact with curing putty sometimes died, but hardened putty appeared totally nontoxic, and the crusts grew over it readily. Most crusts had some "control" transplants in being placed back into a habitat close to their source. Only *Peyssonnelia pacifica* showed long-term negative transplant effects; it died or lost much percent cover in all transplants. Experiments in Maine (C. Pfister, pers. comm.) suggest that this genus does much better when an individual thallus is not fragmented. *Peyssonnelia* is excluded from analyses except where changes in cover can be corrected for by changes in controls (e.g. in laboratory experiments). Crustose coralline (*Lithophyllum impressum*) transplants onto exposed intertidal surfaces also failed due to desiccation, although they survived in submerged treatments.

Transplants were performed at two sites in the San Juan Islands (YI and PP), each with experiments in high, mid-north-facing (mid-N), mid-south-facing (mid-S), and low zones. Tidal heights and rock aspect for experimental habitats are listed in Table 2. To include the environment that was the source for two of the crust species, and to examine the effects of another type of stress, the high zone at PP consisted of a set of pools that were assumed to be stressful because of highly varying temperature and salinity. The intent was to vary parameters causing stress (tidal height, insolation, submerged vs. emerged), but as these experiments were begun prior to the recommendations of Hurlbert (1984), they are pseudoreplicated for some of these variables. While each transplant location contained five patties for each of three disturbance treatments and are thus properly replicated for disturbance, there are only two replicates (with subsamples) for the tidal height variable (i.e., 2 mid-S, 2 mid-N, and 2 low transplants), and only one replicate each for the high pool treatment and the high emergent treatment.

For each intertidal location, molluscan grazers (limpets and chitons) were removed from areas $\sim 1 \text{ m}^2$ and kept out by means of copper paint strips ($\sim 5 \text{ cm}$ wide) on the rock. Littorinids moved freely over these strips but have very little impact on crusts (see below), and urchins were not present in any of the zones. Recruited or immigrant limpets and chitons were removed monthly, so that grazer biomass remained very low

Table 2

Transplant habitats for artificial disturbance experiment and limpet manipulations. Rock aspect is given as general slope and compass bearing (magnetic)

Site	Tidal height (m)	Type	Rock aspect	Date begun	Duration (mth)	No. of crust species
<i>Disturbance expts.</i>						
PP	+ 2.3, High	Pool	Horizontal	9.83	34	6
PP	+ 0.9, Mid-north	Emergent	Steep, 344°	5.84	25	6
PP	+ 0.8, Mid-south	Emergent	Steep, 162°	5.84	25	6
PP	+ 0.2, Low	Emergent	Steep, 332°	9.83	34	6
YI	+ 2.0, High	Emergent	Steep, 340°	9.83	34	5
YI	+ 1.2, Mid-north	Emergent	Steep, 334°	9.83	34	5
YI	+ 1.0, Mid-south	Emergent	Steep, 194°	9.83	34	5
YI	0.0, Low	Emergent	Gentle, 16°	9.83	34	5
FHL	RAFT	Submerged	Horizontal	10.85	24	8
<i>Limpet manipulation</i>						
PP	+ 0.1, Low	Emergent	Steep, 10°	9.83	34	5

at all times. Copper paint appeared to affect algal growth only within about 3 cm; all patties with crusts were placed at least 5 cm away.

In an attempt to quantify crust growth in an "optimal" habitat – grazer-free, never desiccated, and with plenty of light and water motion – another set of transplants was placed on a raft hung from the floating breakwater at the Friday Harbor Laboratories. Here 15 patties were put onto an unshaded half, and 15 more under a shade of two layers of teflon window screening, which reduced the light by 50–75% (depending on sun angle). The raft (of PVC slats, with plenty of circulating water around the patties) was hung 0.5 m below the surface, and the patties were cleaned weekly. Again, artificial disturbance treatments were properly replicated on each side of this raft, but the light treatment was pseudoreplicated.

Major sources of disturbance to algae in this region are herbivores, waves, log damage, and sand scour (not important at my study sites). Herbivores are probably of broadest importance and were manipulated in one set of experiments, but a form of experimental disturbance was needed that was more precisely manipulable and not affected by possible palatability differences among species. Thus crusts were disturbed mechanically in a controlled fashion using brushes. In one set of experiments, I varied disturbance intensity (or biomass removed per event) by using different kinds of brushes; at each habitat, replicated patties ($N = 5$ per treatment) with 5–8 species of crusts were either left unbrushed, or brushed with a nylon brush or a steel brush for 1 min each month (techniques of Steneck, 1982b). Thus frequency of disturbance was kept constant. Pressure was kept consistent by having only one person doing all the brushing on one sampling date, so that all replicates were equally disturbed. Steel brushing appeared to mimic the damage caused by limpet or chiton grazing, making visible scratches in coralline crusts and thinning non-calcified crusts. No crusts were entirely removed by a single (or even several) brushing episodes. Nylon brushing appeared to "dig into" only the softest crusts, thus mimicking grazers such as littorinids

that mostly remove epiphytes. Unbrushed patties were plucked clean of macroalgae and lightly cleaned monthly to avoid a competitor- or fouling-effect. However, these patties were usually more fouled than the brushed ones, confounding some of the results (although this situation is realistic for natural, few-grazer habitats). Intertidal treatments were assigned in a pattern that avoided any treatment always being placed higher or lower on sloping faces. On the raft, treatments were randomly assigned.

Pilot experiments indicated that some crusts visibly regenerated tissue between monthly brushings. To examine crust sensitivity to steel brushing while minimizing regeneration, 1 steel-brushed patties (like those in the field) in the laboratory twice over 2 wk.

An additional field experiment examined the effects of varying disturbance frequency while controlling intensity, using real grazers. Limpets and chitons were excluded ($0 \times$ density) from an area with five patties (same crust species as above), left at normal density (free access: $1 \times$) on five others, and kept at artificially high densities (roughly $2 \times$ limpet densities) on five others. This experiment succeeded at a low site at PP, but failed due to predation on the limpets (by oystercatchers) on YI. This experiment, too, was pseudoreplicated. All patties were cleaned regularly, but fouling was consistently heavier in the $0 \times$ treatment than elsewhere.

Survivorship and growth were monitored to determine the response of each crust sample to the experimental treatments. Since growth of most crusts in most habitats was extremely slow, field experiments ran for over two yr (Table 2), and some for as long as three. The percent cover of each crust on its rock chip was estimated visually (Dethier et al., 1993) at the beginning of the experiment and twice yearly thereafter. Rock chip sizes were measured with a fine grid. Photographs (regular and infrared) were not sufficient to "see" the dark, fleshy crusts used in these experiments, preventing successful digitizing. For crusts that grew out over the putty, maximum extent of lateral growth was measured twice yearly, and area grown (over the putty) was measured at the end using a grid. Changes in percent cover were converted to changes in area to incorporate this new growth. All results are presented as the proportion of the original crust area on each chip; that is, as area at end (including area grown)/area at beginning. The correction for initial area is necessary because not all crusts began as 100% cover on their chips, nor were all chips the same size.

Since assumptions of normality and homogeneity of variances were violated for most of the data sets, non-parametric statistics are used for examination of treatment effects and differences among species. One-way Kruskal-Wallis ANOVAs were followed by the non-parametric version of the Student-Newmann-Keuls test for a posteriori multiple comparisons (Zar, 1984). *P* values ≤ 0.05 are termed significant.

Relative consumption rates of the common intertidal crust species by different species of local grazers were also examined in laboratory experiments. Patties with 6–8 species of crusts were made up in Petri dishes and surrounded with Vexar fences to enclose the grazers. Individual grazers (numbers and sizes varying with species; Table 3) were added to some of the dishes, leaving others as controls. Changes in percent cover of the crusts were monitored through time, with experiments run until obvious changes in crust cover were seen. If significant changes in percent cover among crust species occurred in the controls, the mean change in the control dishes for each

Table 3
Design of laboratory grazer-feeding experiments

Grazer	No. of dishes	No. of indiv./dish	Mean size	Length of expt.	No. of crust species	Controls subtracted?	<i>p</i> value
<i>Katharina tunicata</i>	4	1	40	4 wk	7	no	0.003
<i>Lottia strigatella</i>	4	10	10	4 wk	7	no	0.48
<i>Lottia pelta</i>	1984 3	1	16	3 wk	8	yes	0.004
	1986 5	4	16	2 wk	7	no	0.013
<i>Tectura scutum</i>	1984 3	1	15	3 wk	8	yes	0.008
	1986 5	4	18	2 wk	7	yes	0.006
<i>Littorina scutulata</i>	4	20	8	4 wk	7	no	0.41
<i>Littorina sitkana</i>	3	8	8	13 wk	8	yes	0.04
Steel brush	10	–	–	2 wk	7	no	0.0001

Mean grazer size is given in mm (length). The *p* value indicates differences among crust species in amount (% cover) consumed by each grazer species at the end of the experiment.

species was subtracted from the values with grazers. Differences in susceptibility among crusts were tested with non-parametric ANOVAs.

Tissue water contents of various crust species were measured to look for a correlation with desiccation tolerance. Samples ($N = 5$ –26 per species) were collected at low tide, hydrated in seawater in the laboratory for > 24 hours, blotted thoroughly and weighed, then dried in an oven at 60 °C for 48 h and reweighed. For crustose corallines, other samples were weighed before and after decalcifying with 5% acetic acid and drying, producing estimates of CaCO₃ mass and water mass.

3. Results

3.1. Zonation patterns of crusts

Most crust species showed some zonation in abundance across the range of intertidal environments examined (Fig. 1). Intertidal zones at Tatoosh were ranked as “lower” than comparable zones in the San Juan Islands because of the more benign conditions created by fog, spray, and the timing of low tides there. In both regions, species dominating the high shore are primarily lichens and Cyanobacteria (the latter form thin, indistinct films and were not quantified). Mid zones are dominated by *Hildenbrandia* spp. (grouped for illustration because they overlap highly in distribution and because they cannot be distinguished when sterile), and by the crustose tetrasporophyte of *Mastocarpus papillatus* (referred to henceforth as “Petrocelis” for brevity). Diversity increases in the low intertidal; crustose corallines and several fleshy species are confined to this zone. All species had low mean percent covers but many were locally abundant (patchy), as indicated by the high variances in Fig. 1. This is in part due to the range of habitats surveyed; although tidepools and environments impacted by sediment were avoided, I did include horizontal, sloped, and vertical surfaces facing a variety of compass directions (aspects). Rock aspect was manipulated in the trans-

plant experiments (below), and found to be an important variable. A number of species listed in Table 1 are not illustrated in Fig. 1 because of their very low abundances on rock surfaces exposed to desiccation and associated stresses, although they can be common in other habitats. Tidepools have much less "Petrocelis" and lichens than do exposed surfaces (data in Dethier, 1987), but more of other species, e.g. *Isactis*, "Ralfsia californica", *Rhodophysema*, *Peyssonnelia*, and most of the crustose corallines.

Herbivore biomasses in these same zones are illustrated in Fig. 2. Shallow-grazing molluscs (primarily littorinid snails) are most abundant high on the shore, but are small and never reach high biomass in the areas sampled. Deep-grazing molluscs (limpets and chitons) become steadily more abundant lower on the shore in the San Juans, but are

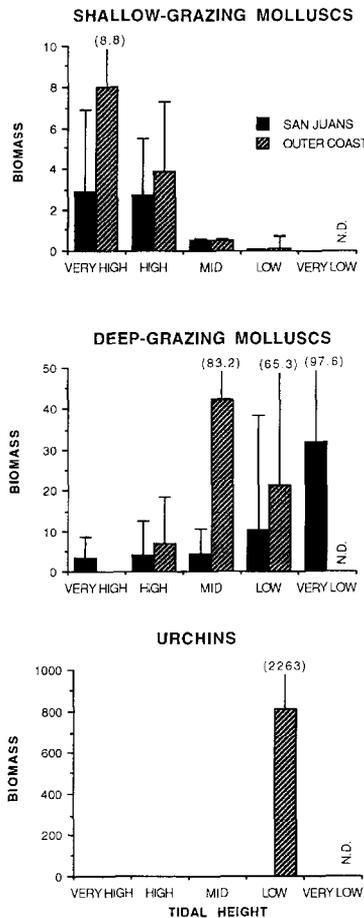


Fig. 2. Abundance of various herbivore groups in the survey quadrats, calculated as dry biomass per m². N's as in Fig. 1. Shallow-grazing molluscs in both regions include *Littorina sitkana* and *Littorina scutulata*, and on the coast include *Onchidella borealis* and *Siphonaria thersites* as well. Deep-grazing molluscs at both sites include the limpets *Lottia pelta*, *Lottia digitalis*, *Lottia strigatella*, *Tectura scutum*, and *Acmaea mitra*, and the chitons *Katharina tunicata*, *Tonicella lineata*, *Mopalia* spp., and *Lepidochitona dentiens*. Urchins are *Strongylocentrotus purpuratus*.

replaced (perhaps competitively displaced) by urchins in the low regions on the coast. In each region, the net result is an increase with decreasing tidal height of potential disturbance (i.e., potential consumption, both in terms of biomass and grazing intensity) to crusts (and to other algae).

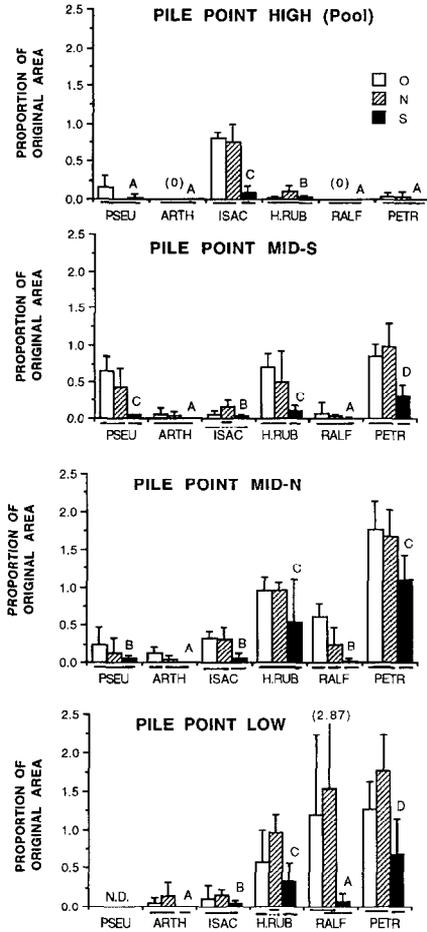


Fig. 3. Effects of brushing treatments on area of transplanted crusts in Washington, at four tidal heights at the Pile Point site. Histograms indicate mean and 1 SD for the five patties in each treatment. Transplanted crusts that showed an overall increase in area during the course of the experiment (2 yr) are those with proportion of original area > 1.0, while < 1.0 indicates a net loss of area. O = unbrushed treatment (low intensity); N = nylon-brushed (moderate intensity); S = steel-brushed (high intensity). Species abbreviations as in Table 1. Lines beneath the bars indicate significant ($p \leq 0.05$) differences among treatments within a species. Letters above the solid bars indicate differences among species within the steel brush treatment; bars with the same letter are not significantly different (Kruskal-Wallis tests with non-parametric SNK tests). N.D. = no data; that species was not transplanted into that habitat.

3.2. Manipulating disturbance potential

3.2.1. Artificial disturbance experiments

Figs. 3–8 illustrate the responses of all transplanted species to the three brushing regimes, including the results of the statistical comparisons both within and among species. All species responded negatively to being steel brushed (intense disturbance) and less negatively (or even positively) to being nylon-brushed, although the latter still caused significant declines in many. Growth rates for all species were extremely slow, with some species showing no measurable lateral growth over 3 yr, and the fastest growing at <20 mm/yr. Growth rates are graphed (e.g. Fig. 4) only if >2 of the 5

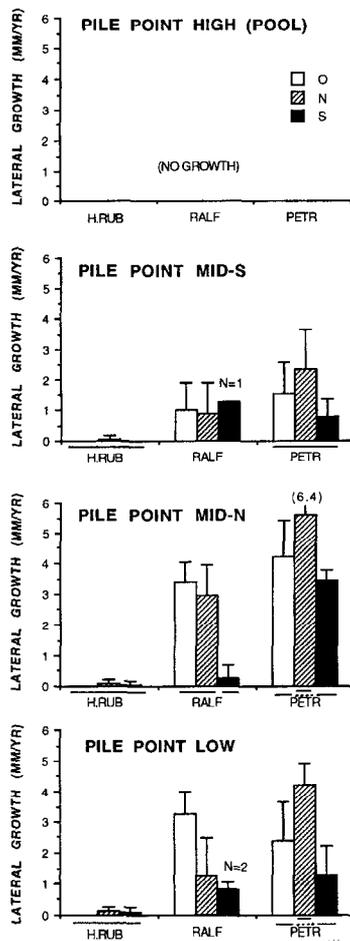


Fig. 4. Effects of brushing treatments on lateral growth of transplanted crusts at the Pile Point site. Symbols and analyses as in Fig. 3. Growth of the other three species transplanted at this site was negligible. Multiple comparisons were not run with variable N 's, e.g. if growth could not be measured in some treatments (such as when some chips were overgrown by another species, or died).

samples in a treatment grew. In general, growth rates responded in the same direction as survival under the different brushing treatments. The 10 species examined are discussed below in rough order of sensitivity to disturbance (i.e., damage done by disturbance agents), based on statistical tests for both the field (Figs. 3–8) and laboratory (Fig. 9) experiments.

Arthopyrenia orustensis is a thin marine lichen common in sunny, mid and high zones (0.2–1.5 m above MLLW; Dethier, 1987). It is a soft crust, composed of clumps of cyanobacterial cells interspersed with fungal filaments (illustrated in Dethier, 1987). It was transplanted only to the PP sites (Fig. 3), where it fared poorly in all the treatments. In both field and laboratory brushing experiments it was the crust most sensitive to disturbance, vanishing totally under the steel brush and mostly under the nylon (Figs. 3 and 9). It also died when submerged (e.g. in the high pool at PP) or fouled by

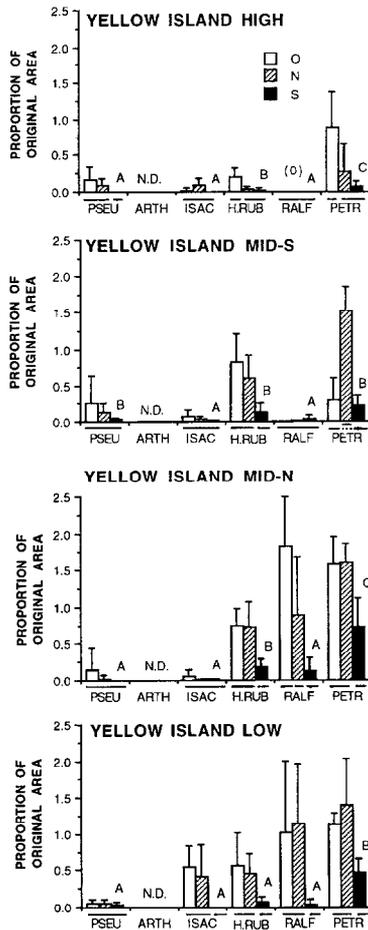


Fig. 5. Effects of brushing treatments on area of transplanted crusts in Washington, at four tidal heights at the Yellow Island site. Symbols as in Fig. 3. *Arthopyrenia* was not transplanted at this site.

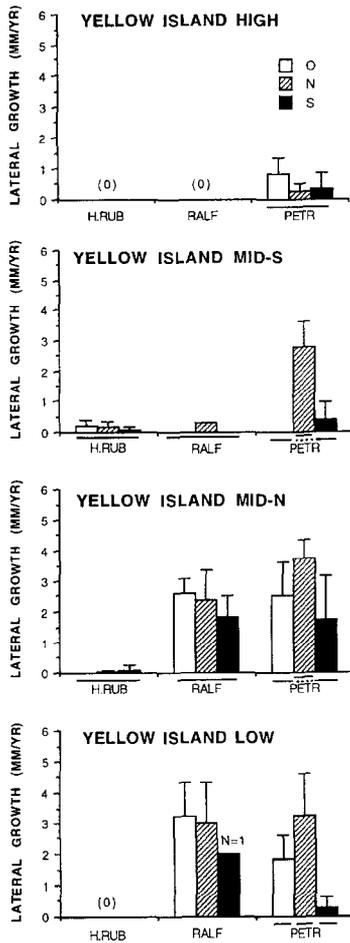


Fig. 6. Effects of brushing treatments on lateral growth of transplanted crusts at Yellow Island. Symbols and analyses as in Fig. 3.

erect algae (as in the unbrush treatments). Lateral growth was observed in none of the 60 samples in this experiment. Transplanting per se was not lethal, as the lichen survived and grew (3 of 15 samples) in the experiment with real grazers (Fig. 13); the limpets kept the habitat un fouled but did not consume the lichen (see below).

Pseudulvella consociata is an enigmatic green crust collected from limpet-free high intertidal pools (Dethier, 1987), where it forms very thin films (usually less than 50 μm thick). I never observed it growing, probably because it was never thick enough to form a conspicuous growing edge. The transplants and laboratory experiments showed it to be very sensitive to steel and nylon brushing.

Rhodophysema elegans, a thin rose-red crust, lives intertidally only in pools. All transplants onto emergent rock (even very low) died, presumably due to desiccation. Data from the raft (Figs. 7 and 8) imply that it is one of the crusts least sensitive to

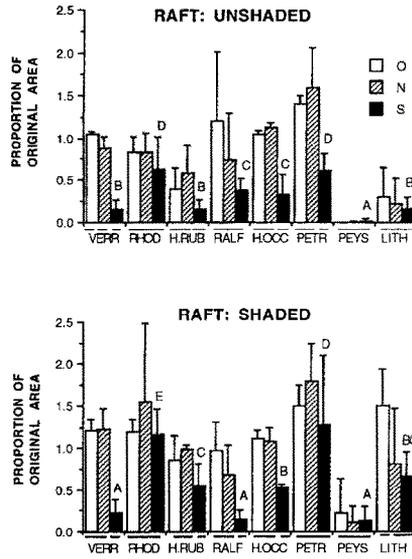


Fig. 7. Effects of brushing treatments on area of transplanted crusts under two light regimes on the raft in Washington (herbivore-free, submerged). Symbols and analyses as in Fig. 3; species abbreviations as in Table 1. *Peyssonnelia* suffered significant transplant artefacts (see Methods).

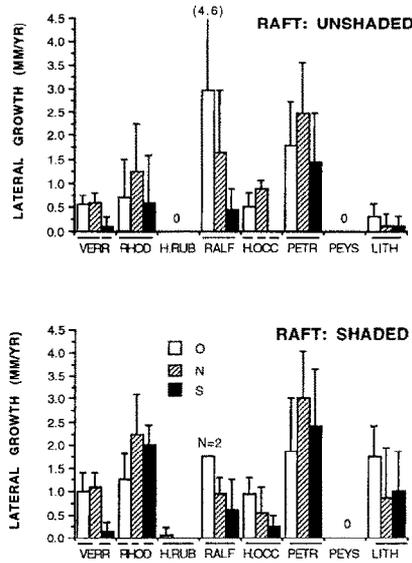


Fig. 8. Effects of brushing treatments on growth of crusts transplanted onto the raft in Washington. Symbols as in Figs. 3 and 7.

disturbance; brushing had no significant effect on area, although declines in percent cover were seen in the steel-brushed samples. In contrast, the short-term laboratory experiment showed that *Rhodophysema* is highly sensitive to being steel-brushed, ranking third out of eight crusts tested (Fig. 9). The explanation for this discrepancy may lie in its very rapid vertical tissue regeneration following disturbance (Dethier & Steneck, in prep.) and in its fairly rapid lateral growth (Fig. 8). In the raft experiments, damaged crusts had time to regenerate between monthly brushings, reducing the apparent brushing effect.

Verrucaria mucosa is a marine lichen normally found in shaded areas above mean high water. Its phycobiont is a green alga, and its thallus is more cohesive than that of *Arthopyrenia*; it is not easily scraped off the rock, and in laboratory experiments it was significantly less susceptible to the steel brush (Fig. 9). *Verrucaria* was not used in the intertidal transplants, but was put on the raft (Figs. 7 and 8), where it survived and grew (despite constant submergence). Both its area and lateral growth showed significant treatment effects. It fared quite poorly when steel brushed, while the nylon brush had a significant negative effect only in the unshaded patties.

Isactis plana is a blue-green crust found naturally as small (<100 mm²), disjunct patches in high tidepools. Like *Arthopyrenia*, it fared poorly in most transplants, although its sensitivity to brushing was much lower than the lichen's. In habitats where it survived, it clearly suffered the most under the steel brush (e.g. Fig. 3, high), but in general the nylon-brushed and unbrushed samples lost equal amounts. Like *Arthopyrenia*, *Isactis* is readily overgrown by other crusts and erect algae; it continued to live in unbrushed (fouled) treatments, but lost cover gradually. Normal lateral growth out over the putty was almost never seen; rather, this crust spreads via propagules distributed over short distances (1–2 cm), where they form new small patches. This behavior was seen only in transplants in the crust's native habitat type (the high pools at PP).

Ralfsia pacifica is a thick brown crust with a thallus composed of a large hypothallus (lower, laterally-directed filaments) giving rise to tightly-packed assurgent filaments. Despite its thickness and tightly-packed filaments, it was one of the crusts most sensitive to disturbance; in most transplant habitats it lost more cover under steel brushing

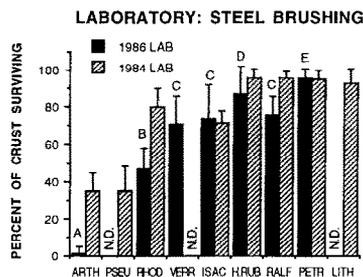


Fig. 9. Tissue remaining (% of original coverage) of nine crust species under steel brushing in the laboratory. Crusts were brushed once a week for 2 wk. $N = 3$ chips (replicates) per species in the 1984 experiment; $N = 10$ in 1986; N.D. = that species was not tested in that experiment. Statistics were run only for the 1986 data, since N 's were too low in 1984. Species with the same letter above the solid bar were not significantly different in survival.

than did many of the thinner crusts, and its growth rate was affected similarly. Even nylon brushing (in the intertidal and on the raft) caused large declines relative to unbrushed samples, although rapid growth helped mask this effect in low intertidal habitats. Nylon-brushed plants grew much faster than steel-brushed (Figs. 4 and 6) but slower than undisturbed ones. Further indication of its sensitivity to disturbance is seen in Fig. 10, which shows the percent cover of *Ralfsia* that recruited onto other chips during the course of the experiment; none appeared on steel-brushed samples, and much more was generally present on unbrushed samples than on nylon-brushed. This sensitivity, and the loss of *Ralfsia* cover in all transplants, appears due to the senescence and sloughing of older basal tissue. Old hypothallus dies and disintegrates, leaving no firm attachment for the overlying tissue, which then pulls away under any disturbance. Short-term experiments such as the steel brushing in the laboratory (Fig. 9) showed lower but variable sensitivity to brushing, presumably because some of the specimens were older than others and because all the thalli did not have time to senesce, as occurred in the field transplants.

Two species of *Hildenbrandia* were studied, although only *Hildenbrandia rubra* was transplanted to all the habitats. *Hildenbrandia rubra* is the thinner species (Table 1) and extends into more marginal habitats (very high pools and freshwater seeps) than does *Hildenbrandia occidentalis*, but otherwise the two overlap in distribution. *Hildenbrandia rubra* showed a distinct negative response to steel brushing in the field in most habitats, although it lost less of its area than any of the species except "Petrocelis". In the laboratory, it was one of the most resistant species tested (Fig. 9). Nylon brushing usually had a mild negative effect, with the exception of the samples on the raft (Fig. 7) and at PP Low (Fig. 3, LOW), where nylon brushing improved survival, probably by reducing settlement and overgrowth by fouling crusts (*Ralfsia* spp.: Fig. 10). *Hildenbrandia rubra* grew too little to observe treatment effects on lateral growth rates; after 4 yr, the maximum total lateral growth seen in any habitat was 1.5 mm.

Hildenbrandia occidentalis is thicker than, but anatomically similar to, *Hildenbrandia*

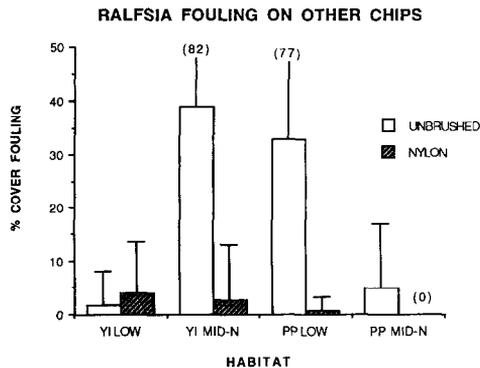


Fig. 10. Percent cover of *Ralfsia pacifica* fouling other experimental chips (except for *Petrocelis* chips, where it did not settle) at the end of the experiment, July 1986. Means and one s.d. are shown for the $N = 15$ –20 chips at each site and treatment.

rubra. On the raft both its area and growth declined under steel brushing but not nylon (Figs. 7 and 8). It grew substantially faster than *Hildenbrandia rubra* under all conditions (Fig. 8).

The fleshy crust most resistant to high artificial disturbance is “*Petrocelis*”. In the laboratory (Fig. 9), only vigorous steel brushing over long time periods reduced its cover, and in the field it was one of only two species that increased in area under the steel brush treatment (Figs. 3, 5 and 7). Its resistance probably stems from its considerable thickness and leathery or rubbery texture; its loose upper filaments seem to move or stretch when brushed, rather than being torn away. However, it did decline gradually in percent cover under steel brushing both on the raft (Fig. 7) and in the intertidal habitats (Figs. 3 and 5), and growth when steel brushed was usually significantly reduced (Figs. 4, 6 and 8). “*Petrocelis*” was the fastest-growing of the fleshy crusts transplanted; only in a few habitats was *Ralfsia pacifica* faster. Another unique feature of “*Petrocelis*” was its response to nylon brushing. Except in habitats with the lowest productivity potential (both high intertidal sites), area and lateral growth generally were higher at the end of the treatment period under nylon brushing than under no brushing. For “*Petrocelis*” in productive habitats, nylon brushing apparently is not a disturbance but a cleansing mechanism. Unbrushed, submerged samples in the laboratory rapidly became covered with a thick coating of bacteria, and upper cell layers died and sloughed off. In the field, unbrushed samples became fouled with diatoms and green algae, and survival and growth declined significantly (e.g. Figs. 5 and 6, mid-south). The nylon-brushed patties remained clean and thus were more subject to desiccation (no canopy), but the “*Petrocelis*” in this treatment thrived.

Attempts to transplant coralline crusts into intertidal habitats failed, apparently because of desiccation stress on exposed surfaces, and extreme insolation and temperatures in the high pools. Transplants onto the raft of one species, *Lithophyllum impressum*, were successful. Samples on the shaded side of the raft survived and grew (Figs. 7 and 8), but for unknown reasons all the samples on the unshaded side fared poorly (Fig. 7) despite having been collected from well-lit, shallow, mid-intertidal pools (others have successfully transplanted this species using this technique: Paine, 1984). Overall, crust area showed a weak treatment effect, with both steel and nylon brushing resulting in reduced area relative to the unbrushed samples. In the laboratory, only pilot experiments ($N = 3$) were done brushing *Lithophyllum* with a steel brush (Fig. 9); two of the samples lost no cover, while the third thinned and declined. The mean cover lost was low, and I expect that under continued brushing it would have lost less cover than any of the fleshy crusts.

3.2.2. Herbivore experiments

Laboratory feeding experiments showed that the four herbivore species tested did not all consume the crusts in the same rank order (Fig. 11), nor did they necessarily eat the crusts that were mechanically the least resistant to removal. For each herbivore species, Kruskal-Wallis tests were run on the percent covers of the crusts at several times during the course of each experiment (durations and p values in Table 3). Ranks (Fig. 11) were assigned based on multiple comparisons following these ANOVAs; crusts are given the same rank (for a given herbivore species) when the percent covers

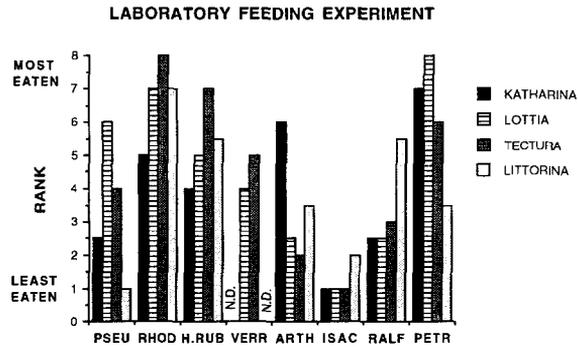


Fig. 11. Laboratory herbivore experiments. Histograms indicate the rank in terms of percent cover of each crust species remaining after being offered as a multi-species choice to different herbivore species. LOTTIA = *Lottia pelta*; LITTORINA = *Littorina sitkana*; other species as in Table 3. N.D. indicates that *Verrucaria* was not offered to those herbivore species. N's are listed in Table 3.

remaining did not differ significantly among those species during any of the censuses. Fig. 11 shows the rankings of eight crust species by a littorinid, each of two limpet species, and a chiton. *Lottia pelta* (Rathke and *Tectura scutum* (Rathke), two limpets similar in size and radular morphology, differed in their rankings of "Petrocelis", *Hildenbrandia rubra*, and *Pseudulvella*, although overall their rankings were highly correlated ($r = 0.83$). *Littorina sitkana* Philippi showed some similarity with the limpets, but removed significant amounts of *Ralfsia pacifica*, which neither limpet species consumed readily. Identical experiments were run with *Littorina scutulata* Gould and with the small limpet *Lottia strigatella* (Carpenter), neither of which had a significant impact on the crusts (Table 3). Yamada (1992) finds that *Littorina sitkana* eats much more rapidly, has sharper teeth, and can bite more deeply into algae than can its congener.

To examine whether the various grazers tested above were showing preferences that related simply to mechanical ease of removal (e.g. versus to taste or caloric value), I compared the sensitivity of the different crusts to being grazed by herbivores with their sensitivity to brushing in the laboratory steel-brushing experiments (the latter provided the clearest data on variation in mechanical toughness). Fig. 12 illustrates the correlation between the mean crust rankings for the four grazer species and for the steel brush. There is no significant correlation between these sets of rankings ($r = 0.24$). Striking differences are seen in the rankings of "Petrocelis" and *Hildenbrandia rubra*, both difficult to brush away but readily eaten. Kitting (1980) also found "Petrocelis" to be readily consumed by limpets. *Pseudulvella* is easily brushed off but not readily eaten, perhaps because it is very thin, compact, and tightly adherent to the substratum. *Arthopyrenia* is also easily brushed but little consumed, at least by the limpet species. It is of interest that of the four least-eaten crust species, two are or contain cyanobacteria (which are often toxic: Carmichael, 1981), and one (*Ralfsia pacifica*) contains very high concentrations of phenolic compounds (5–11% of dry weight, $N = 5$).

While the field experiment in which limpet densities were successfully manipulated was pseudoreplicated, the three treatments were all on one 0.5 m² rock face, and it is unlikely that the patties were subjected to differences other than those relating to the

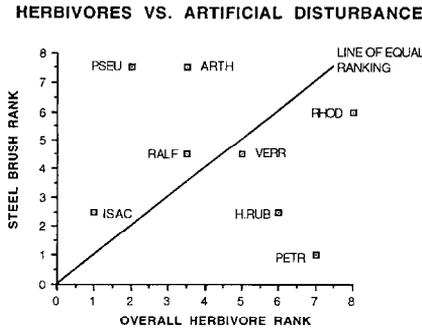


Fig. 12. Correlations between rankings of different crust species by the steel brush and by herbivores (averaged over the four herbivore species tested).

limpet manipulation. ANOVAs run on the data (treating the patties as replicates rather than pseudoreplicates) corroborate the relative susceptibility of the different crusts to grazers. Neither *Isactis*, *Ralfsia pacifica*, or *Arthopyrenia* showed significant differences in area among the 0x, 1x, and 2x limpet treatments (Fig. 13), suggesting that the limpets simply did not eat these species. *Ralfsia* actually grew significantly faster, and *Arthopyrenia* survived and grew slightly better with than without limpets, probably because of the benefits of limpets removing fouling algae. However both “*Petrocelis*” and *Hildenbrandia*, two of the species eaten most readily in the laboratory, lost significantly more percent cover in the 1x and 2x treatments than in the limpet

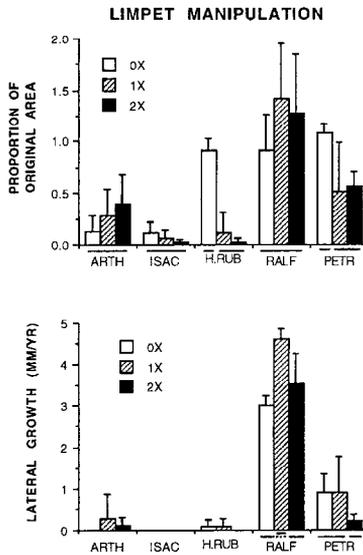


Fig. 13. Crust responses to different frequencies of herbivory (herbivore densities) in the field (low intertidal, Pile Point). 0x = no herbivores; 1x = normal density; 2x = approx. double density of limpets. Other symbols and analyses as in Fig. 3 (N = 5 patties per treatment).

exclusions. These results all suggest a preference for the latter two species and avoidance of the others.

3.3. Results: manipulating productivity potential

By comparing the survival and growth of each species in the various habitats (in the absence of disturbance) along the productivity potential gradient (low to high intertidal), one can determine if all crusts respond similarly to this extrinsic gradient, or if there are intrinsic differences in how they “view” intertidal stress. Since manipulations of this “treatment” (stress) were under- or pseudo-replicated, no inferential statistics were done. Figs. 3–8 and summary Fig. 14 illustrate that in general, for any given brushing treatment most species survived and grew better in the lower intertidal (the hypothesized area of high productivity potential). However, the 11 experimental species discussed below varied in their responses to this gradient. While I assume that the primary stress encountered is desiccation, clearly temperature, UV, and other stresses may be important and follow the same gradient.

The species least resistant to high stress (low productivity potential) situations were *Rhodophysema*, *Peyssonnelia*, and *Lithophyllum*. All are found normally only in pools or subtidally (or in the low intertidal at Tatoosh, where desiccation stress is minimal) and most did well on the submerged raft (Fig. 7), but transplants to emergent rock in the San Juans all died. They survive in tidepools up into mid zones, however; thus they can withstand fluctuating environmental conditions as long as they are submerged.

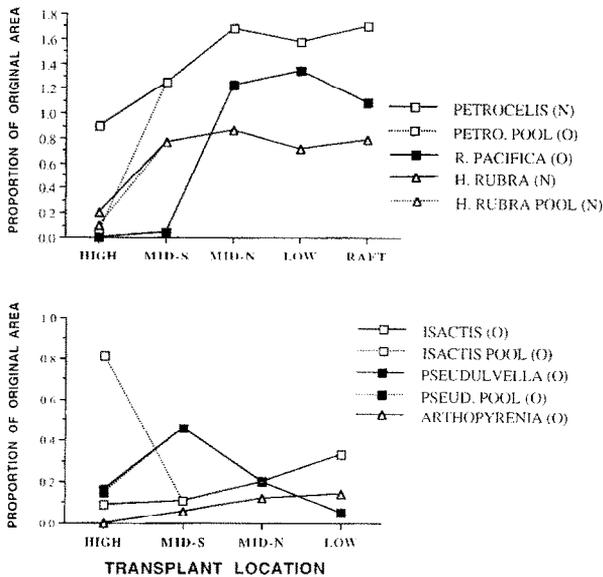


Fig. 14. Summary of crust survival at the transplant sites. For each tidal height, the proportion of the original area is given for the best brushing treatment (e.g. nylon for *Petrocelis*) at that height, averaged for the 2 sites (YI and PP). Since the high treatment was a pool at Pile Point and emergent rock at Yellow Island, these are drawn separately when crust responses were visibly different.

Isactis, *Ralfsia pacifica* and *Hildenbrandia occidentalis* are somewhat more resistant to intertidal stresses than the above three species. Of these, only *Ralfsia* was transplanted to all habitats, and it showed clearly greater survival and growth in the higher productivity potential habitats (Figs. 3–8 and 14). In the mid-intertidal zone, survival was high on north-facing surfaces and very low on south-facing ones, probably due to desiccation. In addition, *Ralfsia* was never seen recruiting onto other chips in the south-facing treatments, but commonly did so on the north-facing ones (Fig. 10). Even in the low zone, *Ralfsia* survival, growth, and recruitment were higher at the north-facing (Table 2) PP site than on the more desiccated, horizontal YI site (Figs. 3–6). *Hildenbrandia occidentalis*, although sometimes found living quite high on the shore, is most abundant in shaded areas and crevices (unlike its congener, see below), suggesting moderate susceptibility to desiccation. *Isactis* survived somewhat better when transplanted to low than to mid or high (emergent) zones (Fig. 14), so I rank it as moderately susceptible as well. However, when submerged, it can withstand extreme conditions; the high pool at PP, where it thrived (Fig. 14), froze during some winters and was hot and hypersaline in the summers.

“*Petrocelis*” tolerates, and perhaps even benefits from, moderate desiccation. It survived in every transplant habitat and was usually the healthiest species at the end of the experimental period. It generally did best in terms of both area and lateral growth in the mid-north habitats (Figs. 3–6). These data corroborate its field distribution; it is common almost everywhere, but covers large expanses of rock on north-facing surfaces in the mid to upper intertidal zone. It did poorly in transplants to high tidepools (Fig. 3) regardless of brushing treatment.

Hildenbrandia rubra and *Pseudulvella* are clearly tolerant of a variety of intertidal stresses, as both can be found on high emergent rock, in high pools, and even in freshwater seeps. However, the “optimal” habitat of each remains uncertain. Neither showed the expected response of greater survival and growth in higher productivity potential habitats, instead surviving well (or even best) in some desiccated mid-south-facing areas (Figs. 3, 5 and 14). *Pseudulvella* was never observed to grow laterally, and growth in *Hildenbrandia rubra* was glacial and variable. The only clear pattern for *Hildenbrandia rubra* is that survival and growth are poorer in the highest zones, although even here the crust experienced only partial, rather than complete mortality as in many other species.

The two lichens, *Verrucaria mucosa* and *Arthopyrenia orustensis*, are clearly the most desiccation tolerant of the manipulated species, normally inhabiting the highest zones on the shore. Their distributions differ, however, in that *Verrucaria* is most abundant in very high but shaded areas, while *Arthopyrenia* predominates on sunny shores (also noted on British shores by Fletcher, 1973). *Verrucaria* thrived on the raft under constant submergence (Figs. 7 and 8), although transplants ($N = 25$) to high pools at different seasons consistently died during the summer, showing that the stresses survived by *Isactis* are lethal to *Verrucaria*. Control transplants into emergent shaded areas ($N = 6$) all survived and grew, while others ($N = 9$) into emergent sunny areas all died. *Arthopyrenia*, in contrast, is totally intolerant of submergence and apparently intolerant of being fouled (discussed above); thus desiccation is necessary for, rather than detrimental to its survival. For this species, and to a lesser extent for *Isactis* and

Pseudovella, the low to high intertidal does not constitute a stress gradient, even though productivity potential for most marine algae probably does decline in this direction.

Tolerance of desiccation did not correlate with tissue water content, at least among the fleshy crusts (Fig. 15). The two least tolerant of the fleshy crusts, *Rhodophysema* and *Peyssonnelia*, had the largest and the smallest water contents, respectively. However, all four coralline species tested had less tissue water (measured as percent of total mass) than all of the fleshy crusts (Fig. 15), presumably because a large proportion of their mass is CaCO₃ (Fig. 15). This dearth of available water may be responsible, in part, for the desiccation intolerance of crustose corallines.

The “quality” of the transplant habitats for algae other than crusts was assessed qualitatively by ranking the level of macroalgal fouling of the patties at each area on 19 dates. The patties were cleaned monthly, and thus fouling represents roughly one month’s growth. High intertidal patties always had the least fouling (mean rank = 1.0); they remained clean or acquired very thin coatings of green or blue-green crusts. Low intertidal patties were the most fouled (mean rank = 3.5), becoming covered with diatoms, ulvoids, and/or filamentous green algae. However, despite the expected negative impact of desiccation, mid intertidal areas with a south-facing aspect often had as much and sometimes more fouling (mean rank = 3.4) than the low habitats, indicating that these areas can be good for growth of these opportunistic algae. Mid intertidal north-facing areas, with less desiccation but less light, had much less fouling than the south faces (mean rank = 2.2). In contrast, most crusts survived and grew better on north-facing surfaces; this was seen not only in the brushing experiments, but in a pilot study (Fig. 16), where crusts were transplanted to each face of an old dock footing. After 4 months, 3 of the 4 species were healthiest on the north face and least healthy on the west; only *Isactis* showed no clear response to rock aspect. It is not clear why the west face should be more stressful than the south, since there are few low tides that fall in the afternoon in this region.

Fig. 14 summarizes the transplant conditions under which each crust species did best (in terms of final area). For some crusts, including the thick “*Petrocelis*” and *Ralfsia*

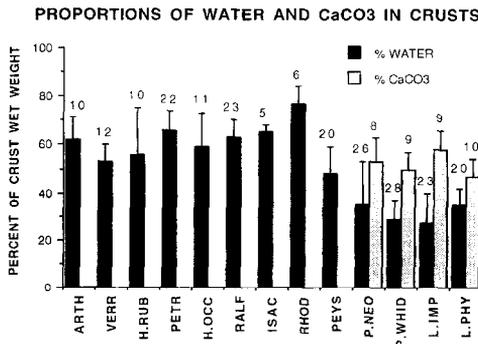


Fig. 15. Proportions of crust wet weight consisting of water and of CaCO₃ for nine fleshy and four coralline crust species. Data are mean percent and 1 SD of total crust wet weight; N's are listed above each bar. Fleshy crusts are illustrated in approximate order of desiccation tolerance. Species abbreviations as in Table 1.

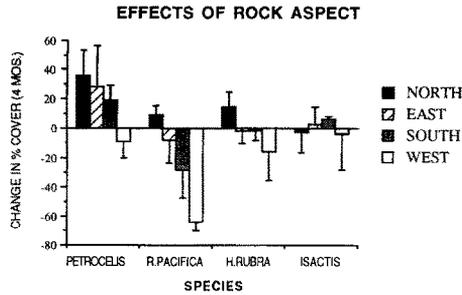


Fig. 16. Effect of rock aspect on survival of crusts outplanted onto an old dock footing ($\sim +1.0$ m tidal height); data are mean and 1 SD of change in percent cover from February to June 1985. Patties were surrounded by fences to exclude limpets, and cleaned on an irregular basis. $N = 4$ chips per species per treatment.

pacifica and the thin *Hildenbrandia rubra* and *Rhodophysema*, best survival and growth occurred under conditions where fouling was minimized: in the nylon-brushed treatments, and in the north-facing transplant sites where relatively few epiphytes appeared. Clearly, nylon brushing is not a major disturbance for these species, and they may benefit from the cleaning action. For other species, including *Isactis* and *Pseudovella*, the complete absence of disturbance was critical. For *Isactis*, good survival was seen only in its “native” habitat; I cannot judge if this was due to the absence of potential competitors and consumers in these stressful pools, or if for some reason this species requires extreme conditions.

4. Discussion

While crustose algae are broadly distributed in the marine realm, they generally dominate the flora only at the ends of environmental continua: (1) they are better than other algal forms at withstanding disturbance (biotic and abiotic), and (2) they are more stress-tolerant than most other algal forms. This study has shown that crusts vary widely both in morphology and in ecological characteristics, presumably enabling them (as a functional group) to occupy this broad range of habitats. Distribution, relative abundance, susceptibility to grazers, tolerance of desiccation, and growth rate all vary among species. Some but not all of this variation can be explained on the basis of straightforward morphological differences among species.

4.1. Mechanisms of disturbance tolerance

The crustose growth form, like clonal growth in terrestrial plants (Bazzaz et al., 1987) and marine invertebrates, is advantageous where horizontal spread is favored over vertical growth, e.g. where upright growth will be removed by disturbance. Similarly crusts, which can spread vegetatively, may be at an advantage where frequent disturbances or physiological extremes kill propagules. In general, the disturbance tolerance

of crusts stems from their being flat, attached to the rock along half their surface, difficult to remove from the rock in their entirety, and effective at regenerating following tissue loss (Daly & Mathieson, 1977; Slocum, 1980; Kitting, 1980; Menge & Lubchenco, 1981; Littler & Littler, 1983, 1984a; Littler et al., 1983b; Stewart, 1989; Steneck et al., 1991; this study). In addition, post-grazing tissue loss due to dislodgement (Lowell et al., 1991) is probably negligible. Although some grazers will eat some crusts (e.g. Branch, 1975; Kitting, 1980; Dungan, 1986), macroalgae appear to be more readily consumed (refs. above), probably because of crust toughness and low caloric content (Littler & Littler, 1983; Littler et al., 1983b). Because of these qualities, there evidently has been selection for the inclusion (or maintenance) of a resistant crustose phase or basal system in many algal life histories (Slocum, 1980; Lüning, 1980; Lubchenco, 1980; Lubchenco & Cubitt, 1980; Dethier, 1981; Littler & Littler, 1983; Jara & Moreno, 1983).

Within this functional group, there is a diversity of means of surviving potential disturbance. Many of the characters predicted to confer ability to survive disturbance (Table 1) do appear to be important. First, some crusts *resist* disturbance, i.e. lose little biomass, by being relatively inedible. The clearest and most predictably important morphological character conferring resistance is the degree of calcification. Calcified crusts (corallines) dominate environments of high herbivore-induced disturbance (Steneck, 1986 and data presented here: Fig. 9). In parallel experiments in Maine (Steneck, unpubl. data), coralline crusts were consistently the least susceptible to artificial removal of tissue by brushing. Although calcified crusts are brittle relative to uncalcified forms (Padilla, 1985, 1989), they are consumed less readily than fleshy species by urchins, limpets, littorinids, and brushes (Dethier et al., 1991; Steneck, unpubl. data). Thus, corallines are relatively inedible for many more types of grazers than are fleshy crusts, giving them a “coexistence escape” from herbivory (Lubchenco & Gaines, 1981). The broad generality of coralline resistance to disturbance leads to the worldwide phenomenon of “urchin barrens”, where the only algae coexisting with dense urchin populations are crustose corallines.

Among the uncalcified crusts there is high variation in resistance to artificial disturbance and to herbivory. Most of the crusts examined in this study have another character that confers resistance: tightly adjoined filaments. Those that do not, including *Arthopyrenia*, are much more susceptible to disturbance than are tightly constructed crusts of similar thickness. Another pertinent variable may be cell size, since species with smaller cells are likely to contain a higher proportion of cell wall material and therefore be tougher. The best example of this is *Hildenbrandia rubra*, which is composed of very small (Table 1), tightly packed cuboidal cells (also noted by Kitting, 1980; Bertness et al., 1983). These authors found substantial tooth wear in limpets eating *Hildenbrandia*. Pueschel (1988) believes that the abundant secondary pit connections among cells in adjacent filaments in this species may further improve coherence of the filaments, and thus toughness. In the laboratory, however, the tight construction of *Hildenbrandia rubra* could not compensate for its thin nature, and grazers removed it from the rock.

Tenacity to the substratum is an additional feature that appears important in resistance to disturbance potential. Crusts differ dramatically in how well they are attached to the rock, from those that are virtually impossible to remove (e.g. *Hildenbrandia* spp.,

“*Petrocelis*”) to those that are held on only loosely (e.g. many *Ralfsia* species, some corallines).

A second, very different means of surviving disturbance is to *tolerate* it, i.e. to lose tissue to a disturbance agent (such as a grazer or sand scour) but suffer proportionately low impact by being thick, or by readily regenerating the tissue by lateral or vertical regrowth. The importance of thickness is somewhat self-evident; thicker crusts take more bites or scratches with a brush to remove. Thinner crusts were much more susceptible to brushing than thick ones; the thick crust “*Petrocelis*” continued to survive and grow under intense disturbance (in non-stressful habitats), while many thin fleshy species did not (Figs. 3–8). *Ralfsia pacifica* is a thick fleshy crust which loses the benefits of this character because of its senescence of underlying tissues (other crusts showed no obvious senescence). Thickness may also confer a competitive advantage among crusts (Sebens, 1986; Steneck et al., 1991), especially if it can be maintained in the face of herbivory. “*Petrocelis*” remains thick in the field even though it is readily consumed by grazers, and this thickness may give it a competitive edge.

Crusts vary widely in regenerative capacities (e.g. Steneck et al., 1991). Relative to all the other crust species studied, *Hildenbrandia rubra* and *Rhodophysema elegans* both can regrow filaments rapidly from basal cells (vertical regeneration) (Dethier & Steneck, in prep.), contributing to their surprisingly high survival in the brushing experiments (Fig. 7).

Third, some crusts appear to reduce biomass loss to herbivores by *detering* them, or being unpalatable. For *Arthopyrenia*, *Isactis*, and *Ralfsia pacifica* (Figs. 11–13), crust sensitivity to artificial disturbance suggests that the herbivores should have been able to bite them. However, both laboratory and field experiments showed that little consumption actually occurred, suggesting a behavioral avoidance based on taste or noxiousness.

Crusts also survive potential disturbance in some cases by *avoiding* it, i.e. by reducing the probability of encounter. One reason why crusts are able to survive high in the intertidal (and deep in the photic zone) is because these are essentially refuges from herbivory (non-coexistence escapes). Presumably no plants can survive under high herbivory in such areas of low growth potential, and no herbivores can survive on such low productivity. Many crusts survive herbivory by growing in crevices and other microtopographic features not available to grazers. For example, *Hildenbrandia* is eaten by grazers and grows laterally extraordinarily slowly, but often is found in crevices and is capable of prolonged survival under other organisms (see also Bertness et al., 1983).

4.2. Mechanisms of stress tolerance

The stress tolerance of crusts as a group may stem in part from their low metabolic rates (Adey, 1970), two-dimensional growth form (for low light conditions: Hay, 1986), and low exposed surface area (for desiccation). Physiological adaptations must also be important, but are unstudied. Intrinsic factors making particular crust species successful in particular types of stressful habitats remain elusive. Clearly thin crusts, with minimized self-shading and no non-photosynthetic tissue, are favored at low light levels (Dethier et al., 1991). Thicker crusts, especially corallines, have non-photosynthetic

lower layers which presumably exact a metabolic cost. In the intertidal zone, tolerance of desiccation stress is seen in both relatively thick (“*Petrocelis*”, *Verrucaria*) and thin (*Hildenbrandia rubra*, *Pseudovella*) fleshy crusts, and does not correlate (for fleshy crusts) with tissue water content (Fig. 15). The loose, mucilage-bound upper filaments of “*Petrocelis*” may retain water and help it resist desiccation, although the higher-dwelling *Hildenbrandia rubra* does not possess this feature. Calcified crusts have very low desiccation tolerance, perhaps in part due to their very low water content per crust mass (Fig. 15). Most adaptations to desiccation and temperature fluctuations are likely subcellular and biochemical rather than structural in nature.

The biomass of a crust in a given habitat is a function of the intrinsic growth rate of that crust and the growth allowed by extrinsic conditions, balanced against its intrinsic ability to resist disturbance and the extrinsic disturbance potential in the habitat. Crust survival in the transplants demonstrated the critical nature of this balance between productivity and disturbance along the manipulated gradients of each parameter. When natural disturbance was eliminated and the transplants were left unbrushed, a number of species were able to survive for years in stressful habitats. For example, “*Petrocelis*” is normally rare in the desiccated south-facing mid intertidal, but when limpets were removed it survived there. Under intense (steel) brushing, however, it gradually disappeared (Fig. 3). For other crusts (e.g. *Pseudovella*) even a low disturbance potential (nylon brush) tipped the balance so that biomass lost > biomass grown, leading to gradual losses in cover. In low-stress habitats, the brushes presumably removed the same amounts of tissue as from the stressed crusts, but recovery was rapid and often complete. Since unproductive (stressful) environmental regimes essentially enhance the impact of herbivores by imposing energetic constraints on the plants (Hay, 1981; Gaines and Lubchenco, 1982), crusts (or other algae) growing in stressful habitats that also contain herbivores must have effective anti-herbivore defenses (Hay, 1981; Lubchenco & Gaines, 1981), whether this be calcification (deep water corallines), toughness (*Hildenbrandia* in the high intertidal), or chemicals (perhaps *Arthopyrenia* and *Isactis*). Normal distribution patterns of any alga cannot be understood without knowledge of how it responds to these two gradients.

4.3. Adaptive strategies

Numerous organisms show “contrasting patterns of correlated life history traits” (Hughes & Jackson, 1985), or adaptive strategies. Experiments with crusts strongly suggest that there are tradeoffs among the morphological and life-history “choices” available to species within this functional group. Stress-tolerant species are usually disturbance-intolerant, and vice versa. A few species are exceptionally broadly adapted (e.g. “*Petrocelis*”) but no species can occupy the full ranges of productivity and disturbance potentials. Table 4 illustrates the diversity of ecological characteristics within this functional group (from one region), summarizing information from experiments and additional observations. While crust recruitment was not investigated systematically, observations suggest there is also very high variation among crust species in the frequency of successful recruitment (Table 5).

A range of crust strategies can be seen even within one habitat; for instance, the most

Table 4

Summary of experimental and observational results for al species listed in Table 1

Species	Max. growth (mm/yr)	Sensitivity to:				Recruit. freq.
		Dist.	Desic.	Foul.	Subm.	
<i>Lithophyllum impressum</i>	5.0	L	H	nd	nd	nd
<i>Lithothamnion phymatodeum</i>	22	L	H	nd	nd	nd
<i>Pseudolithophyllum whidbevensense</i>	16	L	H	nd	nd	nd
<i>Pseudolithophyllum neofarlowii</i>	4.3	L	M	nd	nd	nd
<i>Corallina</i> basal crust	12	L	M	nd	M	H?
<i>Ralfsia fungiformis</i>	15	nd	nd	nd	nd	nd
"Petrocelis"	13	L-M	L	M	H	L
<i>Peyssonnelia pacifica</i>	16	M	H	nd	nd	H
<i>Ralfsia pacifica</i>	17	M	M	M	H	H
<i>Hildenbrandia occidentalis</i>	2.0	M	M	nd	nd	L
<i>Hildenbrandia rubra</i>	1.2	M	L	H*	L	L
<i>Isactis plana</i>	1.5	M-H	M	H	L	L
<i>Arthopyrenia orustensis</i>	14	H	L	H	H	H
<i>Verrucaria mucosa</i>	2.0	M-H	L-M	nd	H	M?
"Ralfsia californica"	nd	nd	H	H	L	H
<i>Rhodophysema elegans</i>	4.0	H	H	H	H	H
<i>Pseudovella consociata</i>	0	H	L	M	L	H?

* But survives overgrowth.

L = low, M = medium, H = high, nd = no data or direct observations. Maximum growth is the fastest recorded for that species under any conditions. "Sensitivity" ratings indicate potential damage or low survival for the conditions listed. Dist. = disturbance, Desic. = desiccation, Foul. = competition by other species recruited onto or next to the crust, Subm. = submergence in very high tidepools. Recruitment frequency data are given in Table 5.

abundant species in the mid intertidal zone in Washington are "Petrocelis" (edible and a poor recruiter but thick, fast-growing, long-lived), *Hildenbrandia rubra* (edible, thin, a poor recruiter, and very slow growing, but seemingly immortal), and *Ralfsia pacifica* (less readily eaten, good recruiter, fast-growing, but short-lived). It is this broad range of life history and morphological characteristics that allows crusts to occupy so much of the hard bottom photic zone.

As a group, crusts have very low photosynthetic and growth rates, and are very poor competitors (Branch, 1976; Wanders, 1977; Slocum, 1980; Ayling, 1981; Dethier, 1981; Menge & Lubchenco, 1981; Steneck, 1982a; Littler & Littler, 1983; Bertness et al., 1983; Menge et al., 1985; Sebens, 1986; Morrison, 1988; Stewart, 1989; Zupan & West, 1990; but see Padilla, 1984). As a result, they are often reliant on herbivores or physical disturbance to keep them from being overgrown and thus outcompeted, or to create open habitat for their spores (Kitting, 1989). Some species can reduce settlement of potential competitors (Masaki et al., 1981; Menge & Lubchenco, 1981; Sebens, 1983; Singletary & Shadlou, 1983; Bertness et al., 1983; DeWreede, 1983; Breitburg, 1984; Dungan, 1986; Johnson and Mann, 1986), although they usually cannot resist overgrowth from the side. A feature that balances this ease of overgrowth is that some species can survive being covered for years (Sebens, 1986; Miles & Meslow, 1990;

Table 5

Recruitment frequency of intertidal crust species, based on observations of available substrata and data from cleaned rocks experimentally attached in different habitats

Species commonly seen recruiting:

- Ralfsia pacifica*: many sites and tidal heights
- "*Ralfsia californica*": in pools and on raft
- Pseudulvella*: thin green crust (ID?), both in and out of pools
- Arthopyrenia*: many sites, especially sunny surfaces
- Cyanobacteria crust ("Dermocarpa"-like): many surfaces
- Petroderma maculiforme*: many herbivore-free surfaces, especially damp
- Rhodophysema elegans*: pools, raft, and low intertidal
- Verrucaria* spp.: herbivore-free surfaces, mid and upper shore
- Peyssonmelia pacifica*: low pools and subtidal

Species occasionally seen recruiting:

- Coralline crusts (various species): pools and raft
- Mastocarpus papillatus*: crustose base of gametophyte, mid and low zones
- Iridaea splendens*: crustose base, low zone and raft
- "*Haematocelis*": low pools
- Isactis*: directly adjacent to populations in "native" high pool habitat only

Species virtually never seen recruiting:

- Hildenbrandia rubra**
 - Hildenbrandia occidentalis* (one documented recruitment onto a transplant patty, YI mid-north)
 - Petrocelis*: only seen on Tatoosh Island, artificial substrates (non-tetraspori: could have been crustose base of gametophyte)
-

* But noted as a good recruiter in the Atlantic (Peckol & Searles, 1983) and in Australia (Underwood, 1980).

Kendrick, 1991; unpubl. data). Other species are the site of selective larval settlement of invertebrates, including grazers that aid in removing competitors (Gee, 1965; Barnes & Gonor, 1973; Morse et al., 1979; Steneck, 1982a; Rumrill & Cameron, 1983; Sebens, 1983; Rowley, 1989; Pearce & Scheibling, 1990). In general, however, crusts require some external mechanism, either disturbance or stressful conditions, to keep competitors from excluding them. A few crusts even avoid competitors by having opportunistic life histories (Dethier, 1981), colonizing new substrata and growing and reproducing rapidly (e.g. *Rhodophysema*, "*Ralfsia californica*").

Harper (1980) noted that there are two facets to understanding why an organism inhabits a given environment: how it is adapted to its habitat, and what hinders it from living elsewhere. These questions are particularly intriguing for species found in environments of low productivity potential (e.g. the high intertidal zone): how completely are they "adapted" to such habitats? Do they grow better there than elsewhere? If not, what processes (e.g. disturbance, competition) exclude them from less stressful environments? What tradeoffs do they suffer for their adaptations to stress? Many of the intertidal crust species have broad tolerances and slow growth, and seem to be restricted to marginal habitats by both herbivory and competition from faster-growing algae. No species showed clear release from repressive conditions in terms of increased growth when transplanted; they may not have the physiological flexibility to do so (Chapin, 1980). Most species did not perform better when placed on the theoretically

“optimal” raft, although only *Arthopyrenia* actually seems to require drying conditions; individual success does not always correspond with a generalized optimum. Several species did show surface tissues invaded by a green endophyte after two yr of continuous submergence; such pathogens/competitors may be subtly important in excluding species from more physically benign regions. Thus while for some species it is clear that biotic processes (competition, predation) limit their distributions to marginal habitats, for others we need to learn more of their physiology and life histories.

A central problem in ecology is to identify and understand patterns of distribution and abundance of species. I have identified such patterns for intertidal crusts in Washington, and discussed some of the processes that determine these patterns. It appears, however, that a thorough understanding is difficult for a group of species whose growth is measurable only over a span of years, and that primarily use “leftover” space – space that other, more competitive plants and animals cannot use because of high disturbance potential or low productivity potential. Understanding crust patterns involves not only understanding how competition, herbivory, and stress affect them, but how these factors affect their competitors. “*Petrocelis*” owes its dominance not only to its resistance to grazers and rapid growth rate relative to other crusts, but to the preference of local grazers for erect algal forms that otherwise would outcompete them. *Isactis* appears to be distasteful to grazers and tolerant of high physiological stress, but is found only in high pools because it cannot compete for space at all. Thus, all crusts are “fugitives”, in a sense, but with a range of morphologies and life histories that correspond in complex ways to the range of marine and maritime environments they inhabit.

5. Acknowledgements

Bob Steneck was a key source of ideas, methods, and energy for this research. Help in the field and laboratory was provided by P. Mace, K. Irons, A. Haskins, K. Paull, M. Woodbury, and D. Duggins. Access to field sites was provided by The Nature Conservancy, the Ragens, and the Makah Tribal Council. D. Duggins, C. Pfister, R. Steneck and several anonymous reviewers improved various versions of the manuscript. Space and facilities at the Friday Harbor Laboratories were provided by A.O.D. Willows. The research was supported by NSF grants OCE 8315136 and OCE 8600262. To all I am grateful.

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