Biodata of David J. Garbary, author of the chapter “The Margin of the Sea: Survival at the Top of the Tides”

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THE MARGIN OF THE SEA:
Survival at the Top of the Tides

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With deep respect and gratitude I dedicate this chapter to George Russell – consummate scholar and mentor.

1. Introduction

From the upper reaches of the intertidal zone to the beginnings of terrestrial vegetation is a region of shoreline that is often sparsely inhabited by algae, and typically includes conspicuous expanses of bare rock. Inspection of the habitat reveals scattered or even abundant lichens, and often extremely patchy to extensive populations of macroscopic algae. The physiological ecology of photosynthetic algae in this part of the intertidal zone comprises the primary theme of this chapter. The organisms discussed here typically have extensive populations above mean high water neap tide (see Lüning, 1990; Lobban and Harrison, 1994; Little and Kitching, 1996, for introduction to tides and zonation). In general, these organisms are found exposed on bare rock and not in the rock pools where greater species richness occurs and less stringent environmental conditions are imposed. In terms of physiological constraints, the high intertidal and adjacent supratidal zone is among the most stressful encountered by organisms in general (Tomanek and Helmuth, 2002), and by marine macroalgae in particular (Davison and Pearson, 1996).

First, the rigors of the environment are explored, and then the various adaptive strategies of algae to survive and thrive in this habitat are discussed. Davison and Pearson (1996) reviewed stress tolerance in intertidal seaweeds as a whole; however, here the focus is on the upper intertidal zone and on disruptive stresses that cause damage or limit growth.

Physiological responses and survival strategies have been explored in organisms in a diversity of seaweeds including red, brown and green algae (Table 1). In addition to purely physiological studies, extensive research has been carried out on ecological strategies involving features of life history. This high intertidal zone is already a highly stressful one for its inhabitants; however, climate change, in particular the increase in ultraviolet radiation (UV), is impacting these organisms (e.g. Hanelt et al., 1997; Robinson et al., 2003). Because of the relative ease of access, the stressful nature of the environment, and the relatively few species involved, this part of the shore and its inhabitants have become model systems for research in physiology and ecology.
Table 1. Summary of genera of marine macroalgae used as model systems for the upper intertidal zone with respect to environmental tolerances.

<table>
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<tr>
<th>Taxonomic group</th>
<th>Nature of tolerance</th>
<th>References</th>
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<tr>
<td>Chlorophyta</td>
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<tr>
<td>Blidingia</td>
<td>Osmotic</td>
<td>Karsten and Kirst (1989) and Karsten et al. (1992)</td>
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<td>Prasiola</td>
<td>Osmotic</td>
<td>Smith and Berry (1986), Jacob et al. (1991, 1992a, b), Bock et al. (1996) and Smith and Gremmen (2001)</td>
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<td></td>
<td>Desiccation</td>
<td>Davey (1989), Bock et al. (1996) and Smith and Gremmen (2001)</td>
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<td></td>
<td>Ultraviolet radiation</td>
<td>Jackson and Seppelt (1997), Lud et al. (2001a) and Holzinger et al. (2006)</td>
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<td></td>
<td>Temperature</td>
<td>Smith and Berry (1986), Davey (1989) and Jackson and Seppelt (1997)</td>
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<td>Ulothrix</td>
<td>Osmotic</td>
<td>Karsten et al. (1991a, b, 1992)</td>
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<tr>
<td>Phaeophyceae</td>
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<td>Fucus</td>
<td>Temperature</td>
<td>Davison et al. (1989), Pearson and Davison (1993) and Li and Brawley (2004)</td>
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<td></td>
<td>Osmotic</td>
<td>Li and Brawley (2004)</td>
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<td></td>
<td>Desiccation</td>
<td>Schonbeck and Norton (1979)</td>
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<td></td>
<td>Ultraviolet radiation</td>
<td>Hanelt et al. (1997)</td>
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<td>Hesperophycus</td>
<td>Desiccation</td>
<td>Oates and Murray (1983)</td>
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<td>Temperature</td>
<td>Pfetzing et al. (2000)</td>
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<td>Silvetia</td>
<td>Desiccation</td>
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<td>Apophlaea</td>
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<td></td>
<td>Ultraviolet radiation</td>
<td>Lamare et al. (2004)</td>
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<td>Bangia</td>
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<td>Gloiopeltis</td>
<td>Desiccation</td>
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<td>Hildenbrandia</td>
<td>Desiccation, osmotic, temperature</td>
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<td></td>
<td>Ultraviolet radiation</td>
<td>Hoyer et al. (2001), Peinado et al. (2004) and Korbee et al. (2005)</td>
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2. The Environment

The relatively benign environment of shallow subtidal to mid-intertidal zones of marine environments is a region of high biodiversity. As one moves up the intertidal zone, the environment becomes increasingly stressful as a consequence of increasing variations in temperature, wave action and salinity. There is a consequential loss of biodiversity and general increase in bare space as one approaches the high intertidal zone. Similarly, when one approaches the shore from the
terrestrial side, the increase in salt and the impact of desiccation gradually decreases the vegetation and soil integrity to produce the bare substratum of rocky shores. Organisms growing here are clearly able to survive, and important ecological questions surround the importance of sublethal stresses and the various physiological strategies that organisms have for survival and how these impact interspecific competition (Davison and Pearson, 1996). Algal genera that have been used as primary model systems for studying the upper intertidal zone are listed in Table 1 along with the primary aspects investigated.

2.1. TEMPERATURE

Because of the importance of elevated temperature in desiccation rate and sub-zero temperatures in relation to freezing tolerance, temperature may be the single most important environmental variable in determining survival in the upper reaches of the intertidal zone. At the bottom of the intertidal zone temperature largely reflects seawater temperature and is relatively stable over diurnal cycles. The greater the time out of the water during low tide the greater the extent to which organisms are exposed to air temperature and the number and rapidity of events associated with tissue freezing (Davison et al., 1989; Pearson and Davison, 1993) or tissue dehydration. With increasing tidal elevation, elevated air temperatures have greater impact although thalli have some protection from evaporative cooling, and thalli under multiple layers of overlapping algal fronds would remain cool. As the vegetation thins and solar radiation reaches rocky substratum there is considerable heating of the substratum that can exceed air temperature. The higher in the intertidal zone the greater the extent to which this occurs. Thus while water temperature may be a temperate 10–15°C, and air temperature on the order of 25°C, the algae may experience even greater temperatures as a consequence of substratum heating. At a temperate site in California when air temperature varied from 18°C to 25°C, the actual temperature range that _Porphyra fucicola_ experienced was from 13°C (i.e. seawater temperature) to 33°C, all within a 6-h period (Biebl, 1970). When air temperatures were higher, thalli of _P. fucicola_ would be exposed to even greater temperature fluctuations. Even without substratum heating, Lipkin et al. (1993) used 35°C in experiments with _Porphyra_ because this reflected maximal temperatures during the growing season.

Extreme temperatures are also experienced by intertidal algae as a consequence of low temperature. While seawater typically reaches only −1.5°C, air temperatures in temperate and polar regions may reach −20°C or even lower. Organisms in the mid-intertidal zone might be protected from the most extreme low temperatures as a consequence of ice cover; however, at the top of the shore organisms may be exposed to the full brunt of these lower temperatures. Some temperate intertidal algae can survive freezing at −20 to −40°C and cultivation nets of _Porphyra_ are typically air dried and stored at −20°C for several months before use.
Davison et al. (1989) showed that the extent of freezing tolerance in intertidal algae was related to their position on the shore with the high intertidal *Fucus spiralis* being unaffected by freezing for 3 h at −20°C, whereas a low intertidal zone fucoid showed a reduction of 97% for the same treatment. In a comparative study of intertidal fucoids Pearson and Davison (1993) showed that *F. spiralis* was much more tolerant to rapid freezing than species lower on the shore, and that full photosynthesis returned more rapidly following thawing. Thus freezing tolerance is associated with shore zonation (Chapman, 1995). Freezing intolerance was accompanied by a large efflux of amino acids, and freezing tolerance is considered an adaptation of the plasmalemma (Davison et al., 1989). In Antarctic green algae; however, high concentrations of dimethylsulphoniopropionate (DMSP) were suggested to function as a cryoprotectant (Karsten et al., 1992).

Membrane proteins called lipocalins have been identified in a diversity of land plants where they are associated with cold tolerance. Charron et al. (2005) demonstrated the presence of lipocalins in *Porphyra yezoensis* and suggested that these proteins may provide the basis for the desiccation tolerance of this high intertidal species.

The role of heat-shock proteins in marine algae has received limited study. Li and Brawley (2004) showed a 30% increase in survival of embryos of *Fucus vesiculosus* (mid-intertidal) and *F. spiralis* (high intertidal) following acclimation of parent thalli to sublethal conditions. This was attributed to the production of heat-shock proteins. *Chondrus crispus* (low intertidal) also produces heat-shock proteins among a wide variety of stress response genes (Collen et al., 2006). To date, none of the algae from the extreme high intertidal zone have been examined for production of heat-shock proteins.

### 2.2. SALINITY

From the bottom to the top of the intertidal zone the most conspicuous change in salinity to which organisms are exposed is the increase in variance of salinity. At the bottom of the shore algae are only out of seawater for short periods during low water, and wave action limits the extent to which thalli are exposed to reduced salinity. At higher positions in the intertidal zone organisms are more exposed to low-salinity rainwater for greater periods during precipitation. In the high intertidal and splash zone further exposures to rainwater occur as well as increased exposures to higher salinity water as a consequence of evaporation. Shallow rock pools in the splash zone may vary from low to high salinity depending upon rain and wave frequency. Thus organisms in the high intertidal zone must be tolerant of salinities at both extremes, and be able to survive or resist both water loss and ion loss during exposures to high and low salinities, respectively. Physiological studies have been carried out on numerous intertidal seaweeds. Intertidal seaweeds can tolerate short-term exposures to reduced salinity. Physiological adaptations are similar to those required for desiccation, since both stresses function to reduce water potential (Smith and Berry, 1986; Lobban
and Harrison, 1994). Similarly, freezing induces equivalent physiological constraints in that cellular water becomes inaccessible, and then adds the potential damage of ice crystal formation (Davison et al., 1989).

Different classes of low molecular weight carbohydrates have been identified as being important in osmoregulation in different algal groups (Kirst, 1990). In green algae osmotic regulation is typically associated with various ions and various organic solutes that include proline, sucrose and DMSP (Karsten et al., 1991b, 1992). In Phaeophyceae, mannitol is found in osmotically significant concentrations in many taxa (Reed et al., 1985), while volemitol can be abundant in Pelvetia canaliculata (Pfetzing et al., 2000). In the red algae Porphyra and Bangia, floridosides may play a similar role, although floridoside concentrations are often independent of salinity in the surrounding medium (Karsten et al., 1993; Karsten, 1999).

Physiological responses to salinity were examined in Blidingia minima (Karsten and Kirst, 1989). This species showed a remarkably stable photosynthetic rate over salinities from 7‰ to 50‰ and only declined at 70‰. A continual decline in tissue water and an increase in K+ and sucrose concentrations corresponded with the salinity gradient. Thus this species is clearly highly adapted to salinity extremes. The Antarctic filamentous green algae Ulothrix impexa and Urospora subflaccida showed little reduction in cell viability from salinities of 7%o to 60‰, and the latter species showed major decline in cell viability only at 102‰. These responses were mirrored in specific growth rates and photosynthetic oxygen production (Karsten et al., 1991a, b).

Hildenbrandia rubra and Prasiola crispa may be the most tolerant marine algae to salinity stress in that H. rubra can recover its full photosynthetic response after 96 h at 4‰ (Kim and Garbary, 2006) while the latter can survive treatments from 0.35‰ to 175‰ (Jacob et al., 1991, 1992a, b). Adaptations for low salinities in P. crispa included the absence of vacuoles in exposures between 0.35‰ and 35‰. Growth and photosynthesis were almost unaffected at low salinities, but were strongly inhibited by extreme hyperosmotic conditions. In these experiments intracellular levels of inorganic ions (Na+, K+, NH4+ Cl−, PO4−) were unaffected by decreased hypoosmotic conditions, but reached a maximum at 70‰. At extreme hyperosmotic levels the organic solutes sucrose and sorbitol were greatest.

2.3. DESICCATION TOLERANCE AND AVOIDANCE

Despite some exceptions and specialized modifications associated with cell walls and the intercellular matrix, the survival of marine algae following desiccation is considered to be based on tolerance of dehydration rather than avoidance. Populations of P. canaliculata may be emersed for up to 8 days between spring tides and thus require extreme tolerance in what is morphologically a highly complex organisms (Pfetzing et al., 2000). This is exceeded by Porphyra from Israel that can recover photosynthesis following 20 days of continuous exposure to air (Lipkin et al., 1993).
Although desiccation rates are largely a function of surface/volume ratio, a few studies have shown that higher intertidal organisms have a greater ability to resist desiccation. Some of the most extreme desiccation tolerant species have adaptations that slow desiccation and allow for more rapid rehydration. For example, *Prasiola crispa* showed slower water loss than for a *Fucus* species under similar humidity (Jacob et al., 1992b). This was attributed to lipophilic materials on the thallus surface and pectic compounds in the cell walls. Oates and Murray (1983) compared desiccation in *Herperophycus* relative to *Silvetia* (as *Pelvetia*) and found that the rate of water loss was against expectation based on surface/volume relationships.

Despite the above results, tolerance of desiccation and recovery of physiological processes following dehydration are the primary mechanisms of survival of the high intertidal algae. Extreme desiccation disrupts membranes and energy transfer during photosynthesis. This was evident in *Porphyra* where comparisons between the high intertidal *P. perforata* and the subtidal *P. nereocystis* showed greater phycobilin fluorescence in both osmotically challenged and air-dried thalli of *P. nereocystis* (Smith et al., 1986). In *P. linearis* fronds only began to show reductions in photosynthesis after a relative water content (RWC) of 0.60 had been reached, and even at a RWC of 0.2 photosynthesis was at 20% of maximum (Lipkin et al., 1993).

Overall, there does not appear to be a relationship between position in the intertidal zone, water content and resistance to desiccation (Dromgoole, 1980). The primary factor explaining desiccation rate is the surface/volume ratio of the plant. Ji and Tanaka (2002) found no relationship between photosynthetic rate following desiccation and tidal height. Smith and Berry (1986) however, reported that the recovery of photosynthetic rate following desiccation or high temperature was highly correlated with height in the intertidal zone. Even within a single species (*Porphyra perforata*) high intertidal fronds were more tolerant of desiccation.

Although adaptations to desiccation are thought to be similar to adaptations to salinity stresses, different physiological phenomena have been examined. In *Prasiola crispa*, Bock et al. (1996) showed changes in phosphate metabolism during exposures to a medium of the non-ionic osmoticum, polyethylene glycol. There were initial changes in cytoplasmic inorganic phosphate (increased) and polyphosphate (decreased) concentrations, followed by an increase in extracellular inorganic phosphate. Within 4 h of return to normal media, control levels of photosynthesis occurred. This work should be repeated on other algae to determine if this is a generalized response, or if it is unique to *Prasiola*.

2.4. SOLAR RADIATION

The only major environmental factors that show less variation at the top rather than the bottom of the intertidal zone are photosynthetically active radiation (PAR) and
UV. Organisms at the top of the shore are clearly more exposed to the damaging effects of excess light from the perspective of photoinhibition and damage from UV radiation. The possibility of light limitation increases down the intertidal zone; however, the potential for damage to photosystems and DNA decreases because of dramatically less exposure times and the increasing possibility of recovery during tidal submergence. Protection mechanisms against reactive oxygen species are clearly important but have not been well studied (see Dring, 2005, for review).

*Prasiola* species have been extensively studied from the perspective of the impacts of UV on growth, survival and physiology (Jacob, 1992; Jackson and Seppelt, 1997; Karsten et al., 2005; Holzinger et al., 2006). Like many other marine organisms, production of mycosporine-like amino acids (MAAs) is inducible in *Prasiola crispa* as a response to increased UV radiation. This is critical because high doses of UV will cause DNA damage and affect photosynthetic performance (Lud et al., 2001a).

*Prasiola crispa* has become a model system for the study of UV effects. Using pulse amplitude modulated (PAM) fluorescence Holzinger et al. (2006) showed that exposure to 6 h of PAR + UV had little effect on photosynthesis; however, 24-h exposure reduced photosystem II efficiency (Fv/Fm) to about 30% of control levels. There was also a major decline to 63% of control levels in relative electron transport rate (rETR) over a range of photon fluence exposures. The controls in this experiment showed photoinhibition at the higher levels of PAR tested; however, this was not apparent in the UV treated thalli. These changes were accompanied by changes in ultrastructure that included occasional dilations to thylakoids, a three to four times increase in 0.4–0.8 μm diameter plastoglobuli and slight damage to mitochondria. It would be of interest if the ultrastructural changes were associated with the physiological changes in photosynthesis. It remains to be demonstrated if the plastoglobuli are merely a damage response or if they are an adaptation providing protection.

Similar experiments were conducted by Lud et al. (2001a) on *Prasiola crispa* var. antarctica. Photosynthetic performance was not impaired by higher levels of UV exposure (2.0 mW m$^{-2}$ vs. 0.2 mW m$^{-2}$ UVB), although there was apparent damage to DNA. The UV tolerance shown by *Prasiola* species is also present in the high intertidal *Fucus distichus* that Hanelt et al. (1997) considered almost impervious to UV. This differs markedly from the greater impact of UV on subtidal red algae that do not form MAAs (Karsten et al., 1998).

The Holzinger et al. (2006) experiments are highly informative; however, they need to be extended to determine impact and recovery over more realistic time periods reflective of the polar and high latitude summers. Survival, despite the pathological changes, would emphasize the tolerance of this species.

*Porphyra* species have high concentrations of MAAs and accumulation of these amino acids reflects the overall exposure to UV radiation (Hoyer et al., 2001; Peinado et al., 2004; Korbee et al., 2005). The related genus, *Bangia*, also produces MAAs; however, it may not be able to adjust concentrations based on environmental conditions (Boedeker and Karsten, 2005).
3. Key Taxa of Rhodophyta, Chlorophyta and Phaeophyceae

3.1. FILAMENTS

There are species of red and green filamentous algae that grow in the high intertidal zone, but this habitat seems devoid of brown algal filaments. The primary taxa of green algae are *Ulothrix* and *Urospora* whereas the primary genus of red algae is *Bangia*. These genera are cosmopolitan. The strong seasonality and the ease with which species can be grown in culture makes them excellent models for physiological adaptations to environmental extremes (Table 1, e.g. Karsten and West, 2000).

3.2. FLAT BLADES AND TUBES

There are over 100 species of *Porphyra*. This is a cosmopolitan genus and different species occur from strictly subtidal habitats to the high intertidal zone. The range of habitats in related species of similar morphology makes this genus particularly attractive as models for adaptation to environmental stresses. Species from the high intertidal zone, e.g. *P. perforata*, *P. linearis* and *P. yezoensis* have remarkable tolerance to extremes of temperature and desiccation (e.g. Lipkin et al., 1993). Because of the extremely high surface to volume ratios, these species desiccate and rehydrate rapidly, and thus are useful models for physiological changes associated with water content.

*Prasiola stipitata* and its relatives are among the most conspicuously desiccation tolerant species of marine algae. Not only are species associated with the high intertidal zone, but they can also thrive in terrestrial communities in humid areas (e.g. Ireland, Rindi et al., 1999). These species have carved out a niche on exposed rocks high in the splash zone, and regularly undergo extreme desiccation. The monostromatic blades and their filamentous forms range from a few millimetres to several centimetres in height. In addition, the high nitrogen of bird droppings also characterized the habitat of *P. stipitata*. The latter is not a case of tolerance, but positive adaptation since populations can decline in adjacent areas even though space is apparently available for colonization. In *Porphyra*, MAAs are stimulated when thalli are exposed to high nitrogen (Korbee et al., 2005). If this is also the case in *Prasiola* it would help explain the apparent association of some species with avian feces.

*Blidingia* species have received little attention as physiological models. Exceptions include studies of salinity impacts on photosynthesis (Karsten and Kirst, 1989) and the impact of environmental factors on the production of DMSP (Karsten et al., 1992). The strong seasonality and wide distribution should provide the basis for further experimental work on environmental tolerances.
3.3. THICK LEATHERY FORMS

3.3.1. Fucoids and Cartilaginous Red Algae

Unlike the species discussed above that are annuals, *P. canaliculata* is a true perennial. Although there are species in western North America that appear similar to *P. canaliculata* (e.g. *Pelvetiopsis* and *Silvetia*), none occur at the same tidal heights, and none are as resistant to desiccation (Rugg and Norton, 1987; Pfetzing et al., 2000). Indeed, *P. canaliculata* may be a model organism for the high intertidal zone inasmuch as it cannot survive when transplanted to lower levels on the shore, and it decays when kept continuously immersed for six or more hours out of 12 h. The key to the tolerance of *P. canaliculata* may be the occurrence of a symbiosis with the ascomycete fungus *Mycophycias ascophylli*, the same fungus that plays such a prominent role in the biology of *Ascophyllum nodosum* (Garbary and Deckert, 2001).

Harker et al. (1999) examined photosynthetic reactions of *P. canaliculata* as a consequence of light and desiccation stress. They concluded that non-photochemical quenching was greater in *P. canaliculata* than in *Laminaria saccharina* (a subtidal species) in both fully hydrated and dehydrated thalli. The high level of non-photochemical quenching in *P. canaliculata* is a strong indicator of the physiological adaptation of the species to the high light levels on the upper shore. Pfetzing et al. (2000) showed that the alditols (mannitol and volemitol) were produced in high amounts by *P. canaliculata* and these were inferred to be stress metabolites based on dynamic changes in concentrations associated with temperature and emersion.

Henry et al. (1996) described a phenomenon in *Silvetia compressa* (as *Pelvetia fastigiata*) that might represent an adaptation to high salinity in developing zygotes. When exposed to 1.5 M sucrose, zygotes and developing embryos became highly plasmolyzed; however, there were specific positions (termed adhesions) where the plasma membrane remained attached to the cell wall. These attachment points were uniformly distributed in ungerminated zygotes, but were localized at the tip of developing rhizoids. The adhesion points were associated with F-actin staining in the cytoplasm. Adhesions occur in other plant systems where they can provide positional information for cytokinesis (e.g. Cleary, 2000). In the large cells of fucoid embryos this might minimizing damage from plasmolysis by retaining positional information for directional growth following relaxation of plasmolysis. Accordingly, adhesions would be predicted to be less prominent in small-celled species (e.g. *Prasiola* spp.) or fucoids lower in the intertidal zone, and more prominent in fucoids higher on the shore (e.g. *P. canaliculata*).

*Mazzaella parksii* (=*Iridaea cornucopiae*), *Gloioptis furcata* and *Endocladia muricata* are three cartilaginous red algae from the high intertidal zone in the temperate North Pacific. The former occurs in extremely dense populations (see below) whereas the other species occur at lower tidal elevations and typically as scattered individuals or clumps rather than as continuous populations. Both *G. furcata* and *E. muricata* become conspicuously desiccated during low tides, whereas *M. parksii*, despite its higher shore elevation, does not normally dry to
the extent of becoming brittle. Little physiological work has been done on these species, although in a range of species from various tidal heights examined during desiccation, *G. furcata* had among the slowest rates of water loss and the most stable relative photosynthetic rate (Ji and Tanaka, 2002).

### 3.3.2. Crustose Red Algae

*Hildenbrandia* and *Apophlaea* are non-calcified crustose red algae that occur in the high intertidal zone. The former genus is cosmopolitan and has species that occur from the high intertidal zone (e.g. *H. rubra*) to the subtidal zone, whereas the latter has two species endemic to New Zealand (*A. sinclairii* and *A. lyallii*), both of which occur in the high intertidal zone. These crusts vary from extremely thin to several millimetres thick, and only *Apophlaea* has erect axes.

Both *Hildenbrandia* and *Apophlaea* must be highly adapted to the rigors of this habitat, and this was demonstrated experimentally. Over a 13-day period, winter collections of *H. rubra* from a mid-intertidal rock pool survived −17°C to 27°C, extreme desiccation and hyposaline conditions (4‰). Following each treatment, plants resumed control levels of photosynthesis within minutes. *Hildenbrandia* is extremely slow growing, and this contrasts with the rapidity of recovery following stresses imposed by Kim and Garbary (2006). Unlike algae from lower in the intertidal zone, *Apophlaea* showed almost complete recovery of photosynthesis following desiccation and there was little difference between loss of 10% of tissue water and 95% of tissue water (Brown, 1987). Brown also obtained similar results for the high intertidal red alga *Bostrychia arbuscula*. In the six species that Brown examined there was a clear response gradient to desiccation that correlated with height in the intertidal zone.

### 4. Survival Strategies

#### 4.1. LIFE HISTORIES

##### 4.1.1. Asexual Reproduction

Two distinct strategies of asexual reproduction are common in algae of the high intertidal zone: clonal growth and formation of asexual spores. Although these reproductive strategies are not limited to the high intertidal habitat, they are a prominent feature of these organisms. Most of the algae discussed here except the fucoids have an asexual spore bearing stage in which mitotically produced spores are formed in large numbers. This provides a rapid means of producing large populations during those short windows when the environment may be suitable. Well-studied examples of this are *P. stipitata* and *P. meridionalis* (e.g. Anderson and Foster, 1999; Rindi et al., 1999).

*M. parksii* is a high intertidal red alga common the Pacific coast of North America in wave-exposed habitats. The alga is perennial and clonal, forming extensive patches with up to 20 fronds cm$^{-2}$ to mostly 2–4 cm in height. Although
the high density of fronds constrains photosynthesis via self-shading, decreased water loss (up to 43% at end of low tide) protects fronds from much higher desiccation than when densities are low (Scrosati and DeWreede, 1998).

4.1.2. Seasonality as an Escape Mechanism
Although the high intertidal zone presents a highly demanding environment year round, there are seasonal cycles of temperature, precipitation and solar radiation (including day length) that allow for seasonal growth of particular species. In cool temperate climates (e.g. western North America from Alaska to California) the high intertidal zone during winter often has tremendous growths of filamentous or finely bladed algae, including *Rosenvingiella*, *Ulothrix*, *Urospora*, *Blidingia* and *Bangia*. Many coastal habitats have long periods of cloud cover and precipitation accompanied by moderate temperatures. In the upper intertidal zone of Nova Scotia many rocky shores have a dense cover of *Bangia* and *Ulothrix* from winter to late spring (Garbary, unpublished). With the onset of summer most of these populations disappear or become highly reduced, except in shaded microhabitats. The tendency of these species to produce extensive populations in winter and spring has been attributed to both ameliorated environmental conditions and to a reduction in grazing pressure (e.g. Cubit, 1984; Anderson and Foster, 1999).

4.1.3. The High Intertidal Zone as an Escape from Herbivores
An explanation generally used for intertidal zonation has been that the upper distribution limits of species are limited by environmental constraints, and that the lower distribution limits of species are regulated by biological interactions of grazing and competition (Lüning, 1990). This generalization has been shown to be somewhat simplistic for the intertidal zone as a whole, as well as for the high intertidal zone (reviews by Foster, 1990, 1992). In addition, algal abundances can be regulated by site-specific processes that include distribution and abundance of grazers whose impact may be on the macroalgae or the microalgae (e.g. Anderson and Foster, 1999; Mak and Williams, 1999). These grazers are typically mollusks, but may include insect larvae and even mites. For example, herbivorous chironomid larvae in California regulated the high intertidal community of ephemeral green algae (Robles and Cubit, 1981). Also in California, populations of the high intertidal *P. meridionalis* were regulated seasonally not only by environmental factors, but also by herbivory of mollusks and mites (Anderson and Foster, 1999).

In addition to being an extreme environment for the algae, the high intertidal zone is also an extreme environment for potential herbivores. Thus, part of the reason these algae can grow in this environment is they may experience reduced herbivory. Chapman (1989) demonstrated that recruitment of *F. spiralis* was not dependent upon the consumer animals even though presence of grazers enhanced the cover of ephemeral algae including *Bangia*, *Ulothrix* and *Urospora* during the late winter and early spring. In experimental studies slightly lower in the intertidal zone Farrell (1991) showed that algal colonization was preceded by barnacle colonization. This was a secondary effect, in that the presence of barnacles
reduced foraging activity by limpets, and thereby gave the algae (*Silvetia, Fucus, Endocladia*) an opportunity to grow. Additional direct and indirect effects of herbivores were observed in algal succession in the high intertidal of Vancouver Island (Kim, 1997).

In conclusion, while environmental factors may be of greater significance in the high intertidal zone than lower on the shore, biological phenomena associated with competition and herbivory are also critical in determining the distribution, abundance and succession of species in this zone.

### 4.2. SYMBIOSES – ALGAL FUNGAL INTERACTIONS

#### 4.2.1. Prasiola borealis and Turgidosculum complicatum

Two associations of the green algal genus *Prasiola* involve symbioses with fungi and have been described as lichens. These associations are geographically disjunct and are found in the high intertidal zone of northwestern North America and Antarctica where this mycophycobiosis is known as *P. borealis* and the lichen *T. complicatum* (= *Mastodia tessellata*). Although there has been some question as to whether this symbiosis was a fungal parasitism of *Prasiola crispa* or a true lichen, Lud et al. (2001b) showed a morphogenetic influence by the fungus on the alga, and that the association is established at the few-celled stage of the alga. Photosynthesis of the lichen has been studied by several authors (Huiskes et al., 1997; Smith and Gremmen, 2001). The latter found that photosynthesis declined at full salinity and that CO₂ assimilation was negatively affected by NH₄NO₃. When hydrated to a least 30% thalli underwent full photosynthesis, and the authors predicted that near maximal photosynthesis was possible for most of the year in the sub-Antarctic region (Smith and Gremmen, 2001).

As noted previously, *Prasiola* species are highly tolerant of UV exposure (Holzinger et al., 2006). The role of the fungal partner in the *Prasiola*–lichen association may be to heighten the UV tolerance of the association. This potential basis for a mutualism may be less significant in northwestern North America where solar radiation is reduced in the winter by cloud cover when *Prasiola* species in general are more conspicuous. In Antarctica, however, where UV radiation has increased as a result of the depletion of upper atmosphere ozone, this may be an important adaptation. It would be of interest to determine if lichenized *Prasiola* species are becoming more prevalent and able to survive greater exposures to UV than their non-lichenized forms.

#### 4.2.2. Apophlaea and Pelvetia

*A. sinclairii* is an endemic red alga from the high intertidal zone of New Zealand in which perennial leathery crusts produce short, terete axes to 30 mm high. This alga is associated with the ascomycete fungus *Mycophycias apophlaeae* (previously *Mycophylessella apophlaeae*) (Hawkes, 1983). Although no experimental studies have been published on the interactions between these species, this associ-
ation is similar to *A. nodosum* and *P. canaliculata* with their systemic populations of *M. ascophylli* (see Garbary and Deckert, 2001, for review). Thus the *Apophlaea/Mycophycias* association is also likely a mutualistic symbiosis. Pfetzing et al. (2000) suggest that the high volemitol production in *P. canaliculata* may be stimulated by the fungal symbiont. It would be of interest to know if volemitol is also produced in the *Apophlaea* symbiosis.

Lamare et al. (2004) showed that *Apophlaea* had the highest concentration of MAAs of the marine organisms they examined, and it was the species from highest in the intertidal zone. It has not yet been established whether production or accumulation of MAAs is associated with the fungal partner, but we hypothesize that desiccation tolerance in *Apophlaea* is associated with its mycobiont similar to juvenile stages of *Ascophyllum* (Garbary and Deckert, 2001). The perennial crusts of *Apophlaea* would be a useful model system for studies of induction of MAAs and the role of heat-shock proteins in annual cycles of physiological adaptation.

*Apophlaea* is closely related to *Hildenbrandia*, a cosmopolitan red algal crust found from the high intertidal to subtidal habitats. Although some authors have reported fungal hyphae in *Hildenbrandia* species, these structures may be an artifact of sporangial cell walls. Regardless, these supposed fungal growths do not appear to form a systemic infection throughout the host (Pueschel, 1982).

5. The High Intertidal as a Model for Extraterrestrial Environments

Extraterrestrial environments are unlikely to be suitable for terrestrial organisms from most earth habitats, whether these habitats are aquatic or non-aquatic. Even the most earth-like of planets may preclude terrestrial organisms because of constraints of physical or chemical conditions. Thus, if there is the potential for terrestrial organisms to survive on exposed surfaces elsewhere, these species must be preadapted for survival in extreme earth habitats. Among the physiological adaptations that one would predict for survival in extraterrestrial environments are the following: tolerance of extremes of temperature, ability to tolerate extreme desiccation and intermittent water availability, as well as tolerance to extremes of solar radiation. Such organisms would likely be autotrophic, although not necessarily photosynthetic. These species are likely to occur in habitats with low biodiversity and few trophic levels, where there are few required interactions with other species for growth and reproduction. If the organisms are composite (i.e. lichens), then the symbionts would likely be tightly bound so that there is no stage at which the partners are required to be independent. They should also be capable of vegetative and asexual reproduction to maximize growth opportunities, and to allow rapid recovery after extensive mortality. This combination of features is met in many lichens and the algae that are discussed here, that is those that inhabit the upper reaches of the intertidal and supratidal zones of marine shores.
The combination of extremes of environmental factors that include temperature, solar radiation, and hyper- and hyposalinity make the high intertidal and supralittoral fringe among the most stringent (Tomanek and Helmuth, 2002). These coastal habitats have fluctuating conditions that make opportunities for growth and reproduction intermittent. These stresses result in the production of reactive oxygen species (Dring, 2005) for which metabolic protection mechanisms remain to be explored, but for which high intertidal organisms should provide ideal model systems. This combination of conditions may be a useful analogue for approximating the harshness of extraterrestrial conditions. Although relatively few algal species can survive in these conditions, these species are well adapted to this habitat.

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7. References


