Chapter 11
Form and Function in Antarctic Seaweeds: Photobiological Adaptations, Zonation Patterns, and Ecosystem Feedbacks

Iván Gómez and Pirjo Huovinen

Abstract Morpho-functional traits of Antarctic seaweeds are modeled by different physical and biological factors. Due to the extreme seasonality, which imposes light limitation for extended periods, Antarctic seaweeds are shade-adapted organisms that are physiologically able to thrive at considerable depths down to 40 m. This vertical distribution is defined by a suite of bio-optical and morphological features that allow algae occupying habitats with different environmental conditions in the water column. However, various species can also colonize the highly perturbed intertidal zone where environmental setting, e.g. ice scouring, high solar radiation, extremely variable temperature, limit growth, and reproduction. In the maritime Antarctic region, large endemic brown algae attaining a massive (leathery) morphology and perennial life history dominate at depths below 10 m or less. Here, they coexist with perennial highly shade-adapted coarsely branched rhodophytes, which show understory characteristics. At shallower locations, various annual species with very rapid growth can be found. The intertidal zone, characterized by a depauperate diversity, is populated mostly by ephemeral and delicate green algae. In the present chapter, form and function of seaweeds is revisited in the context of a changing Antarctic environment. Here, the functional groups display different acclimation mechanisms, which can operate at different temporal scales and consequently with variable impact on the biogeochemical coastal processes. The role of canopy-forming algae, whose "bioengineering" processes alleviate the impact of environmental variability, is fundamental in determining the fate of the benthic communities in the coastal system.

Keywords Canopy-forming algae · Life strategy · Light absorption · Morpho-functional traits · Vertical zonation

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11.1 Brief Overview of Form and Function in Seaweeds

In contrast to unicellular algae, organisms bearing multiple cells (from simple pluricellular colonies to more advanced forms attaining, e.g. parenchyma) have to synchronize a more complex structural organization, characterized by different function-specific elements that follow a morpho-genetic-based program. Thus, multicellular algae adjust form and function through an intricate molecular network that allows them to interact with their physical, chemical, and biotic environment (Grosberg and Strathmann 2007). A suite of morphological models found in benthic organisms (e.g. seaweeds, sponges, corals, bryozoa) coexist in a physical environment, which raises a question of how similar convergent forms have evolved even in species phylogenetically very distant or, alternatively, how related organisms display completely different growth patterns and shape (Kaandorp and Kübler 2001).

A striking characteristic of almost all seaweeds is their morphological plasticity, i.e. although the basic thallus plan is based on a determined morphogenetic design, body shape can change through the life span of an organism or within the life history sequence. These variations in the morphological traits within a genotype can be subtle or drastic depending on the intensity of the endogenous and environmentally driven shifts (Innes 1984; Taylor and Hay 1984). Especially in sites where the physical perturbations are extreme, seaweeds display complex mechanisms to adjust form and function to the prevailing environmental condition (Hay 1986). Phenotypic plasticity, one of the most well-known types of intrinsic morphological variability, is normally prompted by environmental conditions and thereby complicates efforts to identify the routes of morpho-functional responses within a multi-specific assemblage: intrinsic properties at an organismal level mask the morpho-functional differences at community scale (Steneck and Dethier 1994). Changes in morphology due to ontogenetic development and heteromorphic phase expression within of life cycle are also important to characterize form and function in seaweeds. For example, in the brown alga *Himantothallus grandifolius*, the largest Antarctic seaweed, the thallus undergoes considerable changes with development: while juvenile individuals are characterized by partial cortication and coarsely branched morphology, adult plants are characterized by a thick leathery strap-like anatomical structure, where lateral branches are absent (Moe and Silva 1981; Wiencke and Clayton 1990).

Traditionally, functional groups of seaweeds (which could also be applied to other groups of benthic marine organisms) are defined by their thallus architecture (also called life form). This concept implies intuitively a series of intrinsic properties of an organism, which can or not be shared by other unrelated organisms. Clearly this gives a high value to the anatomical features (form) and less emphasis on the function. Such conceptual framework represented the basis on, which Littler and Littler (1980) and Steneck and Watling (1982) developed their general functional form models, where functionality of algae, e.g. resistance to biotic disturbance, was inferred from gross morphology. Although the general applicability of these models has been questioned since similar morphologies often show different functional responses to, e.g. disturbance gradients (Phillips et al. 1997; Ingólfsson

2005; Padilla and Allen 2000), functionality, which depends on extrinsic factors (e.g. resource utilization, disturbance, biotic interactions, etc.), has an unavoidable expression in the morphology. The rationale to understand in what ways form and function is modeled by the environment, known as "the holy grail framework", considers necessarily different areas of knowledge, e.g. genomics, physiology, ecology, demography, etc., and has been used with different emphasis to explain the structure of different types of vegetation, both in terrestrial and aquatic realms (Littler and Littler 1980; Grime 1981; Steneck and Dethier 1994; Lavorel and Garnier 2002). Thus, if one assumes that different habitats have a different environmental setting, it is possible to argue that they host assemblages of organisms with similar morphology but different functional attributes. For example, in littoral stress, tolerance of macroalgae depends strongly on fine photochemical adjustments, which are related to their position on the shore and less with functional form groups (Aguilera et al. 1999; Gómez and Huovinen 2011; Balata et al. 2011). This has been commonly found in different types of terrestrial vegetation where environmental tolerance, and not gross morphology, defines functional groups (Grime 1981; Ackerly and Reich 1999; Poorter and Bongers 2006).

11.2 Functional Groups of Seaweeds in the Antarctic

The coastal systems around Antarctica may be regarded as highly inhospitable for life, where physical disturbance associated with ice scouring, extreme light limitation, and low temperatures imposes severe restrictions for marine organisms. However, benthic algae thrive in these habitats displaying different functional strategies and morphologies (Fig. 11.1). Based on various surveys, 131 species of seaweeds (Fig. 11.2) are distributed among different types of functional groups: filamentous and finely branched (45); foliose (9); coarsely branched, including corticated species (48); thick leathery, including terete forms (11); and postrate species (18) (Fig. 11.2). However, when the different functional forms are grouped according to the major phylogenetic categories, it is possible to observe that 64% of green algae are filamentous, while practically the totality of thick leathery forms belong to brown algae. In red algae, 58% of the known species can be recognized as finely and coarsely branched morphs. In the case of Chlorophyta, most of the species attain delicate filamentous or sheet-like morphs, and with the exception of the endemic *Lambia antarctica* and *Monostoma hariotii* (Wiencke and Clayton 2002; see also Chap. 2 by Oliveira et al. and Chap. 5 by Pellizzari et al.), all are restricted to intertidal zones. However, it should be emphasized that many species cannot be easily assigned to these major functional categories. For example, the brown algae *Adenocystis utricularis* and *Utriculidium durvillaei* are the only species with a saccate morphology (and thus were not included in this analysis). Moreover, the number of postrate species, which may include crustose, calcareous, and endophytic life forms, is largely underrepresented. In fact, these algae have been very little studied,

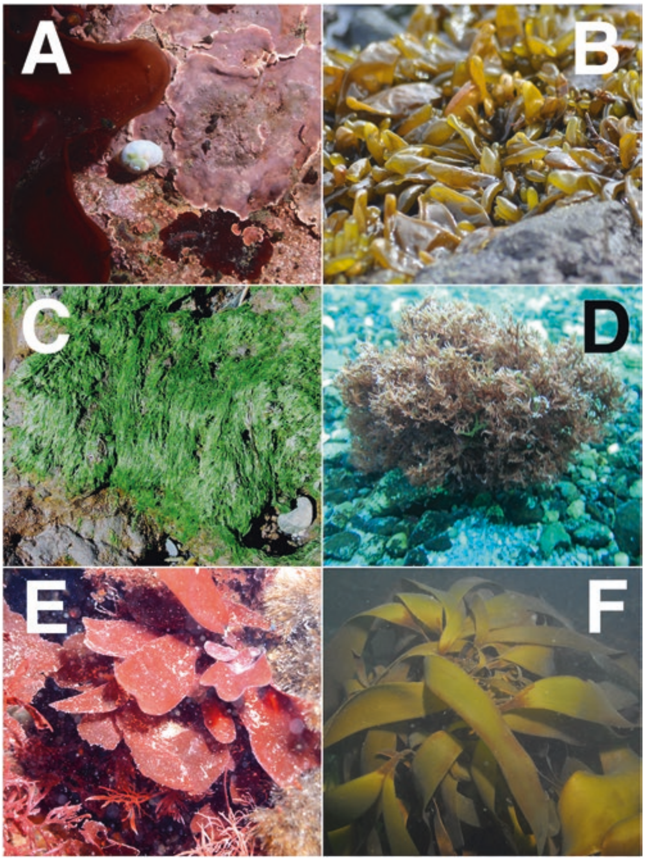
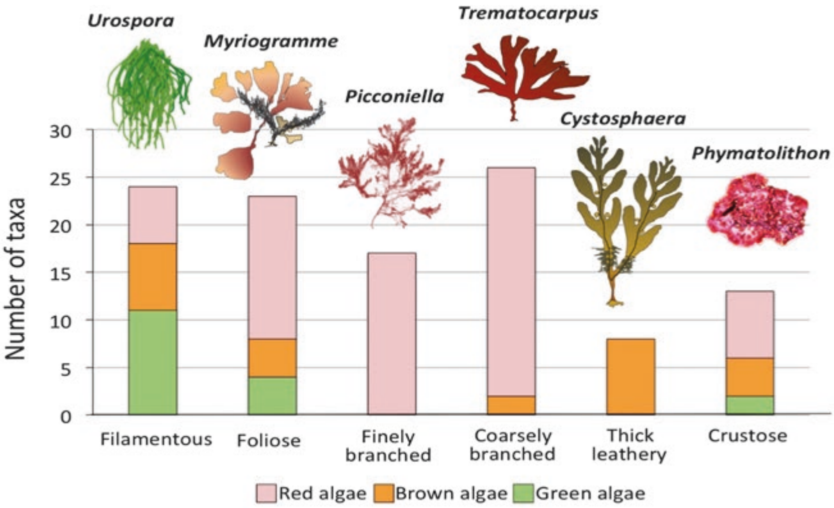


Fig. 11.1 Diversity of gross morphologies in Antarctic seaweeds. (**a**) Crustose Rhodophyta; (**b**) Saccate morphology (*Adenocystis utricularis*); (**c**) Filamentous tubular (*Ulva intestinalis*); (**d**) finely branched *Plocamium cartilagineum*; (**e**) coarsely branched (*Trematocarpus antarcticus*); (**f**) Thick leathery (*Ascoseira mirabilis*). (Photos **a**, **d**, **e** and **f** by Ignacio Garrido; **b** and **c** by Iván Gómez)

due to mostly that they are not ubiquitous (e.g. encrusting morphs) or can inhabit deeper locations (e.g. calcified coralline algae) (Alongi et al. 2002).

The absence of a marked dominance of a given seaweed gross morphology in the Antarctic can only be explained in terms of the distribution of these different functional forms in the mosaic of benthic habitats. In fact, the arrangement of species across different environmental gradients implies also an ordination of organismal traits that can be classified in different functional entities (e.g. gross morphology, size, life forms, physiological responses). Thus, it is possible to understand why similar morpho-functional "solutions" are exploited by different taxa, many of them phylogenetically unrelated. For example, of the 25 species of green algae recorded in the Antarctic, 56% correspond to widely distributed taxa, which normally display



RED ALGAE

Filamentous & Finely branched
Antarcticothamnion polysporum
Audouinella purpurea
Audouinella concrescens
Audouinella membranacea
Ballia callitricha
Ballia sertularioides
Bangia atropurpurea
Erythrotrichia carnea
Ceramium involutum
Cystoclonium obtusangulum
Dasyptilon harveyi
Griffithsia antarctica
Meiodiscus concrescens
Pantoneura plocamioides
Picconiella plumosa
Rhodochorton purpureum
Plocamium cartilagineum
Plocamium hookeri
Plocamium secundatum
Plumariopsis pensinsularis
Polysiphonia abscissa
Pterothamnion antarcticum
Pterothamnion simile

Foliose
Leniea lubrica
Pyropia endiviifolia
Pyropia plocamiestris

Crustose/postrate/endophytic
Antarctocolax lambii
Clathromorphum lemoineanum
Clathromorphum obtectulum
Gainia mollis
Hildenbrandia lecannellieri
Hydrolithon subantarcticum
Synarthrophyton patena
Synarthrophyton schmitzii
Phymatolithon foecundum
Pseudolithophyllum fueguianum

Thick leathery
Gigartina skottsbergii

Coarsely branched
Ahnfeltia plicata
Austropugetia crassa
Callophyllis atrosanguinea
Callophyllis tenera
Callophyllis variegata
Curdiaea racovitzae
Delisea pulchra
Georgiella confluens
Gracilaria sp.
Gymnogongrus antarcticus
Gymnogongrus turquetii
Hymenena sp.
Hymenocladiopsis prolifera
Hymenocladiopsis sp.
Iridaea cordata
Iridaea mawsonii
Microrhinus carnosus
Myriogramme livida
Myriogramme manginii
Nereoginkgo adiantifolia
Nereoginkgo populifolia
Neuroglossum delesseriae
Notophycus fimbriatus
Pachymenia orbicularis
Palmaria decipiens
Palmaria georgica
Paraglossum amsleri
Phycodrys antarctica
Phycodrys austrogeorgica
Phycodrys quercifolia
Phyllophora ahnfeltioides
Phyllophora antarctica
Plumariopsis eatonii
Ptilonia magellanica
Rhodokrambe laingioides
Rhodymenia coccocarpa
Rubrointrusa membranacea
Sarcodia montagneana
Sarcothalia papillosa
Sarcothalia circumcincta
Trematocarpus antarcticus
Varimenia macropustulosa

BROWN ALGAE

Flamentous & finely branched
Elachista antarctica
Geminocarpus austrogeorgiae
Geminocarpus geminatus
Leptonematella falklandica
Scytosiphon lomentaria
Pylaiella littoralis

Coarsely branched
Chordaria linearis
Halopteris corymbosa
Halopteris obovata
Microzonia australe
Phaeurus antarcticus
Scytothamnus fasciculatus

Crustose/postrate/endophytic
Australofilum incommodum
Lithoderma antarcticum
Petroderma maculiformis
Ralfsia australis

Saccate
Adenocystis utricularis
Utriculidium durvillaei
Antarctosaccion applanatum

Thick leathery
Ascoseira mirabilis
Cystosphaera jacquinotii
Desmarestia anceps
Desmarestia antarctica
Desmarestia confervoides
Desmarestia menziesii
Himantothallus grandifolius

Foliose
Petalonia fascia

GREEN ALGAE

Filamentous & Finely branched
Acrosiphonia arcta
Blidingia minima
Chaetomorpha irregularis
Chaetomorpha mawsonii
Cladophora coelothrix
Cladophora repens
Lambia antarctica
Rhizoclonium tortuosum
Spongomorpha pacifica
Ulothrix australis
Ulothrix flacca
Ulothrix implexa
Ulothrix subflaccida
Urospora penicilliformis
Ulva hookeriana
Ulva intestinalis

Foliose
Monostroma hariotii
Prasiola crispa
Ulva compressa
Ulva lactuca
Ulva rigida

Postrate/endophytic
Endophyton atroviride
Entocladia maculans
Entocladia viridis
Ulvella viridis

Fig. 11.2 Major functional-form groups in different divisions of Antarctic seaweeds based on different surveys (Clayton et al. 1997; Wiencke and Clayton 2002; Hommersand et al. 2009; Ramírez 2010; Charles Amsler, personal communication)

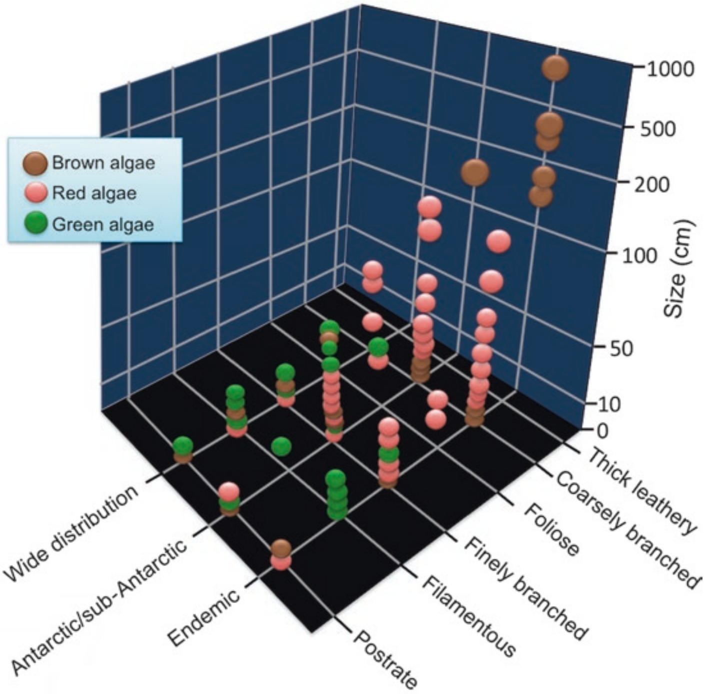


Fig. 11.3 Antarctic seaweeds and their organization in relation to form and function, size, geographic affinity, and taxonomy. Number of taxa extracted from Fig. 11.2

filamentous or sheet-like forms (Fig. 11.3). According to Gómez et al. (2019), form and function and biogeographic affinity are highly correlated in Antarctic green algae. In contrast, only 12% of Rhodophyta can be regarded as widely distributed, contrasting with the high prevalence of endemic (42%) and Antarctic/sub-Antarctic taxa (46%). Similar pattern can be observed in brown algae where endemic and Antarctic/sub-Antarctic species (characterized by thick leathery and saccate morphs) account by 88% of the total numbers of recorded taxa (Fig. 11.2).

11.3 The Vertical Zonation of Antarctic Seaweeds: A Paradigm of Spatial Distribution of Different Morpho-functional Traits

Knowledge on zonation and in general the structure of the submarine landscape in the shallow sublittoral in the Antarctic began to increase in the 1960s and 1970s, along with scuba diving–based surveys (Neushul 1965; Delépine et al. 1966;

Zaneveld 1966; DeLaca and Lipps 1976; Lamb and Zimmerman 1977). These studies across different geographical zones demonstrated that the vertical distribution of macroalgae could be defined in terms of functional groups, which apparently do not follow uniform patterns, principally due to differences in latitude, substrate, influence of ice, associated fauna, etc. The vertical distribution of Antarctic seaweeds has been much more studied in the Western Antarctic Peninsula and adjacent islands, an eco-region known as the Maritime Antarctic. Due to the relatively milder climatic conditions, seaweed assemblages reach their maximal development in terms of abundance and diversity in the north-western part of the Antarctic Peninsula, decreasing the macroalgal biodiversity towards the southern regions (Wiencke et al. 2014; Mystikou et al. 2014). The zonation in the Maritime Antarctic can be characterized by a dominance of large canopy-forming endemic species of the order Desmarestiales (*Desmarestia menziesii*, *D. anceps*, and *Himantothallus grandifolius*) between 10 and 40 m or greater depth (Fig. 11.4a). These three species have thick leathery and terete gross morphology and can alternate their dominance depending on the substrate characteristics, whose consolidation can vary considerably depending on closeness to glaciers, slope of the vertical profile, terrestrial runoff, etc. (Klöser et al. 1994). Coexisting at this level, it is possible to found delicate understory red algae, e.g. *Myriogramme*, *Gymnogongrus*, and *Georgiella* (Amsler et al. 1995). Between 0 and 5 m depth, a zone marked by ice abrasion and waves, the substrate is colonized by fast-growing species, algae with an ability for re-sprout from basal shoots and crustose forms. In contrast, the intertidal rocky shores are dominated by ephemeral, turf species, mainly filamentous Chlorophyceans (e.g. *Urospora*, *Ulva*, *Ulothrix*) and the saccate brown alga *Adenocystis utricularis* (Huovinen and Gómez 2013; Marcías et al. 2017).

In areas outside the Western Antarctic Peninsula, e.g. around the Ross Sea and some sites along the East Antarctica, the diversity and abundance of seaweeds decreases and their vertical distribution is much more constrained by available substrata and the longer permanence of sea ice cover (Zaneveld 1966; Miller and Pearse 1991; Gambi et al. 1994; Johnston et al. 2007; Clark et al. 2011). In these sites, although some large Desmarestiales (e.g. *H. grandifolius* and *D. menziesii*) can be found at deeper locations, in general the coarsely branched red algae *Iridaea cordata* and *Phyllophora antarctica* are the dominant assemblages, especially at intermediate depths (between 2 and 20 m) (Cormaci et al. 2000) (Fig. 11.4b). Another particular feature of these ecosystems is the massive presence of crustose coralline red algae at deeper locations, especially of *Phymatolithon foecundum* (Hommersand et al. 2009), which can cover >70% of the available substrate under the canopy of red and brown algae (Irving et al. 2005). Remarkably, algae have to adapt to very low light conditions for primary productivity, irrespective of their functional form architecture. In fact, due to their extreme shade adaptation, these species can reach considerable depths and live with <2% of surface irradiances (Schwarz et al. 2003, 2005; see also Chap. 7 by Huovinen and Gómez).

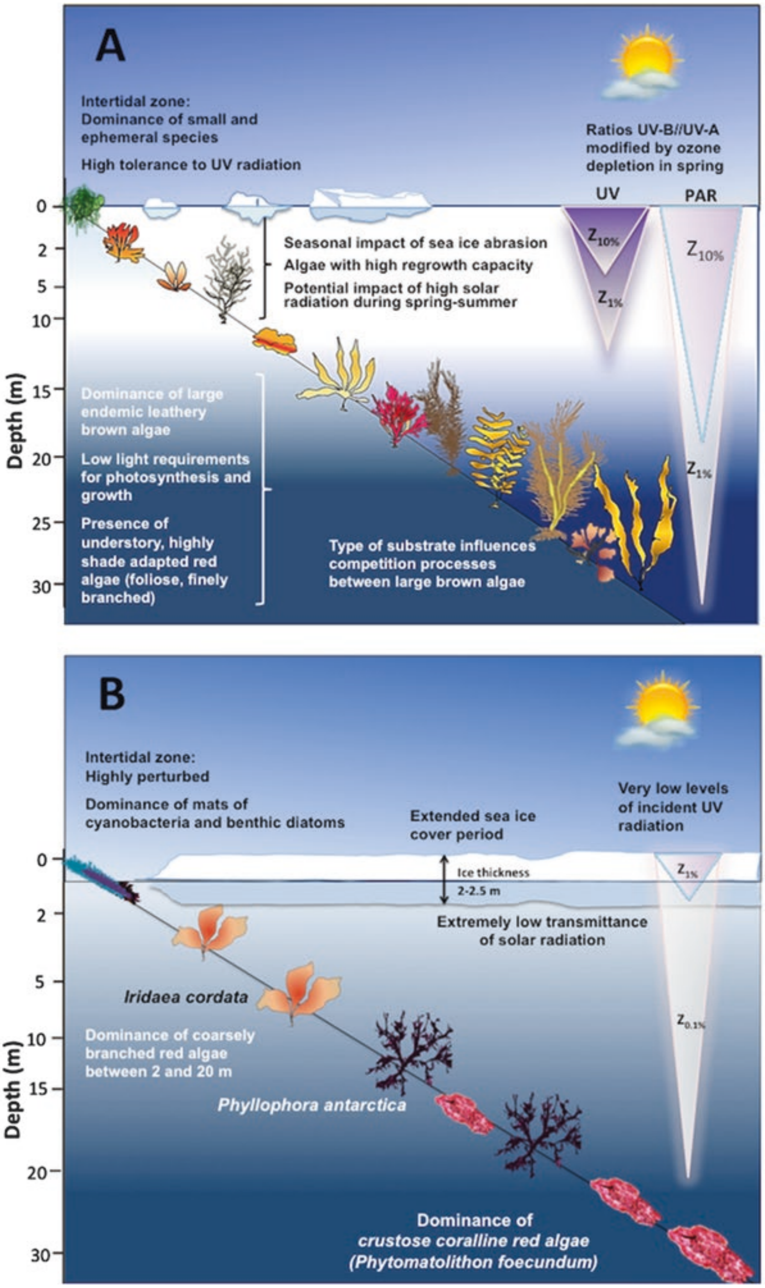


Fig. 11.4 Patterns of vertical distribution of seaweeds in Western Antarctic Peninsula (**a**) and Eastern Antarctica (**b**) indicating major functional groups and photobiological processes. Synthetic schemes from observations reported in Gambi et al. (1994), Johnston et al. (2007), and Huovinen and Gómez (2013)

11.4 Light Use Characteristics as a Major Factor Delineating Physiological Thallus Anatomy of Seaweeds

The arrangement of different functional forms along the depth gradient is strongly determined by different physico-chemical and biological factors. However, spatial and temporal availability of light is probably the most relevant factor by which zonation of Antarctic seaweeds can be explained. Because light governs the primary processes of photosynthesis, and, hence, primary productivity and biomass formation, Antarctic seaweeds, irrespective of their morphological organization, display efficient mechanisms of light harvesting. In fact, in the Antarctic, the marked seasonality in light availability defines strongly an intrinsic shade adaptation of macroalgae. Here the whole phenology of algae is closely tuned with the Antarctic light regime, which exposes organisms to darkness in winter (Wiencke et al. 2009). However, although in summer algae can be exposed to very high doses of solar radiation due to extended daylengths of up to 24 h at the highest latitudes, they do not acclimate and retain the capacity for very low light requirements for metabolism (Gómez and Huovinen 2015). This ability to use very low irradiances for photosynthesis and an intrinsic positive metabolic carbon balance (an indicator of compensation of carbon losses due to respiration) (Gómez et al. 1997; Deregibus et al. 2016) has important implications for the spatial dimension of the algal zonation: it allows Antarctic algae to colonize shaded locations, especially deeper sites. As a consequence, many Antarctic species can occupy extended ranges of depth and hence different light fields (Gómez et al. 1997). This situation contrasts with zonation patterns of various cold and temperate coasts, where the different algal groups are arranged in well-defined “belts” (Lüning 1990). Light trapping, especially under very limited conditions of irradiance, requires not only a specific pigment configuration but also morphological features such as thickness and thallus translucency, which are important in terms of absorptance of the different wavelengths (Gómez and Huovinen 2011). Algae increase light trapping through their thallus architecture, which can result in different in vivo spectral absorptance (Lüning and Dring 1985; Gómez et al. 2019). In Fig. 11.5, the spectral characteristics of several Antarctic macroalgae with different functional form and thickness are exemplified. In the case of thick leathery and coarsely branched morphs (e.g. *Himantothallus*, *Desmarestia*, *Iridaea*), attaining thallus thickness >500 μm, show high absorptance practically along the whole spectrum. In contrast, delicate morphs with thickness <100 μm, mostly foliose and finely branched such as *Monostroma*, *Pantoneura*, *Myriogramme*, and *Pyropia*, show decreased absorptance between 550 and 650 nm. Interestingly, some thin filamentous algae, e.g. *Ulva intestinalis*, *Acrosiphonia*, and *Urospora*, can exhibit high absorptance at these wavelengths, which is related to their turf arrangement, i.e. the overlapping of different filaments equals the several cell layers of thicker algae. Overall, these patterns are related to algal taxonomy and distribution in the zonation profile. In fact, thick leathery forms commonly belong to the brown algae, and their efficient light absorption over an extended range of wavelengths allows using the impoverished light field at higher depths (Gómez and

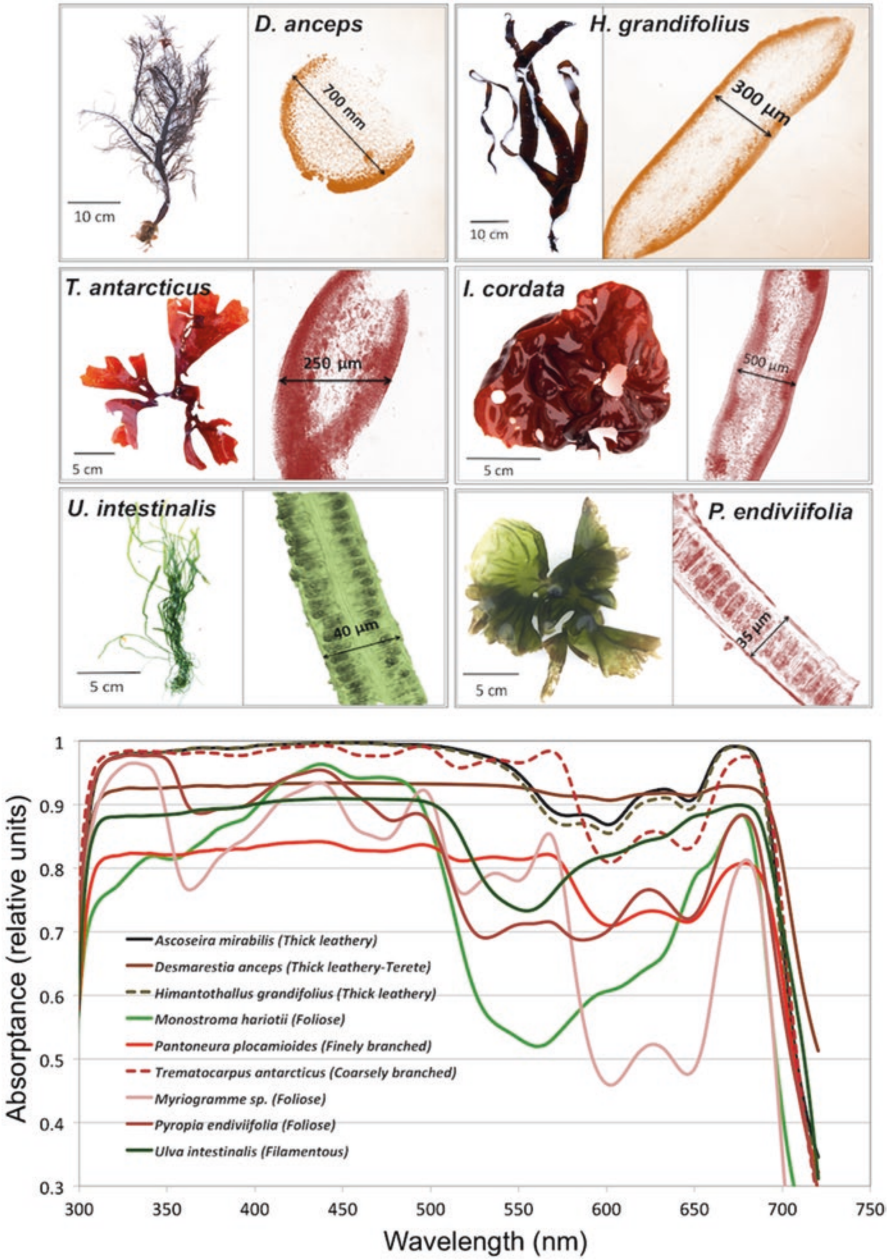


Fig. 11.5 Patterns of spectral in vivo absorptance of several Antarctic seaweeds with different morpho-functional organization. Examples of thallus gross morphology, cross section, and thickness are indicated for selected species. Cross-sectional microphotographs courtesy of Nelso Navarro

Huovinen 2015). Similarly, understory coarsely branched and finely branched red algae, inhabiting deep sites with high absorption between 400 and 500 nm, are well suited to live at these depths (Gómez et al. 2019). Considering that, irrespective of their thallus shape and taxonomical affinity, Antarctic seaweeds are shade-adapted organisms, whose morphological and optical traits (e.g. thickness), pigment composition, and intrinsic photochemical capacities are superimposed in their vertical distribution (Huovinen and Gómez 2013; Gómez et al. 2019).

11.5 Form and Function in the Context of Life Strategies and Stress Tolerance

Since the publication of MacArthur and Wilson in 1967 on r and k selection, which put into a context the evolutionary divergences of organisms in relation to the production and care of offsprings, many studies have tried to expand these concepts to other adaptive traits (concept discussed in Pianka 1970). Because r and k strategies involve normally differences in energy allocation and, hence, body size, the form and function concept could be easily integrated in the theory (Grime 1981). For the case of marine macroalgae, in the 1980s, Joanna Kain used the terms "season responder" and "season anticipator" to describe the different phenological responses of seaweeds to seasonal changes in the environment (Kain 1987). Accordingly, "season responders" correspond to organisms that grow and reproduce under favourable environmental conditions, which could be analogous to r strategists, while "season anticipators" are organisms whose development is triggered by environmental factors at which they anticipate. The latter classification resembles k-selection strategy. Although not a strict rule, most of the season responders identified in the literature seem to correspond to delicate, small-sized forms, which normally exhibit an opportunistic strategy. In contrast a number of season anticipators can be associated with long-lived (perennial) seaweeds attaining normally large thalli (Kain 1989). However, although intuitively one may argue that differences in thallus complexity (including size) are correlated with differential responses to season, in general they are complex and depend on different environmental factors, type of biological indicator (growth, photosynthesis, reproduction, etc.), age and life history phase, and endogenous rhythms, all which can show complementary or divergent patterns (Kain 1986; Lüning and Kadel 1993; see also Chap. 10 by Navarro et al.).

In the Antarctic benthos, seaweeds are exposed to a marked seasonality, and thus, the concepts of "responders" and "anticipators" could explain well the different phenological patterns found in Antarctic seaweeds. In fact, various Antarctic species, e.g. *Iridaea cordata*, *Ulva intestinalis*, *Acrosiphonia arcta*, and *Adenocystis utricularis*, have been regarded as "season anticipators", while Antarctic Desmarestiales, *Ascoseira mirabilis* and *Palmaria decipiens*, can be considered as "season anticipators" (Wiencke 1990a, b). Although these classifications were based mostly on growth responses to the Antarctic light regime, it has been shown that photosynthetic light use characteristics can respond in the same seasonal manner. For example, the brown alga *Adenocystis utricularis* and the red alga *Iridaea cordata*, two species regarded as responders, maintain high photosynthetic functionality still in winter, when light is very limited (Gutkowski and Maleszewski 1989; Weykam et al. 1997). This strategy is completely different in large Desmarestiales and *Ascoseira mirabilis*, as well as the red alga *Palmaria decipiens*, which activate their photosynthetic apparatus during early spring to optimize the available irradiance after the ice break-up (Gómez et al. 1995a, b; Wiencke et al. 2009). For large brown algae whose thalli can have length of various meters, these responses have important morpho-functional implications: Firstly, photosynthesis and growth during early spring are strongly synchronized to potentiate the use of newly fixed and stored carbon. Secondly, there is spatial separation between carbon production and sink zones with different metabolic activity, which can also be exposed to very contrasting light fields. Because these massive thick leathery species require compensation for the enhanced carbon burning due to high rates of dark respiration during the rapid biomass formation, the lamina elongation is powered by carbon stored in the previous season (Gómez and Wiencke 1998), similarly as in high-latitude kelps (e.g. *Laminaria*, *Saccharina*) (Dunton and Schell 1986). A well-studied case is *Ascoseira mirabilis*, which grows through the action of an intercalary meristem and presents "conducting channels" in medullary cell regions (Clayton and Ashburner 1990; Gómez et al. 1995b). In this species, during the growth phase, carbon stored as laminarin in distal parts is remobilized through the conducting cells (normally as mannitol and some amino acids) towards the meristem to replenish carbon substrates in the so-called light-independent carbon fixation (LICF) reactions (Kremer 1981; Gómez and Huovinen 2012). Such morpho-functional strategies have not only been demonstrated in large brown algae: in the perennial, coarsely branched red alga *Palmaria decipiens*, LICF reactions accounting 9% of the total fixed carbon have been reported (Weykam et al. 1997), suggesting that this type of mechanisms are operating in algae with complex thallus anatomy and season anticipation phenology, which allow them thriving at high depths and under extreme seasonality in the Antarctic.

Form and function in the context of stress tolerance have been revisited in the last years. Interestingly, several anatomical traits related to resistance to physical disturbance, e.g. multilayered architecture, thickness, and large size, are also functional to increase light trapping, e.g. efficient absorptance (Gómez and Huovinen 2011). Recently it was claimed that populations of three species of Desmarestiales (*D. anceps*, *D. menziesii*, and *H. grandifolius*) and *Ascoseira mirabilis* extending between 5 and 30 m depth show similar photosynthetic characteristics along the depth profile (Gómez and Huovinen 2015). However, not only the efficient and highly conserved light use across different irradiances but also an intrinsic capacity for UV stress tolerance was shown in these algae (see Chap. 7 by Huovinen and Gómez). Although all these traits conferring UV shielding show a strong overlapping with other factors, e.g. competence for space and overgrowth, scape from herbivores, there appears to exist a trade-off between photoprotection against enhanced solar UV radiation, mostly due to an increased thallus cross section (low area/weight ratio) and ultrastructural compounds, and highly efficient shade adaptation (Gómez and Huovinen 2015). A key element explaining this feature in algae rarely exposed to UV radiation is their constitutively high levels of phenolics (phlorotannins) (Flores-Molina et al. 2016). These secondary metabolites in Antarctic brown algae represent multifunctional compounds with putative roles in, e.g. resistance to grazing, temperature, and UV radiation (Amsler et al. 2005; Iken et al. 2009; Huovinen and Gómez 2013; Rautenberger et al. 2015) (for a description of functional roles of phlorotannins in Antarctic seaweeds, see Chap. 17 by Amsler et al. and Chap. 18 by Gómez and Huovinen).

In the case of delicate morphs, mostly filamentous and finely branched green algae, the opportunistic life strategy of these organisms allows them to respond rapidly to environmental stressors and, in virtue of their high metabolic rates per weight, to restore the homeostasis at short term (Holzinger and Karsten 2013). Albeit stress tolerance of seaweeds living in the intertidal zone would rely on highly efficient metabolic adjustments (Holzinger and Lutz 2006; Karsten et al. 2009; Gómez and Huovinen 2011), some structural adaptations have been described. For example, in *Urospora penicilliformis* a dense cell wall, presence of mucilage and external mineral deposition provide efficient shielding from high solar radiation and desiccation (Roleda et al. 2010). In many cases, filamentous green algae can form mats or turf-like structures that are effective to minimize the harmful effects of changing environment (Bischof et al. 2006). In all, in terms of photosynthetic characteristics and physiological responses to stress, form and function of some Antarctic seaweed assemblages have been related to biogeographic affinity and depth. Based on 31 species from King George Island, three major groups of species were defined: (a) coarsely branched Rhodophyta are mostly found at shallow subtidal sites and have an Antarctic-sub-Antarctic origin; (b) endemic Antarctic brown algae are dominant at depths between 10 and 30 m and practically all attain thick leathery morphology; and (c) filamentous and sheet-like green algae, mostly intertidal species, normally can be categorized as algae with wide geographic distribution (Gómez et al. 2019).

11.6 Functional Traits of Seaweeds and Properties of Benthic Communities

Seaweeds in practically all cold-temperate and polar coastal ecosystems represent foundational organisms, whose processes and fate determine key community indicators, such as structure and functional and taxonomic richness (Chapman 1987; Lüning 1990). In King George Island, the distribution and composition of different functional groups in both intertidal and subtidal sites are regulated by different factors, which are defined by some species that account by 90% of the dissimilarities between depth strata (Valdivia et al. 2014). When representative taxa are analysed, effects are scale dependent: variance components increase at the finer scale of variation (from centimeters to meters) compared to shore level (hundreds of meters) (Valdivia et al. 2014). In the intertidal system dominated by filamentous and finely branched morphs, the grazing by the limpet *Nacella concinna* is probably one of the most important biological interactions (Kim 2001; Segovia-Rivera and Valdivia 2016). Apart from green algae, *N. concinna* exerts control on periphyton, thus determining far-reaching ecological processes, e.g. the fate of re-colonization and succession in these systems (Campana et al. 2009; Valdivia et al. 2019; see also Chap. 12 by Campana et al. and Chap. 13 by Valdivia).

At the subtidal zone, facilitative interactions held by large brown algae through bioengineering seem relevant for the structure and maintenance of the benthic communities (Valdivia et al. 2015). These canopy-forming seaweeds are important as they shelter other species of algae and invertebrates from harmful environmental conditions and thus have an important effect on the community biomass of the whole ecosystem (Valdivia et al. 2015; Ortiz et al. 2016; see also Chap. 15 by Momo et al. and Chap. 16 by Ortiz et al.). However, in locations exposed to severe impact of physical disturbance, small organisms can be favoured while canopy-forming algae would be more sensitive (Smale 2007). For example, in eastern Antarctica where ice cover can be considerably extended through spring, canopy-forming macroalgae were only abundant at sites where sea-ice cover break-up occurs during spring, but absent at sites that retained ice cover until summer (Johnston et al. 2007). Thus, these organisms appear to respond slowly to the changing environment due, for example, to enhanced warming. For example, in new ice-free areas originated from glacier retreat where enhanced sediment input limits light penetration, establishment of large brown algae is highly constrained (Quartino et al. 2013). In these highly perturbed sites, ice scouring and unconsolidated substrate affect considerably the presence of canopy-forming algae and hence the taxonomic richness (Klöser et al. 1994; Smale 2007; Smale et al. 2008; Valdivia et al. 2015). On the other hand, environmental shifts driven by climate change can affect the morpho-functional responses of Antarctic species. For example, physiology of canopy-forming algae (e.g. *Desmarestia* spp.) may have consequences for the whole benthic community (Schoenrock et al. 2015). In the case of crustose species, fleshy encrusting forms (*Hildenbrandia*) could be favoured in scenarios of changing pH and temperature compared to calcified Coralline species (*Clathromorphum*) (Schoenrock et al. 2016). In general, morpho-functional and anti-stress mechanisms of macroalgae to cope with sharp physical gradients percolate towards upper hierarchies through insurance of functional richness in the community, which set high degree of resilience to physical perturbation (Ortiz et al. 2016, 2017) or to minimize the impact of alien species (Arenas et al. 2006; see Chap. 16 by Ortiz et al.).

Considering some functional form models for marine seaweeds, similitudes and analogies with terrestrial vegetation strategies can be identified. For example, according to the functional groups described by Grime (1981) for terrestrial vegetation, opportunistic green algae growing at the intertidal zone could correspond to the “ruderal” species, permanently subjected to strongly physical perturbation. In contrast, large endemic brown algae, which thrive in sites with lower physical

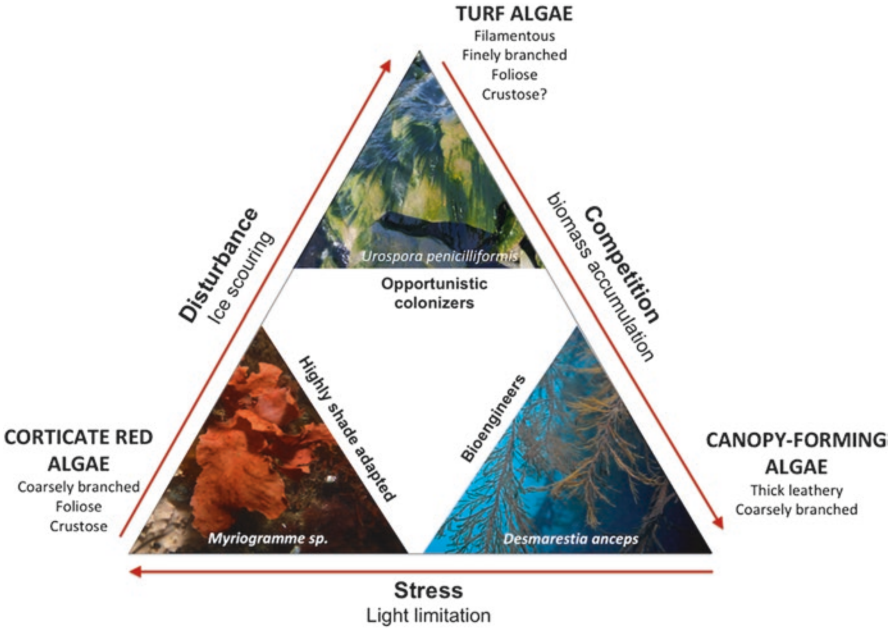


Fig. 11.6 CSR Grime's triangle describing the main strategies and environmental trade-off of the major functional groups of Antarctic seaweeds. (Photos *Myriogramme* and *Desmarestia* by Ignacio Garrido; *Urospora* by Iván Gómez)

perturbation, can be analogue to "competitive species" in virtue of their exuberant canopy and perennial characteristics. For many temperate ecosystems, the life history traits conferring advantages under high levels of disturbance are convergent in different types of algal assemblages, suggesting that some patterns could be generalized (Steneck and Dethier 1994). However, in Antarctic communities some factors associated with disturbance and stress require adjustment to the extreme Antarctic conditions. In the conceptual framework in Fig. 11.6, three major functional groups of Antarctic seaweeds (turf algae, dominated by intertidal green algae; canopy-forming algae, especially large brown algae; and corticated red algae, grouping many understory species) can be oriented through the three axes following a Grime's CSR triangle schema. Here, the extreme action of ice (perturbation), light limitation (stress), and biomass (competition) dimensions determine the separation among algal groups. Corticate red algae in virtue of their extreme shade adaptation represent the stress tolerant group. Here, many crustose species growing at very low light conditions in the eastern Antarctic can also be added to this group. In the perturbation axis, filamentous and finely branched green algae and some little saccate brown algae (*Adenocystis utricularis*) exemplify the colonizers, well adapted to occupy sites highly perturbed by ice, terrestrial run-off, and high solar radiation. Under these conditions abundance and species richness are less influenced by biological interactions (Valdivia et al. 2014; Segovia-Rivera and Valdivia 2016).

Finally, the canopy-forming algae, represented by species of the order Desmarestiales, and *Ascoseira* and *Cystosphaera* that exhibit high biomass production, are dominating at sites with lower physical perturbation. However, they show competitive abilities for light and substrate (Gómez et al. 1997; Valdivia et al. 2015).

11.7 Concluding Remarks

The main ecological expression of the morpho-functional adaptation of Antarctic seaweeds is the macroalgal zonation, which is not only a vertical arrangement of species but also represents an ordination of organismal traits that can be classified in different functional entities (e.g. gross morphology, life forms, physiological responses). These attributes can be scaled up to community structure and ecosystem functioning. The concept, well studied in plants, has been revitalized in the last decade in the context of the contemporary climate change.

Due to the seasonally changing light conditions, characterized in the highest latitudes by several months of very dim light, Antarctic seaweeds are adapted to very low light levels. In contrast, after the ice break-up in spring, they suddenly can be exposed to strong solar radiation. Thus the adaptations of Antarctic algae are finely tuned with the daylength, changes in water turbidity, and ice perturbations. This environmental variability is fully exploited by seaweeds in virtue of their efficient morpho-functional adaptations. However, due to climate change, the environmental settings in which Antarctic seaweeds have evolved for millions of years are changing. In these new scenarios, the adaptive capacities of these organisms as well as the ecosystem functions they provide will be challenged (Constable et al. 2014; Gutt et al. 2015). Although one can recognize that polar seaweeds are particularly susceptible to these changes with unpredictable consequences for the whole coastal ecosystem, we have still a limited understanding on how physiological and morphological traits respond and how they will be integrated in, for example, molecular mechanisms of environmental tolerance and stress resilience.

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