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Authors	Chandler, CJ; Wilts, BD; Brodie, J; Vignolini, S
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Structural Color in Marine Algae

Chris J. Chandler, Bodo D. Wilts, Juliet Brodie, and Silvia Vignolini**

Structural coloration is widespread in the marine environment. Within the large variety of marine organisms, macroalgae represent a diverse group of more than 24 000 species. Some macroalgae have developed complex optical responses using different nanostructures and material compositions. In this review, we describe the mechanisms that are employed to produce structural color in algae and provide a discussion on the functional relevance by analyzing the geographical distribution and ecology in detail. In contrast to what is observed in the animal kingdom, we hypothesize that structural color in algae predominantly functions for a non-communicative purpose, most likely protection from radiation damage, e.g., by harmful UV light. We suggest that the presence of structural color in algae is likely influenced by local factors such as radiation intensity and turbidity of the water.

1. Introduction

Structural colors are the result of the interaction of light with nanostructured materials. Such nanostructures, with features on the mesoscale (i.e., ≈100 nm), are capable of producing vivid, saturated colors through interference.[1] Different organisms exploit a variety of nanostructures and materials which, often combined with underlying pigmentation, can produce a wide range of complex optical effects,[2,3] ranging from metallic and iridescent colors[4,5] to bright whites.[6] In nature, structural color occurs in the marine and terrestrial environments in organisms across the tree of life, including birds,[7–9] insects,[10–14] land plants[15,16] (e.g., in the leaves,[17,18] flowers[19–21] and fruit[22,23]), bacteria,[24] fungi,[25] slime molds,[26] viruses,[27] diatoms[28] and macroalgae.[29] The biological significance of structural color is mainly studied and understood in insects[30,31] and other animals[32,33] in terms of intra- and inter-specific communication,[34] mate attraction[35] and predator deterrents.[33,36–38] In flowers, structural color is hypothesized to function in relation to attracting potential pollinators.[20] However, in organisms such as algae the function of structural color remains unclear.

C. J. Chandler, Dr. S. Vignolini
Department of Chemistry
University of Cambridge
Lensfield Road, Cambridge CB2 1EW, United Kingdom
E-mail: sv319@cam.ac.uk
C. J. Chandler, Prof. J. Brodie
Natural History Museum
Department of Life Sciences
Diversity and Informatics Division
Cromwell Road, London SW7 5BD, United Kingdom
E-mail: j.brodie@nhm.ac.uk
Dr. B. D. Wilts
Adolphe Merkle Institute
Chemin des Verdiers 4, CH-1700 Fribourg, Switzerland

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Marine macroalgae (red, brown and green seaweeds) represent a large, diverse group of organisms within the marine kingdom. To date, around 11,000 species of marine algae have been described, however it is suggested that around 10,000 species are still undescribed (Mike Guiry pers. comm.; see further in ref. [39]). Red (Rhodophyta) and green (Chlorophyta) algae originated from the primary endosymbiosis of cyanobacteria around 1500 Mya.[40] In comparison, the divergence of the brown algae (Phaeophyceae), as a consequence of secondary endosymbiosis, occurred relatively recently, at around 200 Mya (**Figure 1**).[41]

Marine algae play a major role in the functionality of coastal ecosystems,[42] provide a significant contribution towards global carbon fixation,[43] contribute to stable food sources,[44] and are employed in various health[45] and medicinal[46] products. Considering the global importance of marine algae and the current declines that many populations face as a result of environmental degradation,[47–49] understanding their structural color may reveal adaptation strategies useful in relation to global environmental change. For example, similarly to leaves,[50,51] structural color in algae may serve to protect species from ultraviolet radiation which may be beneficial considering continual ozone damage. Assuming this hypothesis, structural color may be useful in predicting marine species composition in the future.

Despite the lack of understanding on the biological purpose of structural color, marine algae have received very little attention within this field, most likely as their colors do not function for a communicative purpose.[32] Subsequently, only a few studies have attempted to work on and identify the mechanisms responsible for producing structural color and they have mainly focused on the red algae (Rhodophyta), where intracellular[52] and extracellular[29] structures have been observed. For example, in the red alga, *Chondrus crispus* Stackhouse[53] (Rhodophyta), it has been shown that structural color is produced by a multilayered structure in the cuticle with refractive-index periodicity.[29] Furthermore, virtually no studies have attempted to investigate the vivid and diverse array of structural color patterns found within the brown algae (Phaeophyceae). It has been suggested that intracellular quasi-ordered spherical inclusions in the epidermal cells termed 'iridescent bodies' are responsible for the observed structural color,[54] however there is no clear experimental evidence that correlates these bodies with the optical appearance.

In this progress report, we describe the mechanisms of color production in marine algae and compare them to those observed in land plants. Moreover, focusing on the specific

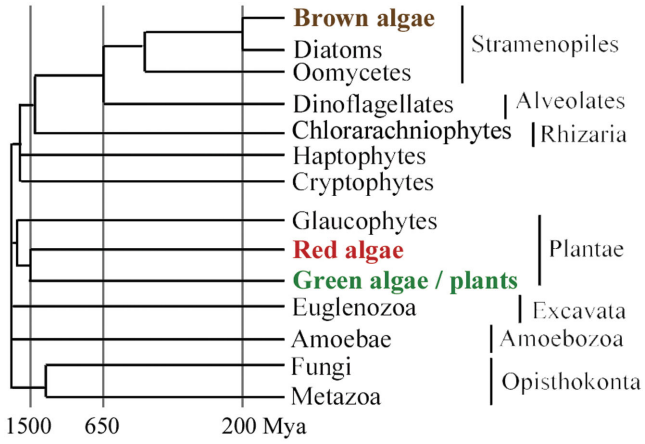

Figure 1. Evolutionary tree of the eukaryotes showing the position of red, green and brown algae and the time of divergence of red algae, dinoflagellates, and brown algae. Adapted with permission.[101] Copyright 2010, Nature Publishing Group.

group of brown algae, where only one mechanism has been observed (so far), we show their distribution, ecology and phylogenetic placement. Finally, we discuss the various functions and biological significance that such coloration may provide.

2. Physical Mechanism of Structural Coloration in Marine Algae

Structural mechanisms capable of producing color can vary in dimensions, complexity and ordering (e.g., ranging from periodic structures to highly disordered).[55] Marine macroalgae employ different strategies to produce complex optical responses using different architectures and materials. **Figure 2** compares the two main types of architectures responsible for structural color in algae. Firstly, extracellular multilayered structures,[29] similar to those of land plants.[16] These structures found in *Chondrus crispus* or *Iridaea* sp. are protein rich (≈50%) and contain around 40% carbohydrates.[56] Structurally colored *C. crispus* individuals (gametophytes) contain kappa and/or iota carrageenan,[57] a linear polysaccharide capable of forming a strong, well-bonded cuticle. Secondly, intracellular structures consisting of three-dimensional not periodic spherical objects.[56–72] These intracellular inclusions, distributed throughout the epidermis, consist of highly packed vacuoles with multiple dense, proteinaceous globules scattered throughout a matrix of polysaccharides and an osmiophilic material (see **Figure 3**a). *Cystoseira stricta* is suggested to contain protein within the inclusions, however the presence of proteins may differ between species.[58]

Early observations of structural color in brown algae revealed "globules responsible for iridescence".[59] Subsequent attempts to clarify the mechanisms responsible for this structural color revealed the identical structures, now referred to as "iridescent bodies".[60–63] Previous studies have identified these bodies in *Cystoseira* spp.,[58,64,65] *Dictyota* spp.[66–70] and *Zonaria tournefortii*[71] (see **Table 1**).

Iridescent bodies are also found in red algae,[52] a distinctly separated group from the brown algae (Figure 1). The occurrence of iridescent bodies in both red and brown algae suggests that they were either retained through the secondary endosymbiosis from which the brown algae were derived or they have

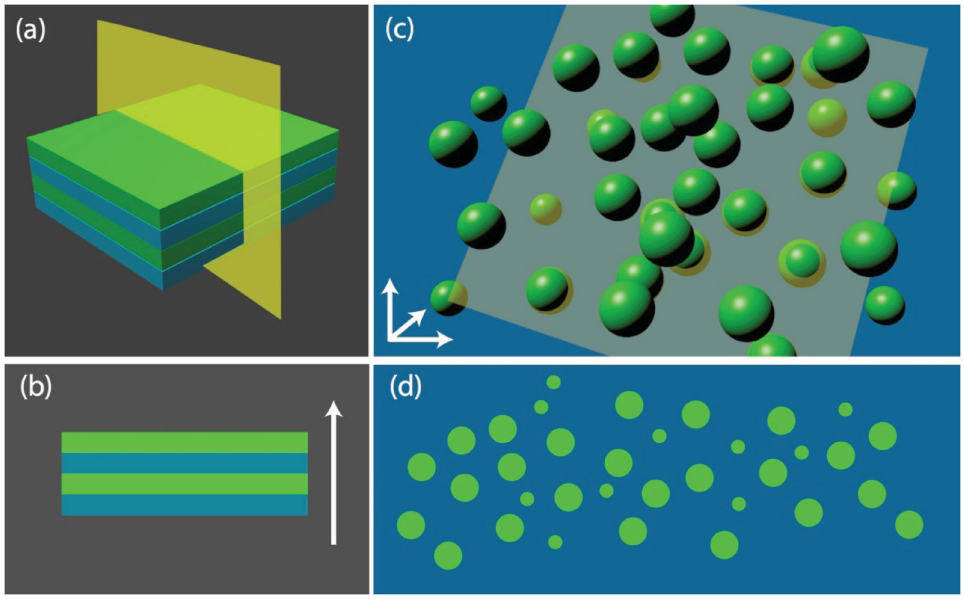

Figure 2. Schematic representation of the common ultrastructures responsible for structural color in algae: a) a multilayered structure and b) the corresponding cross section. In the case of a periodic multilayer structure, the sectioning can give artefacts only when we measure the thickness of the layers. Such artefacts can be taken into account by imaging multiple cross-sections and determining the tilt angle. In general, the measurement error due to this artefact is comparable with natural variations within biological samples. c) Iridescent bodies and d) the corresponding cross section. When the structures are non-periodic (c,d) it is more difficult to evaluate the structural parameters of the full 3D system and more sophisticated tomography techniques are required for a complete characterization.

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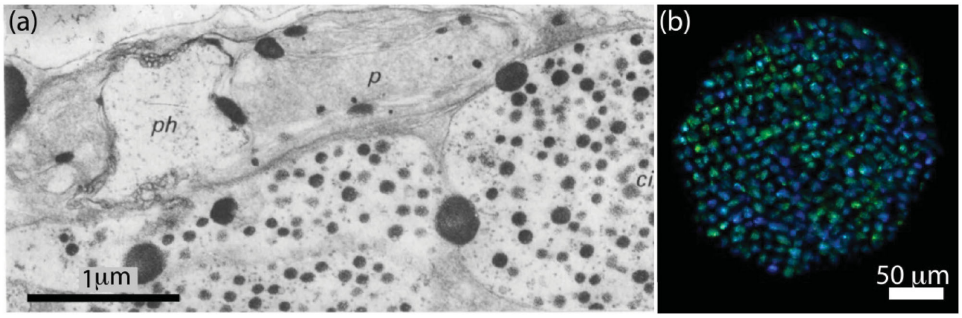

Figure 3. Structural color from iridescent bodies. a) TEM micrographs of iridescent bodies in *Cystoseira tamariscifolia*. Adapted with permission.[102] Copyright 1980, Company of Biologists; iridescent bodies (*ci*), physode (*ph*), plastid (*p*). b) Reflectivity image of a fresh *C. tamariscifolia* sample obtained with a water immersion objective 40× in epi-illumination configuration.

evolved multiple times. It has been shown that structural coloration has evolved independently several times in other taxa,[72] therefore iridescent bodies may have evolved independently in brown algae at a later date.

The physical basis behind the rather disordered iridescent bodies is different from standard multi-layered architectures for two main reasons (see also Figure 2). First, in the case of a multi-layered structure, the mechanism can be described along one direction in space with variation in the refractive index (which is responsible for the multiple reflection of light at the interface between the two materials), while in the case of iridescent bodies the architecture is fully three-dimensional (i.e., the variation of the refractive index is along all the three dimensions in space). Second, in the case of a multilayered structure, the variation of the reflective index is mostly periodic, while for iridescent bodies, the photonic structures are not perfectly periodic but they show a short-range order on length scales comparable to optical wavelengths. This point is particularly important because the use of the term "iridescence" is used to describe color that stems from periodic structures such as multi-layered structures or gratings,[16] but the use of this term should not be used when describing the optical response from the so called "iridescent bodies". Coloration originating from these bodies may not be strictly iridescent because the structure itself is not perfectly ordered,[73,74] although an iridescent or metallic effect may still be produced due to a slight color change from cell to cell giving an iridescent appearance (Figure 3b). Therefore, in this review we avoid the term iridescence for brown algae, i.e., a change in the hue or saturation of color upon variation in the viewing or illumination angle.

Table 1. Nanostructures reported in brown, red, and green macroalgae and evidence of their role in the production of structural color.

Division	Genus	Species	Naming Authority	Structural mechanism	Evidence	References
Phaeophyceae	*Cystoseira*	*amentacea* var. *stricta*	Montagne	iridescent bodies	–	[64,65]
Phaeophyceae	*Cystoseira*	*barbata*	(Stackhouse) C. Agardh	iridescent bodies	–	[104]
Phaeophyceae	*Cystoseira*	*crinita*	Duby	iridescent bodies	–	[58]
Phaeophyceae	*Cystoseira*	*tamariscifolia*	(Hudson) Papenfuss	iridescent bodies	+	[76]
Phaeophyceae	*Dictyota*	*dichotoma*	(Hudson) J. V. Lamouroux	iridescent bodies	–	[67,69]
Phaeophyceae	*Dictyota*	*diemensis*	Sonder ex Kützing	iridescent bodies	–	[70]
Phaeophyceae	*Zonaria*	*tournefortii*	(J. V. Lamouroux) Montagne	iridescent bodies	–	[71]
Rhodophyta	*Antithamnion*	*defectum*	Kylin	iridescent bodies	–	[105]
Rhodophyta	*Chondracanthus*	*exasperatus*	(Harvey & Bailey) Hughey	multi-layered cuticle	–	[106]
Rhodophyta	*Chondria*	*coerulescens*	(J. Agardh) Falkenberg	iridescent bodies	–	[52,107]
Rhodophyta	*Chondrus*	*crispus*	Stackhouse	multi-layered cuticle	+	[29]
Rhodophyta	*Chylocladia*	*verticillata*	(Lightfoot) Bliding	iridescent bodies	–	[108]
Rhodophyta	*Cottoniella*	*fusiformis*	Børgesen	iridescent bodies	–	[109]
Rhodophyta	*Gastroclonium*	*clavatum*	(Roth) Ardissone	iridescent bodies	–	[54]
Rhodophyta	*Iridaea*	*cordata*	(Turner) Bory de Saint-Vincent	multi-layered cuticle	+	[56]
Rhodophyta	*Mazzaella*	*flaccida*	(Setchell & N. L. Gardner) Fredericq	multi-layered cuticle	+	[56]
Rhodophyta	*Mazzaella*	*splendens*	(Setchell & N. L. Gardner) Fredericq	multi-layered cuticle	+	[56]
Chlorophyta	*Valonia*	*macrophysa*	Kützing	array of microfibrils	–	[110]
Chlorophyta	*Valonia*	*ventricosa*	J. Agardh	array of microfibrils	–	[111]

– = no evidence for the mechanism in the production of color; + = evidence for the mechanism in the production of color.

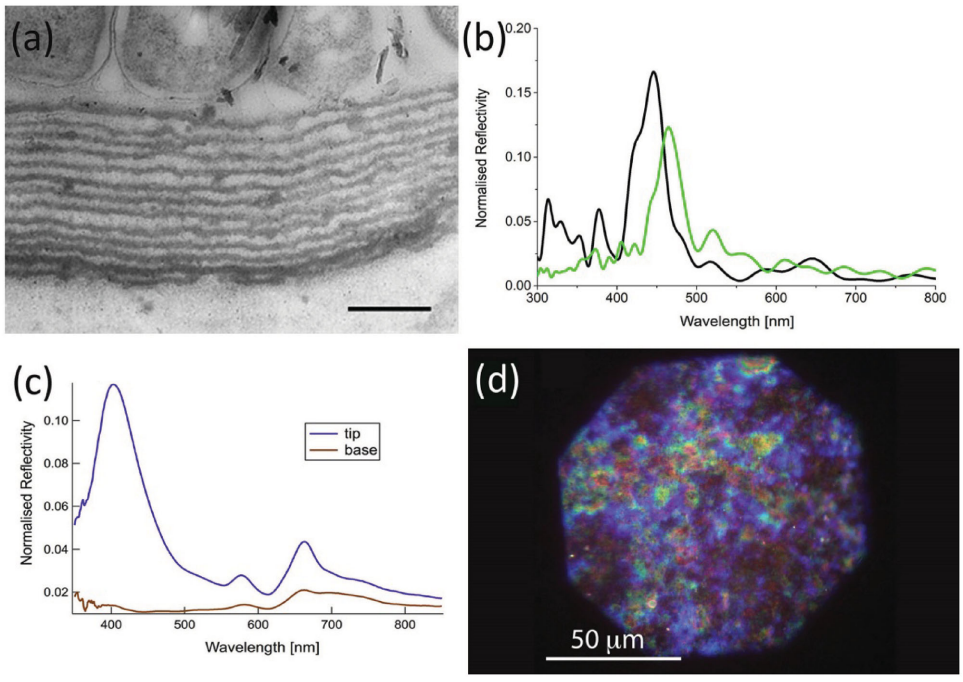

Figure 4. Optical analysis of *Chondrus crispus* a) TEM micrograph of cuticular multilayers, b) reflectance spectra results from FDTD simulations (green line represents simulation from structure in (a); black line represents simulation from another TEM image of the same structure). c) Reflectivity spectra from optical microscopy at the tip and base of the frond and d) optical image of structurally colored specimen. Adapted with permission.[29] Copyright 2015, Nature Publishing Group.

Despite the assumed role of iridescent bodies, there is no clear experimental evidence that correlates the optical appearance to the anatomy/ultrastructure. For a better understanding of this optical phenomenon, small-angle X-ray scattering (SAXS) measurements or TEM tomography combined with optical results would be essential to extract structural information. We speculate that such objects (Figure 3a) may act as coherent scatters that selectively reflect blue color.[74] Similar to the case of the quasi-ordered nanostructures found in bird feather barbs,[75] in algae it is possible to measure a short-range correlation in the position of the vacuoles,[76] however further studies are necessary to confirm this hypothesis.

In contrast, the physical principle of multi-layered structures, commonly referred to as Bragg stacks, is well reported. An example of this system has been shown to produce the blue coloration in the thalli of *Chondrus crispus* (**Figure 4**).[29] Such photonic structures can reflect, in specular direction, an intense color that overcomes the response from the pigment, and the color of the tissue appears to be strongly metallic (Figure 4d).

3. Visual Color Effect in Marine Algae

Interestingly, even if the production of structural color in red and brown algae is limited to two optical mechanisms, the visual effect produced by the organism can vary significantly, e.g., by creating different color responses and changing spatial patterns on the frond surface.[77] In red algae, color can vary between hues of blue and green. However, color often appears purple as a result of the underlying red pigmentation. In Irish Moss, *Chondrus crispus*, structural color is restricted to within 1.5 cm from the tips of the thalli (**Figure 5**g). In contrast, such color found in *Fauchea laciniata* is distributed across the entire frond and not within the area at the tips of the thalli (Figure 5h).

In brown algae, unique patterns of coloration can be seen within certain species of the Dictyotales. *Distromium flabellatum* exhibits structural colors that vary between blue and yellow-green and are often distributed to form a barcode-like appearance across the entire frond (Figure 5f). *D. humifusa* produces a bright blue color restricted to bands that traverse the thallus (Figure 5e).[78] Furthermore, *D. dichotoma* and *D. cyanoloma* can produce blue color restricted to the outer margins of the thalli (Figure 5b,c). We hypothesise that this restricted distribution is likely to be a result of sporangia distribution, as structurally colored margins are only found in fertile specimens whereas the whole thallus exhibits the blue coloration in non-fertile individuals (Figure 5i).[79]

In Fucales, structural color only occurs in *Cystoseira* spp. For example, in *C. tamariscifolia* the reflected coloration varies between strong blue, green and turquoise colors and occurs uniformly throughout the frond, except in juvenile specimens where such color can be confined to the tips of the thalli. Structural color originating from a three-dimensional structure will produce an omnidirectional optical effect appearing strongly colored from all angles in situ (Figure 5a).

4. Distribution and Ecology: the Case of Brown Algae

In brown algae, structural color is confined to two orders, Dictyotales and Fucales. Ancestors of Dictyotales (Sphacelariales and Syringodermatales) diverged from the rest of the brown algae in the Jurassic followed by the divergence of the

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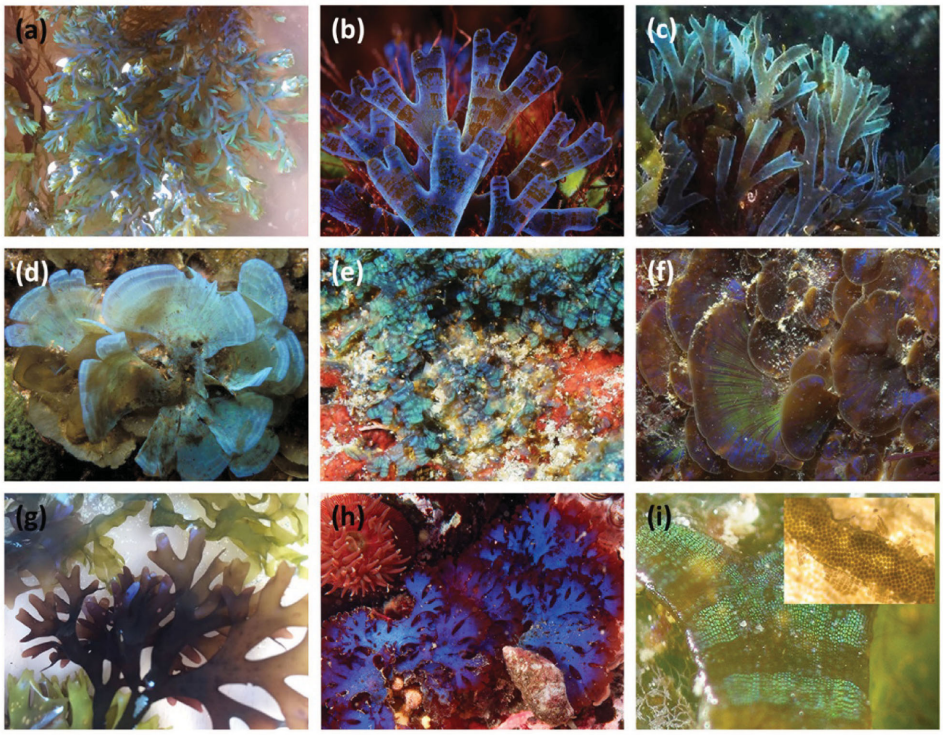

Figure 5. Structural coloration in a) *Cystoseira tamariscifolia* (Credit: Chris J. Chandler), b) *Dictyota dichotoma* (Credit: Gary Bell), c) *Dictyota cyanoloma* (Credit: Joana Aragay Soler), d) *Stypopodium zonale* (Credit: John Huisman), e) *Dictyota humifusa* (Credit: Robert Fenner), f) *Distromium flabellatum* (Credit: Julian Finn), g) *Chondrus cripus* (Credit: Chris J. Chandler), h) *Fauchea laciniata* (Credit: Ryan Murphy), i) Banded structural color on the surface of a *Dictyota* sp. (Inset: a band of non-structurally colored sporangia on the thallus surface of a *Dictyota* sp.) (Credit: John Huisman).

Dictyotales about 110 Mya. Fucales, the only other group to retain or independently evolve structural color, diverged more recently at the end of the Cretaceous, at ca. 65 Mya. The distribution of structurally colored brown algae was determined through an extensive literature search. Structural color in the different species was recorded throughout 10 geographical distributions (adapted from ref. [80]) and three water depths (intertidal, shallow subtidal to 20 m depth and deeper than 20 m). The presence or absence of structural color represents cases only where a species was recorded as structurally colored or nonstructurally colored in situ. For example, *Dictyota dichotoma* is often described as exhibiting such color and is widely distributed geographically, but only four cases were found where it had been recorded as structurally colored in situ (**Table 2**).

Structural color was found in 76 species of brown algae and these species varied widely in their latitudinal as well as longitudinal range. Structurally colored specimens were found to be mainly distributed throughout tropical waters, similar to the non-structurally colored species (**Figure 6**). However, large differences existed in the geographical range between some species. Both *Dictyota ciliolata* and *Dictyota phlyctaenodes* are structurally colored however *Dictyota ciliolata* was found to have a pantropical distribution,[81] whereas *Dictyota phlyctaenodes* occurred only in the shallow waters of Juan Fernandez Island off the coast of Chile.[82] Furthermore, clear differences in distribution are visible between *Cystoseira* spp. and *Dictyota* spp. (see Figure 6c,d). Restricted geographical ranges may be attributed to limitations in dispersal potential or a low ecological tolerance. All of these distributions are dependent on a well-defined concept of the species under study given the high incidence of cryptic diversity that is reported for the algae,[83] particularly in the case of species that are widely distributed. However, we can have confidence in the distribution of these species, such as *Dictyota ciliolata*, which has been subject to a recent taxonomic study.[81]

The majority of structurally colored brown algae occurred in shallow waters ($n = 123$) in comparison to deep waters ($n = 17$) and rock pools ($n = 46$). This may suggest a defense mechanism against high levels of radiation, although it has been shown that algae must be submerged in water in order to produce the necessary contrast in refractive index for structural color to occur. Therefore, considering a loss of structural color out of water, we would expect results to reflect a significantly lower number of cases of structural color in intertidal zones.

5. Functional Purpose

The function of structural color in marine algae remains experimentally unexplored. Previous studies have speculated on various functions of such color in the fronds of algae and the leaves of land plants, including photo-protective mechanisms to dissipate excessive levels of irradiance[84] and the use of angle-dependent coloration as a predator deterrent.[56]

Very few species were found to be structurally colored in deep (>20 m) water, suggesting that structural color may

Table 2. Structurally colored brown algae and the evidence of color or no color, globally.

Genus	Species	Af	Eu	Ind	As	Aus	Na	Ca	Sa	Atl	Pac
Cystoseira	*abies-marina*										
Cystoseira	*algeriensis*										
Cystoseira	*amentacea*										
Cystoseira	*amentacea* var. *stricta*										
Cystoseira	*baccata*										
Cystoseira	*barbata*										
Cystoseira	*brachycarpa*										
Cystoseira	*crinita*										
Cystoseira	*crinitophylla*										
Cystoseira	*elegans*										
Cystoseira	*funkii*										
Cystoseira	*humilis*										
Cystoseira	*spinosa* var. *tenuior*										
Cystoseira	*mediterranea*										
Cystoseira	*nodicaulis*										
Cystoseira	*sauvageauana*										
Cystoseira	*tamariscifolia*										
Cystoseira	*usneoides*										
Canistrocarpus	*cervicornis*										
Canistrocarpus	*magneanus*										
Dictyopteris	*delicatula*										
Dictyopteris	*dichotoma*										
Dictyopteris	*justii*										
Dictyopteris	*repens*										
Dictyopteris	*undulata*										
Dictyota	*adnata*										
Dictyota	*bartayresiana*										
Dictyota	*canaliculata*										
Dictyota	*ceylanica*										
Dictyota	*ciliolata*										
Dictyota	*crenulata (#1)*										
Dictyota	*#2 (canariensis)*										
Dictyota	*cyanoloma*										
Dictyota	*cymatophila*										
Dictyota	*dichotoma*										
Dictyota	*dichotoma* var. *intricata*										
Dictyota	*flabellata*										
Dictyota	*friabilis*										
Dictyota	*grossedentata*										
Dictyota	*hamifera*										
Dictyota	*humifusa*										

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Table 2. Continued.

Genus	Species	Af	Eu	Ind	As	Aus	Na	Ca	Sa	Atl	Pac
Dictyota	*implexa*										
Dictyota	*liturata*										
Dictyota	*mertensii*										
Dictyota	*naevosa*										
Dictyota	*ocellata*										
Dictyota	*phlyctaenodes*										
Dictyota	*pinnatifida*										
Dictyota	*pulchella*										
Dictyota	*rigida*										
Dictyota	*sandvicensis*										
Dictyota	*serrulata*										
Dictyota	*spiralis*										
Dictyota	*stolonifera*										
Distromium	*flabellatum*										
Distromium	*skottsbergii*										
Exallosorus	*harveyanus*										
Lobophora	*variegata*										
Lobophora	*papenfussii*										
Lobospira	*bicuspidata*										
Padina	*boergesenii*										
Padina	*pavonica*										
Padina	*profunda*										
Rugulopteryx	*okamurae*										
Spatoglossum	*schroederi*										
Spatoglossum	*macrodontum*										
Stypopodium	*australasicum*										
Stypopodium	*flabelliforme*										
Stypopodium	*multipartitum*										
Stypopodium	*rabdoides*										
Stypopodium	*schimperi*										
Stypopodium	*zonale*										
Taonia	*abbottiana*										
Zonaria	*diesingiana*										
Zonaria	*tournefortii*										
Zonaria	*zonata*										

Evidence for structural colour	
Evidence for no structural colour	
Evidence for both structural colour and no structural colour	
Presence	
Absence	

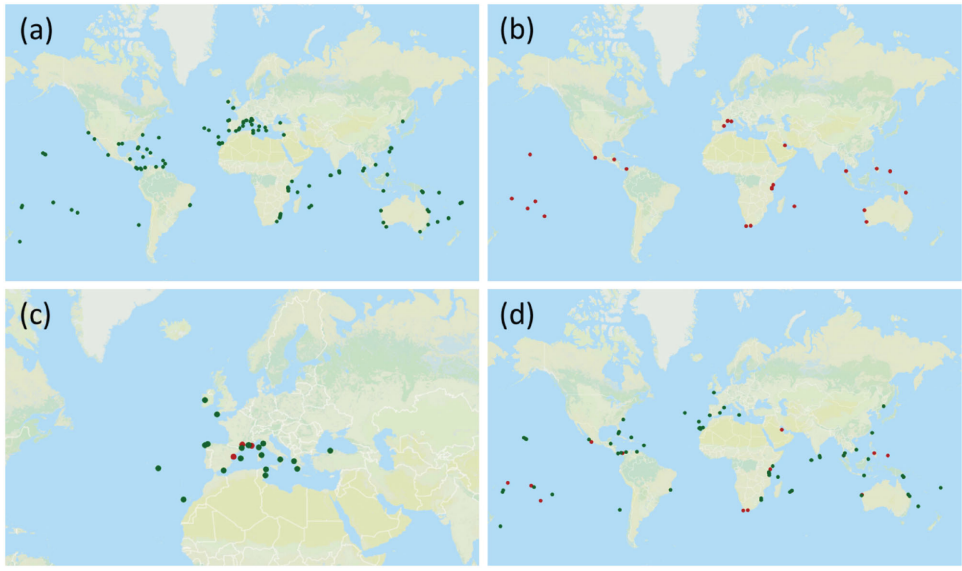

Figure 6. Distribution of structurally colored brown algae and evidence of individuals with no structural color present. a) Evidence of structurally colored brown algae, 76 species ($n = 129$); b) evidence of brown algae where structural color was absent ($n = 29$); c) distribution of structurally colored *Cystoseira* sp. and d) distribution of structurally colored *Dictyota* sp. Green represents a structurally colored individual and red represents a case where there is an absence of structural color.

function to provide protection against high levels of solar radiation in shallow subtidal areas or intertidal rock pools. Macroalgae generally experience levels of photosynthetically active levels of radiation (PAR) that are far in excess of those needed to saturate photosynthesis, especially during the summer months.[85] Therefore, they must protect themselves to avoid photo-damage, particularly in the shallow subtidal and intertidal zones.[86] Macroalgae will be photo-adapted during long term selection. In addition, they have well-developed systems for dissipating energy, including photo-acclimation, a plastic response where e.g., pigments are added or removed, and photo-regulation, e.g., non photochemical quenching via the xanthophyll cycle.[87] Nevertheless, photo-inhibition, whereby excess photons become inhibiting or even damaging to the photosystem complexes, can occur.[88] Therefore, mechanisms such as structural color may offer a physical means whereby the total amount of photo-stress is reduced due to reflecting particularly high-energy photons. Furthermore, it has been shown that such mechanisms can be very efficient in reducing absorption in the blue-UV region, such as in the case of multi-layered structures, with light reflectance of ≈20%.[29] Therefore, the use of photonic structures that reflect blue-UV specific light may provide a useful adaptation to reducing excessive levels of radiation.

Moreover, since structural color is often confined to the growing tips, it may function as an additional photo-protective mechanism during the early stages of growth. A photo-protective mechanism used by intertidal seaweeds includes phlorotannins, which are polyphenolic compounds located in the physodes (membrane bound, spherical bodies) of brown algae, and provide photo-protection for intertidal seaweeds amongst other things.[89–91] Phlorotanins absorb radiation between wavelengths of 190–400 nm, with some absorption occurring within the visible part of the spectrum,[92,93] and thus may reduce excessive UV radiation and high PAR.[90] In the brown alga *Lessonia nigrescens*, a positive relationship was demonstrated between the production of insoluble phlorotannins during summer, and suppression of photoinhibition and DNA damage. The transition of soluble to insoluble phlorotannins was related to growth requirements as active blade elongation occurred during that season.[91] Considering multiple defense mechanisms are common in plants and no negative association has been shown between multiple defensive traits and resource investment,[94] the combination of high phlorotannins and structural coloration may provide an advantage over other species in high light environments, as supported by the extensive speciation and widespread distribution of *Dictyota* spp.

Another hypothesis for the function of structural color is a defense mechanism against predators. Fish are primary grazing predators as well as a range of crustaceans including krill, shrimp and crabs for algae. Considering fish photoreceptors are limited to blue or UV light,[95] the structural color effect could act as a visual defense against potential prey. For example, banded structural color patterns found in *Dictyota* spp. (Figure 5i) may function to mask the true identity of the algae thus confusing potential prey.[96] Similarly, blue coloration can be lost when viewed from one angle but appear vivid when viewed from another, as observed in the red alga *Chondrus crispus,* potentially startling prey. However, in some structurally colored *Cystoseira* spp., such as *C. tamariscifolia*, color is consistently vivid from all angles as well as more evenly distributed across the length of the frond. Therefore, it seems possible that the function of structural color may differ between genera. It could also be hypothesized that structural color to deter predators is related to levels of secondary metabolites in brown algae. The brown algae produce a wide array of secondary metabolites,[97] for example, Dictyotales produce diterpene metabolites that are known to inhibit feeding by several herbivore species.[98,99] However, chemical defense is reported to differ in different

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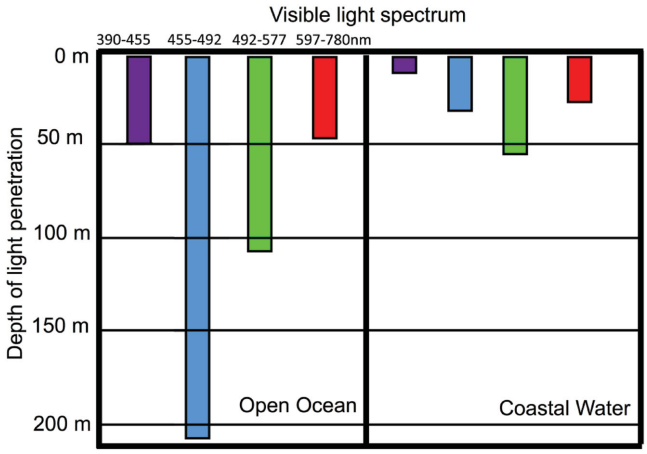

Figure 7. The penetration depth of the visible light spectrum in clear oceanic waters compared with turbid coastal waters. Adapted with permission.[103] Copyright 2016, NOAA Ocean Explorer.

geographical regions and certain metabolites deter some grazers but not others,[97,99] in which case the role of structural color may act as a secondary defense against predators when levels of metabolites are not sufficient to deter certain grazers.

Although much less commonly reported from deeper water, there are a number of species that are found to be structurally colored in deep waters (>20 m). In the intertidal, it is highly likely that the reflection of blue light is necessary in order to reduce excessive radiation, especially in the summer months. It is possible that species would still be compromised by UV radiation at greater depths in clear water: at 30 m in pure water, ca. 74% UV blue remains (the coefficient of absorption is 10^{-4} (cm^{-1}) in the near UV-blue region). Therefore, reflection of blue light would still be necessary to reduce the level of radiation found in clear, low-nutrient, oceanic waters (**Figure 7**). In more turbid, coastal waters, UV-blue light is rapidly attenuated by absorption and scattering from e.g., chlorophyll (phytoplankton), nutrients, sediments and dissolved organic matter which are in greater abundance from an increase in land run-off.[100]

It can therefore be hypothesized that structural color functions to manage appropriate levels of radiation absorption in both the intertidal and subtidal environments. Furthermore, the distribution of structurally colored individuals may be heavily influenced by the level of radiation as well as, on the local scale, water conditions that can significantly alter the depth to which blue-UV light can penetrate. Conversely, in deeper waters where blue light is reduced, and considering blue light is important for photosynthesis and plant development, structural color may function to provide available photons to photosynthetically active parts of the fronds that would otherwise be unable to capture light.

6. Conclusions and Future Directions

This progress report of structural color in marine algae provides new insights into this phenomenon and lays the foundation for future work in this largely unexplored topic. Structural color is reported only in red and brown algae and we found that two mechanisms are responsible for structural color. We found that iridescent bodies are the only photonic structure present in brown algae. However, the presence of these bodies in the red algae raises questions as to whether they have evolved more than once and whether they are of bacterial origin. In addition, discovery of the genetic basis for the iridescent bodies will enable comparative studies to find genes in both brown and red algae, which do not exhibit structural color. Experimental evidence is also required to test the function of structural color as a photoprotective mechanism against UV radiation or as a defense mechanism against predators. Therefore, future work needs to address both experimental and genetic problems to understand the biological significance of structural color in marine algae. Such findings have the potential to reveal novel adaptation strategies useful in relation to a changing climate as well as increasing our understanding of structural color in nature as a whole.

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