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Structural colour in marine algae

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Structural colouration is widespread in the marine environment. Within the large variety of marine organisms, macroalgae represent a diverse group of more than 24,700 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 colour in algae and provide a discussion on the functional relevance by analysing the geographical distribution and ecology in detail. In contrast to what is observed in the animal kingdom, we hypothesise that structural colour 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 colour in algae is likely influenced by local factors such as radiation intensity and turbidity of the water.

1. Introduction

Structural colours are the result of the interaction of light with nanostructured materials. Such nanostructures, with features on the mesoscale (i.e. ~100nm), are capable of producing vivid, saturated colours 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 colours [4, 5] to bright whites [6]. In nature, structural colour 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 fruits [22, 23]), bacteria [24], fungi [25], slime moulds [26], viruses [27], diatoms [28] and macroalgae [29]. The biological significance of structural colour is mainly studied and understood in insects [30, 31] and animals [32, 33] in terms of intra- and inter-specific communication [34], mate attraction [35] and predator deterrent [33, 36-38]. In flowers, structural colour is hypothesized to function in relation to attracting potential pollinators [20]. However, in organisms such as algae the function of structural colour remains unclear.

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 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 [41] **(Figure 1)**.

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 colour may reveal adaptation strategies useful in relation to global environmental change. For example, similarly to leaves [50, 51], structural colour in algae may serve to protect species from ultraviolet radiation which may be beneficial considering continual ozone damage. Assuming this hypothesis, structural colour may be useful in predicting marine species composition in the future.

Despite the lack of understanding on the biological purpose of structural colour, marine algae have received very little attention within this field, most likely as their colours 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 colour 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 colour is produced by a multi-layered structure in the cuticle with refractive-index periodicity [29]. Furthermore, virtually no studies have attempted to investigate the vivid and diverse array of structural colour 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 colour [54], however there is no clear experimental evidence that correlates these bodies with the optical appearance.

In this review, we describe the mechanisms of colour production in marine algae and compare them to those observed in land plants. Moreover, focusing on the specific 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 colouration may provide.

2. Physical mechanism of structural colouration in marine algae

Structural mechanisms capable of producing colour 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 of structural colour in algae. Firstly, extracellular multi-layered 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 coloured *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 polysacharides 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 colour in brown algae revealed ‘globules responsible for iridescence’ [59]. Subsequent attempts to clarify the mechanisms responsible for this structural colour 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 evolved multiple times. It has been shown that structural colouration 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 multi-layered 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 colour 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'. Colouration 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 colour 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 of colour upon variation in the viewing or illumination angle.

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 colour [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 colouration in the thalli of *Chondrus crispus* [29] (**Figure 4**). Such photonic structures can reflect, in specular direction, an intense colour that overcomes the response from the pigment, and the colour of the tissue appears to be strongly metallic (Figure 4d).

3. Visual colour effect in marine algae

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

In brown algae, unique patterns of colouration can be seen within certain species of the Dictyotales. *Distromium flabellatum* exhibits structural colours that vary between blue and yellow-green and are often distributed to form a barcode-like appearance across the entire frond (Figure 5*f*). *D. humifusa* produces a bright blue colour restricted to bands that traverse

the thallus (Figure 5*e*) [78]. Furthermore, *D. dichotoma* and *D. cyanoloma* can produce blue colour restricted to the outer margins of the thalli (Figure 5*b,c*). We hypothesise that this restricted distribution is likely to be a result of sporangia distribution, as structurally coloured margins are only found in fertile specimens whereas the whole thallus exhibits the blue colouration in non-fertile individuals (Figure 5*i*) [79].

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

4. Distribution and ecology: the case of brown algae

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

Structural colour was found in 76 species of brown algae and these species varied widely in their latitudinal as well as longitudinal range. Structurally coloured specimens were found to be mainly distributed throughout tropical waters, similar to the non-structurally coloured species (Figure 6). However, large differences existed in the geographical range between some species. Both *Dictyota ciliolata* and *Dictyota phlyctaenodes* are structurally coloured 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 and 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 coloured brown algae occurred in shallow waters (n = 123) in comparison to deep waters (n = 17) and rock pools (n = 46). This may suggest a defence 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 colour to occur, therefore considering a loss of structural colour out of water, we would expect results to reflect a significantly lower number of cases of structural colour in intertidal zones.

5. Functional purpose

The function of structural colour in marine algae remains experimentally unexplored. Previous studies have speculated on various functions of such colour 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 colouration as a predator deterrent [56].

Very few species were found to be structurally coloured in deep (> 20 m) water, suggesting that structural colour may function to provide protection against high levels of solar radiation in shallow subtidal areas or intertidal rock pools. Macroalgae generally experience levels of PAR (Photosynthetically Active Levels of Radiation) 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 of light become inhibiting or even damaging to the photosystem complexes, can occur [88]. Therefore, mechanisms such as structural colour 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 colour 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 include 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 photo-inhibition 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 defence 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 colouration 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 colour is a defence 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 colour effect could act as a visual defence against potential prey. For example, banded structural colour patterns found in *Dictyota* spp. (Figure 5i) may function to mask the true identity of the algae thus confusing potential prey [96]. Similarly, blue colouration 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 coloured *Cystoseira* spp., such as *C. tamariscifolia*, colour 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 colour may differ between genera. It could also be hypothesised that structural colour 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 defence is reported to differ in different geographical regions and certain metabolites deter some grazers but not others [97, 99]. In which case the role of structural colour may act as a secondary defence 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 coloured 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 hypothesised that structural colour functions to manage appropriate levels of radiation absorption in both the intertidal and subtidal environments. Furthermore, the distribution of structurally coloured 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 colour may function to re-direct the available light to photosynthetically active parts of the fronds that would otherwise be unable to capture light.

6. Conclusions and future directions

This review of structural colour in marine algae provides a new insight into this phenomenon and lays the foundation for future work in this largely unexplored topic. Structural colour is reported only in red and brown algae and we found that two mechanisms are responsible for structural colour. We find 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 colour. Experimental evidence is also required to test the function of structural colour as a photoprotective mechanism against UV radiation or as a defence mechanism against predators. Therefore, future work needs to address both experimental and genetic problems to understand the biological significance of structural colour 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 colour in nature as a whole.

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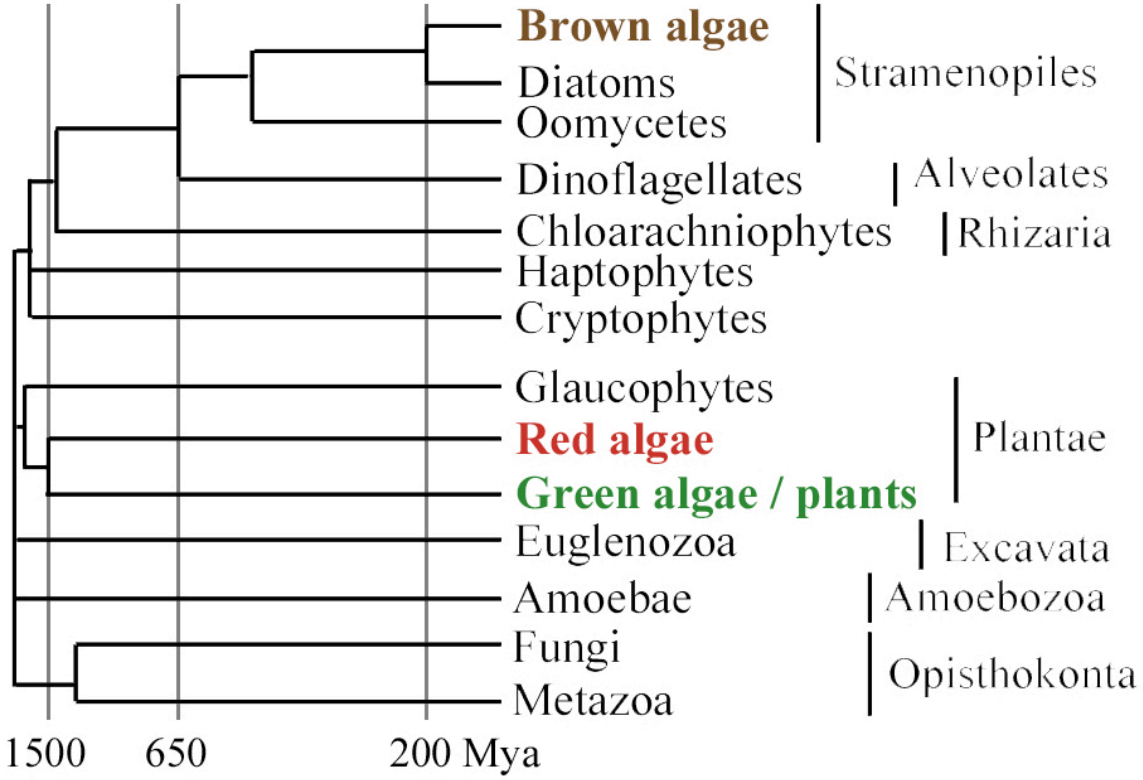

Figure 1. Evolutionary tree of the eukaryotes showing the position of red, green and brown algae and the time of divergence of red algae, dinoflagellates and brown algae (Adapted with permission from [101], 2004, The American Society of Naturalists).

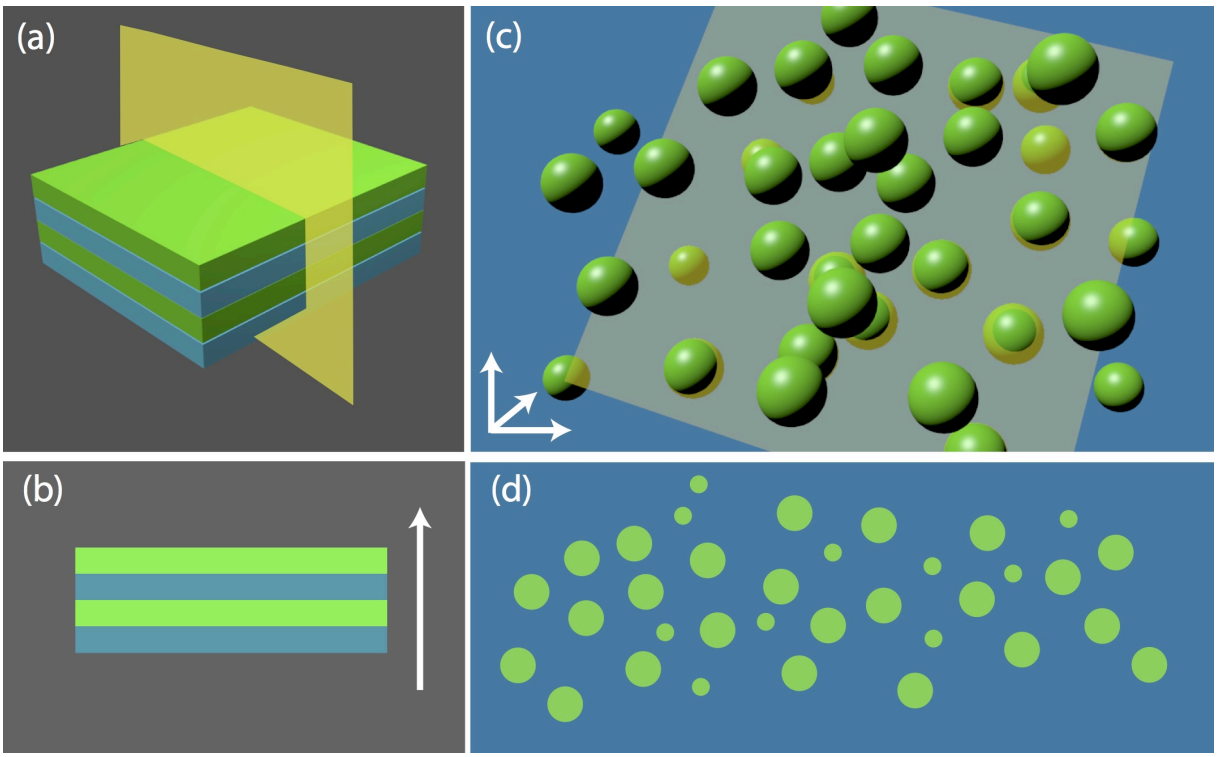

Figure 2. Schematic representation of the common ultrastructures responsible for structural colour in algae: a) a multi-layered structure and (b) the corresponding cross section. In the case of a periodic multilayer structure, the sectioning can give artefacts only when we measure the thickness of the 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 characterisation.

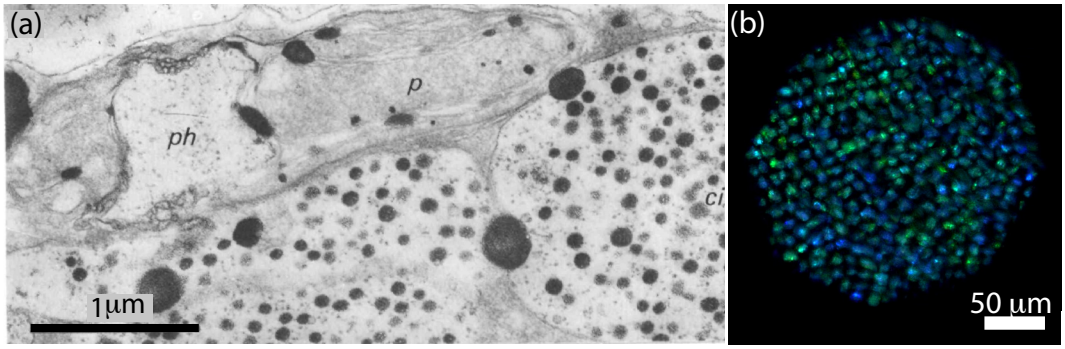

Figure 3. Structural colour from iridescent bodies. (a) TEM micrographs of iridescent bodies in *Cystoseira tamariscifolia,* adapted with permission from [102]; iridescent bodies (*ci*), physode (*ph*), plastid (*p*). (b) Reflectivity image of a fresh *C. tamariscifolia* sample obtained with a water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

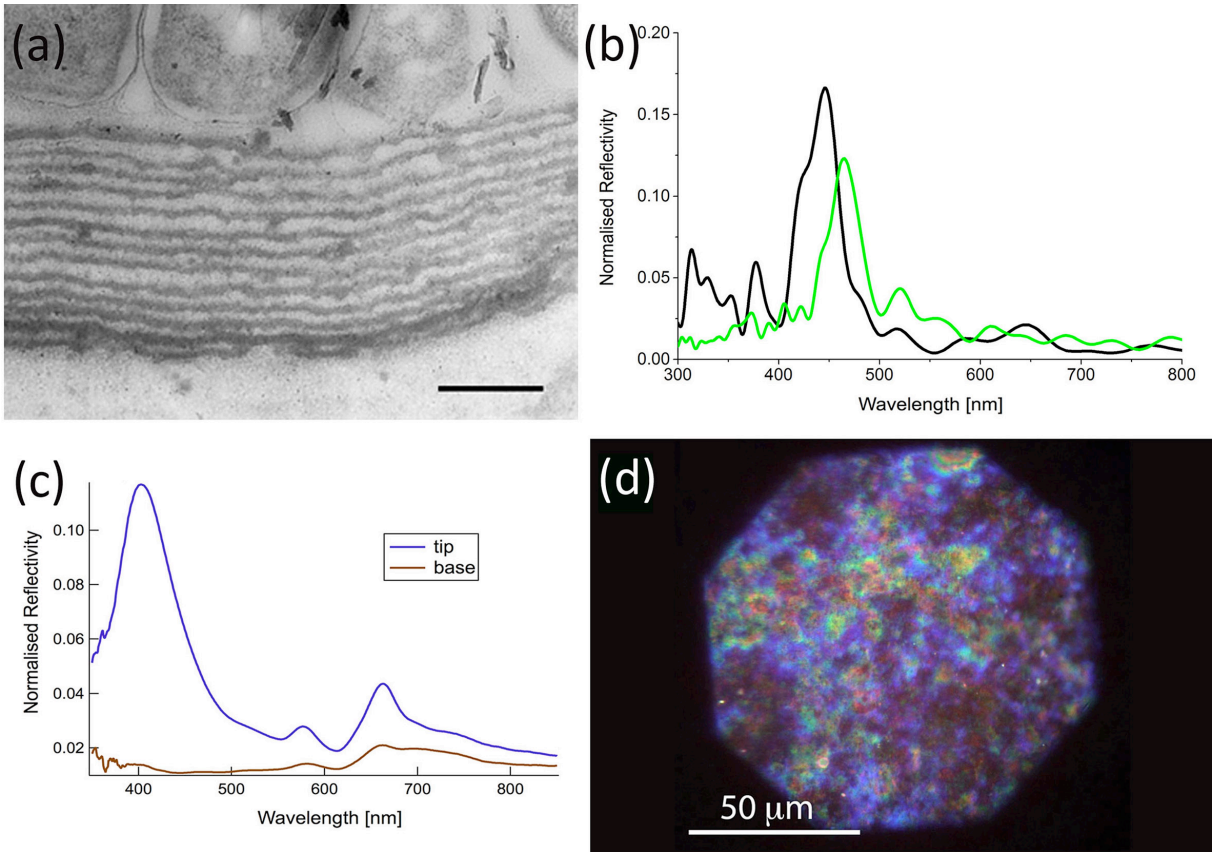

Figure 4. Optical analysis of *Chondrus crispus* (a) TEM micrograph of cuticular multi-layers, (b) reflectance spectra results from FDTD simulations from two different TEM images (green line for structure in figure 4a; black line for another TEM image of the same structure, (c) reflectivity spectra from optical microscopy at the tip and base of the frond and d) optical image of structurally coloured specimen (Adapted with permission [29], 2015, Nature Publishing Group).

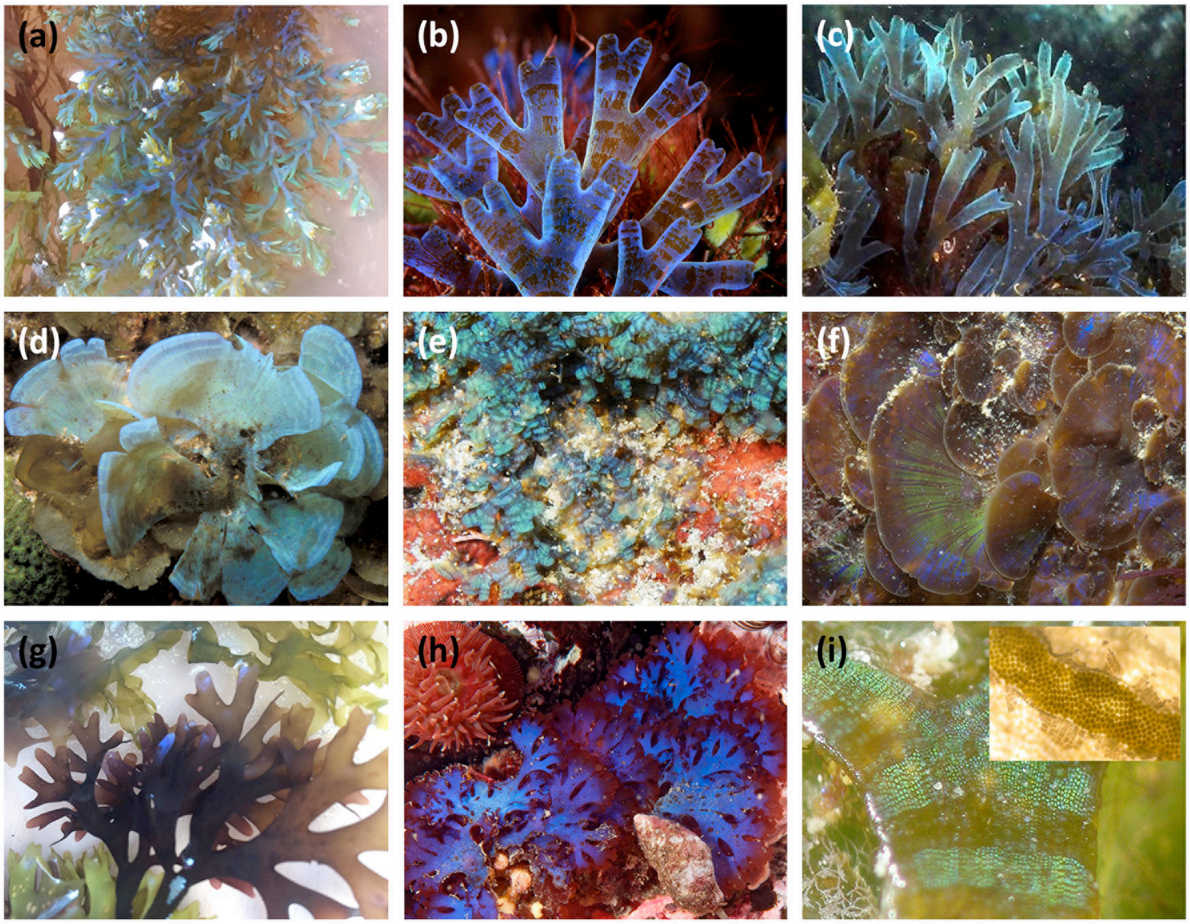

Figure 5. Structural colouration in (a) *Cystoseira tamariscifolia,* (b) *Dictyota dichotoma*, (c) *Dictyota cyanoloma*, (d) *Stypopodium zonale*, (e) *Dictyota humifusa*, (f) *Distromium flabellatum*, (g) *Chondrus cripus*, (h) *Fauchea laciniata*, (i) Banded structural colour on the surface of a *Dictyota* sp. (Inset: a band of non-structurally coloured sporangia on the thallus surface of a *Dictyota* sp.).

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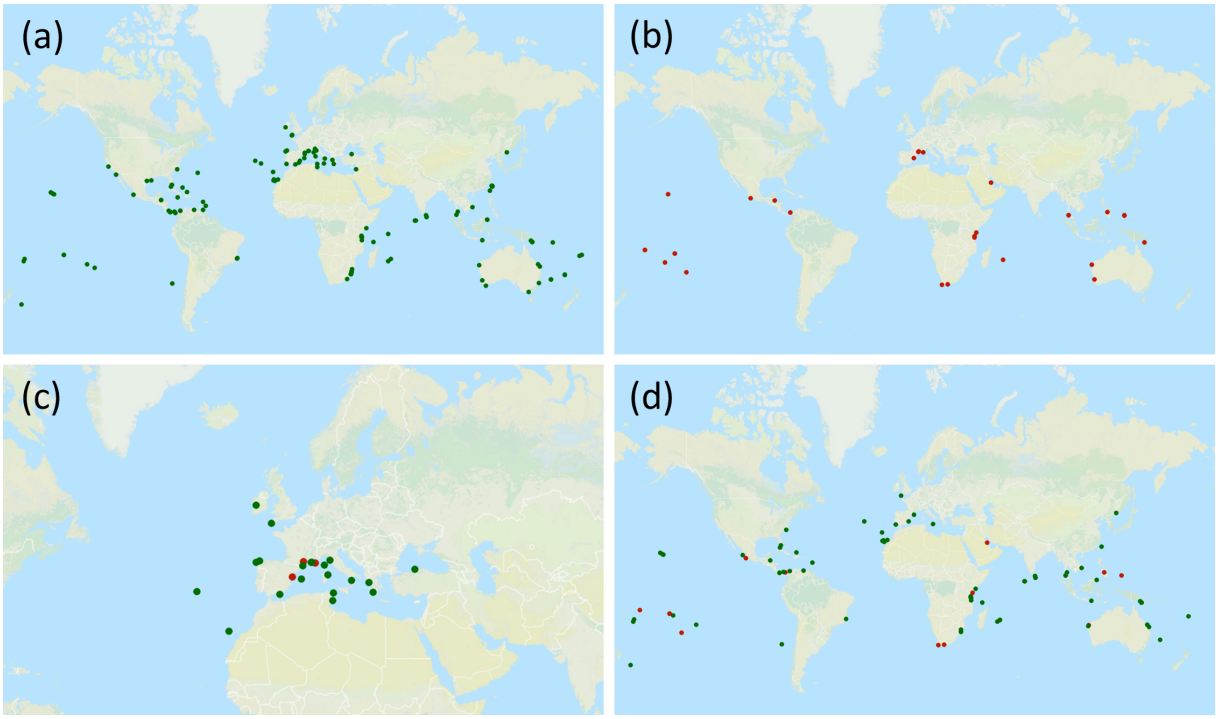

Figure 6. Distribution of structurally coloured brown algae and evidence of individuals with no structural colour present. (a) Evidence of structurally coloured brown algae, 76 species (n = 129); (b) evidence of brown algae where structural colour was absent (n = 29); (c) distribution of structurally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

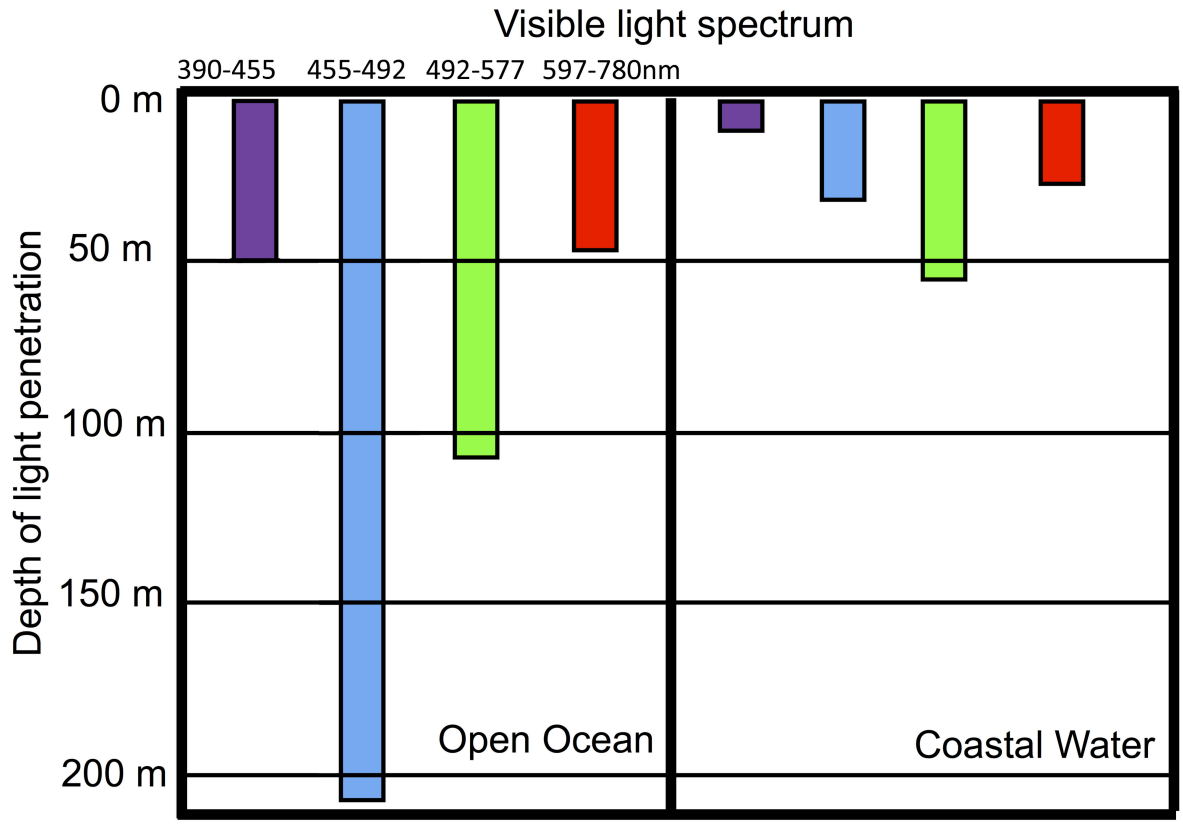

Figure 7. The penetration depth of the visible light spectrum in clear oceanic waters compared with turbid coastal waters. (Modified with permission [103], 2016, NOAA Ocean Explorer).

Table 1. Nano-structures reported in brown, red and green macroalgae and evidence of their role in the production of structural colour.

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 colour; + = evidence for the mechanism in the production of colour.

Table 2. Structurally coloured brown algae and the evidence of colour or no colour, 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*										
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

Af, Africa; Eu, Europe; Ind, Indian Ocean; As, Asia; Aus, Australasia; Na, North America; Ca, Central America; Sa, South America; Atl, Atlantic Ocean; Pac, Pacific Ocean.

Marine algae feature complex photonic structures to manage and reflect incident light. We here review the photonic mechanisms of these marine plants and discuss the geographical distribution, ecology and phylogenetic placement of structurally coloured brown algae as well as their general influence on the global marine ecosystem.