

Ecophysiology of photosynthesis in macroalgae

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Abstract Macroalgae occur in the marine benthos from the upper intertidal to depths of more than 200 m, contributing up to 1 Pg C per year to global primary productivity. Freshwater macroalgae are mainly green (Chlorophyta) with some red (Rhodophyta) and a small contribution of brown (Phaeophyceae) algae, while in the ocean all three higher taxa are important. Attempts to relate the depth distribution of three higher taxa of marine macroalgae to their photosynthetic light use through their pigmentation in relation to variations in spectral quality of photosynthetically active radiation (PAR) with depth (complementary chromatic adaptation) and optical thickness (package effect) have been relatively unsuccessful. The presence (Chlorophyta, Phaeophyceae) or absence (Rhodophyta) of a xanthophyll cycle is also not well correlated with depth distribution of marine algae. The relative absence of freshwater brown algae does not seem to be related to their photosynthetic light use. Photosynthetic inorganic carbon acquisition in some red and a few green macroalgae involves entry of CO₂ by diffusion. Other red and green macroalgae, and brown macroalgae, have CO₂ concentrating mechanisms; these frequently involve acid and alkaline zones on the surface of the alga with CO₂ (produced from HCO₃[−]) entering in the acid

zones, while some macroalgae have CCMs based on active influx of HCO₃[−]. These various mechanisms of carbon acquisition have different responses to the thickness of the diffusion boundary layer, which is determined by macroalgal morphology and water velocity. Energetic predictions that macroalgae growing at or near the lower limit of PAR for growth should rely on diffusive CO₂ entry without acid and alkaline zones, and on NH₄⁺ rather than NO₃[−] as nitrogen source, are only partially borne out by observation. The impact of global environmental change on marine macroalgae mainly relates to ocean acidification and warming with shoaling of the thermocline and decreased nutrient flux to the upper mixed layer. Predictions of the impact on macroalgae requires further experiments on interactions among increased inorganic carbon, increased temperature and decreased nitrogen and phosphorus supply, and, when possible, studies of genetic adaptation to environmental change.

Keywords CO₂ concentrating mechanism · Chlorophyta · Complementary chromatic adaptation · Diffusive CO₂ entry · Phaeophyceae · Photoinhibition · Rhodophyta

Abbreviations

CA	Carbonic anhydrase
CAM	Crassulacean acid metabolism
CCN	Complementary chromatic adaptation
CCM	CO ₂ Concentrating mechanism
DBL	Diffusion boundary layer
DIDS	4,4'-Diisothiocyano-2,2'-stibene disulfonic acid
PAR	Photosynthetically active radiation
PEPc	Phosphoenolpyruvate carboxylase
PEPck	Phosphoenolpyruvate carboxykinase
Rubisco	Ribulose biphosphate carboxylase oxygenase
UVA	Ultraviolet A

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UBB Ultraviolet B
UVR Ultraviolet radiation

Introduction

Macroalgae were, and are, by no means Barry Osmond's major research interest, but he has published on responses of marine macroalgae to variations in photosynthetically active radiation (PAR) and inorganic carbon availability, and on effects of O₂ concentration. The PAR study on the marine macroalga *Ulva* dealt with high PAR and photoinhibition (Osmond et al. 1993), and also on the effect of tissue N status on photoacclimation (Henley et al. 1991). The finding of inhibition by higher O₂ concentration of photosynthetic O₂ production by a number of marine macroalgae (Downton et al. 1976) contrasts with the findings of another group studying O₂ effects on ¹⁴CO₂ assimilation in photosynthesis in many of the same organisms from the same location (Black et al. 1976). Barry also studied on inorganic carbon acquisition, including a search for Crassulacean acid metabolism (CAM) in some seaweeds from Beaufort, NC (Raven and Osmond 1992), and had previously studied on CAM in the amphibious lycopod *Stylites* (= *Isoetes*) *andicola* (Keeley et al. 1984). Also not involving algae, Barry's study on the effect of water flow on the natural abundance of stable C isotopes in freshwater embryophytes (Osmond et al. 1981) was relevant to the effects of boundary layers (Smith and Walker 1980). His insights on the ecophysiology of land plants clearly also have implications for the ecophysiology of macroalgae.

Cardoll and Franck (2010) point out that the greatest diversity of photosynthesis occurs in the eukaryotic algae. Among these, the macroalgae, however defined, are a subset of the eukaryotic algae, defined here as an alga with

the largest linear dimension attained of at least 1 mm. This definition includes some phytoplankton organisms such as the colonial marine prymnesiophycean *Phaeocystis* and the motile multicellular chlorophycean *Volvox*, so we add 'normally benthic' to accord with what most scientists would regard as macroalgae. The marine macroalgae comprise red (Rhodophyta: Bangiophyceae and Florideophyceae), green (Chlorophyta, mainly Ulvophyceae, a few Trebouxiophyceae and a few Streptophyta: Charophyceae in brackish waters) and brown (Heterokontophyta: Phaeophyceae) algae (Table 1). New lineages of marine macroalgae are still being discovered (Zechman et al. 2010). In freshwaters there are red (mainly Florideophyceae), green (Charophyceae, Chlorophyceae, Trebouxiophyceae, Ulvophyceae) and a few brown algae, as well as the chrysophycean (Heterokontophyta) *Hydrurus* (Klaveness and Lindstram 2011) and the tribophyceans (Heterokontophyta) *Botrydium* and *Vaucheria* (the latter also in brackish waters) (Table 1). As for marine macroalgae, photosynthetically interesting new freshwater macroalgae are still being discovered (Entwistle 1989; Vis et al. 2008). Despite this diversity, only a minority of eukaryotic algal classes have macroalgal representatives (van den Hoek et al. 1995; Falkowski and Raven 2007; Graham et al. 2009).

The phylogenetic diversity of macroalgae has important implications for our understanding of pigmentation, the form of Rubisco (ribulose-1,5-bisphosphate carboxylase-oxygenase) which is present, and the organisms' structure (complex acellular or multicellular) with different degrees of complexities as indicated by number of kinds of cells (Raven 1981, 1984a, b, 2003b; van den Hoek et al. 1995; Bell and Mooers 1997; Falkowski and Raven 2007; Sand-Jensen et al. 2007; Graham et al. 2009) (Table 1). Macroalgae are found in both marine and inland waters, usually as benthic haptophytes, but a few benthic rhizophytes or as free-floating pleustophytes [see Lüther (1949) and Raven

Table 1 The phylogenetic range, habitat, structure, Rubisco form, photosynthetic pigments and xanthophyll cycle of macroalgae

Kingdom	Phylum	Class	Habitat	Structure	Rubisco	Pigments	Xanthophyll cycle
Archaeplastida	Rhodophyta	Bangiophyceae	sw > fw	M	Form ID	Chl a, PB	None
Archaeplastida	Rhodophyta	Florideophyceae	sw > fw	M	Form ID	Chl a, PB	None
Archaeplastida	Chlorophyta	Chlorophyceae	fw, t	M, A	Form IB	Chls a, b	v-a-z
Archaeplastida	Chlorophyta	Trebouxiophyceae	sw, fw, t	M	Form IB	Chls a, b	v-a-z
Archaeplastida	Chlorophyta	Ulvophyceae	sw > fw > t	A, M	Form IB	Chls a, b	v-a-z
Archaeplastida	Streptophyta	Charophyceae	fw, bw	M	Form IB	Chls a, b	v-a-z
Chromista	Ochrophyta	Chrysophyceae	fw	M	Form ID	Chls a, c	dt-dd
Chromista	Ochrophyta	Fucophyceae	sw ≫ fw	M	Form ID	Chls a, c	v-a-z
Chromista	Ochrophyta	Tribophyceae	fw, bw	A	Form ID	Chls a, c	dt-dd

From data in van den Hoek et al. (1995), Falkowski and Raven (2007), Graham et al. (2009), Goss and Jakob (2010), and Schubert et al. (2011) *bw* brackish water, *fw* freshwater, *sw* seawater, *A* acellular, *M* multicellular, *a* antheraxanthin, *dd* diadinoxanthin, *dt* diatoxanthin, *v* violaxanthin, *z* zeaxanthin

(1991, 2003a) for definition of haptophytes, rhizophytes, pleustophytes]. Competition with aquatic embryophytes mainly concerns rhizophytes; there are only a few haptophytic seagrasses (e.g. *Phyllospadix*) or freshwater vascular macrophytes (Podostemaceae) but more haptophytic submersed bryophytes (Raven 1991).

Why be a macroalga, when macroalgae generally have lower specific growth rates, a frequently used proxy for evolutionary fitness, than microalgae? It must be borne in mind that there are substantial ranges of specific growth rates among both microalgae and macroalgae which can be related to evolutionary strategies (Lapointe and Tenore 1981; Shepherd 1981; Raven 1984b; Reynolds 1984; Henley and Ramus 1989; Nielsen and Sand-Jensen 1990; Henley et al. 1991; Raven and Taylor 2003; Flynn 2009). The fastest-growing macroalgae (*Ulva* spp.) have specific growth rates of up to 0.5 per day at about 20 °C, presumably related to a low degree of differentiation so that most of the thallus cells undergo cell division (Lapointe and Tenore 1981; Henley and Ramus 1989; Henley et al. 1991).

For the macroalgae with more differentiation and localized growth (Bell and Mooers 1997) there is no universal ‘explanation’ for their large size at reproductive maturity, but in a number of cases the fitness advantage can be related to temporal and spatial variations in resource supply from the habitat. The marine Laminariales (Phaeophyceae) typically have large perennial sporophytes growing at higher latitudes where summers have low nutrient availability, because nutrients are depleted above the thermocline by the growth of photosynthetic primary producers, but have high PAR. In winters, the PAR is lower but the nutrient availability is greater as a result of deeper mixing (Chapman and Craigie 1977, 1978). There are seasonal variations in growth rate, with inverse seasonal relations of quantity of stored organic C (laminarin, mannitol) and quantity of stored N (and P?): Lüning (1990). The Charales (Charophyceae) live in fresh and brackish waters. They are rhizophytes with a small fraction of their biomass in rhizoids in sediment with high N and P but no light; most of the biomass is in shoots in illuminated water with lower concentrations of N and P. The organisms have an effective bidirectional transport involving rapid cytoplasmic streaming through giant cells and plasmodesmata between rhizoids and shoots, and within shoots between the main sites of photosynthesis and the main sites of growth at apices where organic C demand exceeds local supply from photosynthesis (Raven and Smith 1978; Andrews et al. 1984; Box et al. 1984; Raven 2003b).

There are inverse gradients of PAR and nutrients reaching down to and through and (for PAR) below the thermocline: do very large macroalgae capitalize on this, with predominant nutrient uptake at the bottom of the alga

close to the holdfast, and predominant photosynthesis at the top of the alga, with long-distance transport between them (Raven 2003b)? Microalgae can do this with diel vertical migration in some dinoflagellates and *Volvox*, and once per generation for *Ethmodiscus* (Raven and Richardson 1984; Raven 1984b, 1998; Raven and Waite 2004). This may be the case for the giant kelp, *Macrocystis pyrifera*, which can translocate fixed carbon from apical to basal regions and, in turn, the basal blades may export assimilated ammonium (and presumably nitrate) into the stipe, and then upwards to the more apical blades (Lobban 1978; Hepburn et al. 2012), but further study on this translocation is needed to quantify the fluxes, energetics and driving forces (Raven 1984b, 2003b). More generally, large perennials can sequester space and resources over periods of years and, if iteroparous, potentially have the chance to reproduce in each of several years. Some perennial macroalgae are semelparous, i.e. only have one, terminal, reproductive event, e.g. the multicellular marine *Himanthalia* (Brenchley et al. 1997, 1998), and many acellular marine macroalgae (van den Hoek et al. 1995; Graham et al. 2009).

The macroalgae have considerable ecological significance: global productivity estimates vary but are on the order of 1 Pg C per year, with values which are high on a habitat area basis compared to phytoplankton (Smith 1981; Charpy-Roubard and Sournia 1990; Field et al. 1998; Geider et al. 2001). Macroalgae provide a food source for herbivores and decomposers, and a habitat for organisms that feed on them—and those that do not! As for their importance in the study of photosynthesis, the acid and alkaline bands on the ecorticate internodal cells of characean algae in the 1930s (e.g. Arens 1939) set the scene for the study of the role of these zones in inorganic C assimilation in the last four decades, while photoinhibition was studied in *Fucus* in the 1940s by Steeman Nielsen (see Franklin and Forster 1997). Macroalgae were also important in studies of the role of photosynthetic pigments in photosynthesis in relation to the occurrence and interaction of two distinct photochemical reactions through ‘chromatic transients’ and the Emerson enhancement effect (Blinks 1960), and on the use of HCO_3^- in photosynthesis in marine algae (Blinks 1963).

Response to PAR and ultraviolet (UV) radiation in relation to the environment

Energetic considerations in pigment synthesis and light harvesting

Macroalgae start off small, usually from propagules with limited resource reserves compared to seed-plant seeds, and so need photosynthetic self-sufficiency early on; many

of the propagules are themselves photosynthetic (Raven 1984a, b, 1999a, b; Binzer and Middelboe 2005; Binzer et al. 2006). This also applies to the small phase of algae with a heteromorphic alternation of phases (Bell 1997; Thornber 2006; Wang et al. 2011) in the life cycle, e.g. the gametophytes of laminarians. Small photosynthetic structures have smaller package effects (Ramus 1978; Ramus and Rosenberg 1980; Raven 1984a, b, 1996; Dring and Lüning 1985; Lüning and Dring 1985). A small package effect allows variations in pigment composition to be more clearly expressed in terms of fractional absorption of PAR as a function of wavelength (Harvey pointed this out, in terms of seeing the ‘real colour’ of algae for taxonomic assignment, in the mid nineteenth century); this has been explored (Raven 1996) in terms of the range of pigments found in algae which never grow large enough to have a large package effect relative to those that do, as adults, have a large package effect (Raven 1996). A hint in this direction comes from chlorophyll d, which absorbs out to 730 nm as compared to the 700 nm cut-off for most in vivo complexes of chlorophyll a and which was discovered in field-collected red algae by Manning and Strain (1943). The pigment is not found in all red algae, and doubts had been expressed as to whether it was really produced by the red algae rather than by their endophytes. It is now clear that the endophyte suggestion is correct, and that the organisms concerned are cyanobacteria such as *Acaryochloris* which occur as endophytes in red (and other) macroalgae as well as occurring free-living (Larkum and Kuhl 2005; Behrendt et al. 2011). It is of interest that the best-investigated organism with long wavelength-absorbing complexes of chlorophyll a is the marine green ulvophycean alga *Ostreobium* which lives as an endophyte in corals, internal to the zone containing the *Symbiodinium* photobionts (Haldall 1968; Koehne et al. 1999).

Are these small stages in the life cycle where selection could favour one pigment type over others? Presumably competition among young stages (and between young stages and sexually mature laminarian gametophytes) is important in determining zonation after propagules have settled in both the ‘right’ and ‘wrong’ zones, though photosynthesis might not be the major factor: desiccation tolerance, for example, may be more important in the intertidal. A large package effect, as in later developmental stages of algae, especially those with a large optical thickness, is an advantage in limiting photoinhibition (Six et al. 2009; Raven 2011a) and in allowing screening of UV (Raven 1991). There is variation with depth in the tissue of PSII fluorescence characteristics in macroalgae with a large optical thickness (Garbary and Kim 2005).

The hypothesis of ‘complementary chromatic adaptation’ (CCA) for the vertical zonation of marine macroalgae, i.e. green algae in shallowest water, red algae deepest

and brown algae intermediate, has gradually been eroded. Zonation of the three main pigment groups of macroalgae is less clear than Engelmann assumed, and he under-estimated (or ignored) the impact of terrestrially derived gilven/gelbstoff on the transmittance of coastal seawater in many places (Crossett et al. 1965; Larkum et al. 1967). Modelling by Dring (1981) shows that CCA is likely to only have a small role in determining zonation; physiological experiments in which red, green and brown seaweeds, along with green colour mutants of *Gracilaria*, were grown under different light wavelengths resulted in the same conclusion (Ramus 1983; Ramus and Van der Meer 1983). However, the deepest growing macroalgae are generally rhodophytes, at least in clear water (the case Engelmann considered; Littler et al. 1985; Runcie et al. 2008). Further investigation is needed of what contributes to the energy balance of macroalgae at their low-light (depth) limits; the current, understandable, trend to use chlorophyll fluorescence to estimate photosynthesis in situ (Runcie et al. 2008) cannot address the respiratory component of energy balance, and the correspondence of fluorescence-derived electron transport rates with oxygen exchange measurements varies with irradiance (Longstaff et al. 2002).

Considering the synthesis costs of the different pigments (and hence how long it takes to absorb enough PAR to repay the costs of synthesis in a given radiation environment) makes the occurrence of red algae at great depths more difficult to explain, despite CCA (Raven 1984a, b; Raven et al. 2000; see Fujii et al. 2012a, b). The argument here concerns the energy costs of synthesis of the quantity of pigment which, at zero package effect, absorbs 1 mol photons from a 400- to 700-nm radiation field with an equal flux of photons at all wavelengths. The red algal phycobilins have significantly larger construction costs in these terms than do the chlorophyll a–b or chlorophyll a–c complexes (and the various fucoxanthin and siphonein complexes) (Raven 1984a, b, 2011a; Raven et al. 2000; Nielsen and Durnford 2010; Fujii et al. 2012a, b).

Correlation of deeper growing algae with a larger or smaller package effect in the adult stages is also imperfect (Markager and Sand-Jensen 1992a, b; Raven et al. 2000; Johansson and Snoejis 2002; Middelboe and Binzer 2004). Finkel et al. (2004) point out that data from microalgal cultures growing at range of PARs usually show an increased chlorophyll a (and other photosynthetic pigments) content per cell with decreasing PAR for growth, but in some cases there is a decrease in the photosynthetic pigments per cell at the lowest PAR tested. It is not clear if the cells at the lowest PARs were in balanced growth, i.e. with a time-invariant composition if in turbidostat cultures. If the cells were in balanced growth, then the data at very low PAR are consistent with the returns in PAR absorption

per generation for a further increase in energy investment in increasing photosynthetic pigment per cell, giving a longer generation time (less fitness) than does the cell that absorbs less PAR with less pigment but with a larger saving in energy costs of synthesis.

The absolute maximum depth at which an alga with given pigmentation and package effect can grow is determined by the energetic requirements for maintenance processes such as protein turnover (Raven et al. 2000; Quigg and Beardall 2003; Raven 2011a, 2012) and the recouping of leaked solutes (Raven and Beardall 1981a, b, 1982; Raven et al. 2000; Quigg et al. 2006), as well as back reactions in redox reactions associated with photosystem II (Raven and Beardall 1981a, 1982; Raven et al. 2000; Quigg et al. 2006). For leakage of CO₂ from a CO₂ concentrating mechanism (CCM), assuming a constant gradient of CO₂ concentration between inside and outside of the cell, the energy cost of recouping leakage remains constant with increasing depth while the energy available for operating the CCM decreases, so that eventually there is no net influx of inorganic carbon. By contrast, diffusive influx of CO₂ with C₃ biochemistry has loss factors of photorespiration which are a constant fraction of the net forward reaction (Raven et al. 2000), or even a smaller fraction at low irradiances where diffusive limitation of CO₂ entry and O₂ loss are relatively small, so that the steady-state CO₂ concentration around Rubisco is higher and the steady-state O₂ concentration is lower than is the case at higher irradiances. It would then be predicted that algae with diffusive CO₂ entry, rather than CCMs, would occur at the depth limit for macroalgal growth. While red algae lacking CCMs are relatively more common compared to algae with CCMs in low irradiance habitats (Maberly 1990; MacFarlane and Raven 1990; Johnston et al. 1992; Maberly et al. 1992; Raven et al. 2000; Murru and Sandgren 2004; Hepburn et al. 2011; Marconi et al. 2011; Moulin et al. 2011), there are insufficient data on the carbon acquisition characteristics of algae at the depth limit to adequately test the hypothesis (see later).

There are also vertical gradients of CO₂, with higher concentrations in natural waters at the depth limit of benthic macroalgae than at the surface, and of O₂ where the concentration in natural waters is lower at the depth limit of benthic macroalgae than at the surface. These differences would increase the photosynthetic rate of algae with diffusive CO₂ entry at a given photon flux density (see Raven et al. 2000). The higher external CO₂ concentration at depth decreases the CO₂ gradient between Rubisco and the bulk medium in organisms, so decreasing leakage. These considerations show that both the benthic algae with CCMs, and those without, will have the effect of low PAR fluxes at depth partly offset by these vertical gradients of metabolic gases.

Relation of growth at low PAR to nitrogen source

Growth at low light should be favoured by growth on reduced nitrogen sources (NH₄⁺, urea, amino acids) rather than oxidised nitrogen sources (NO₂[−], NO₃[−]), since for an alga growing on NH₄⁺ as a nitrogen source with a carbon:nitrogen ratio of 10, the photon requirement is 12 photons per carbon assimilated, and the additional energy needed for NO₃[−] reduction would mean a total requirement of 14 photons per carbon assimilated (Falkowski and Raven 2007). With a PAR attenuation coefficient of 0.1 m^{−1}, a depth limit of 50 m for growth on NH₄⁺ becomes a depth limit of about 48 m for growth on NO₃[−]. For much clearer waters with an attenuation coefficient of 0.025 m^{−1}, a depth limit of 200 m for growth on NH₄⁺ becomes a depth limit of about 192 m for growth on NO₃[−]. The significance of this difference between NH₄⁺ and NO₃[−] must be considered in the context of the general predominance of NO₃[−] among inorganic nitrogen sources in (particularly) the deeper parts of the zone inhabited by benthic macroalgae (Falkowski and Raven 2007).

A similar argument was applied to growth in less than a metre depth of water of the freshwater red alga *Lemanea mamillosa* by MacFarlane and Raven (1990). This alga grows rapidly in February at 56°N (Dundee, Scotland) with 7.5-h daylength and a low solar angle (MacFarlane and Raven 1990). The measured in situ growth rates are close to the maximum possible from known energy costs of photosynthesis and growth (Falkowski and Raven 2007) for the observed use of NH₄⁺ as nitrogen source and the observed photosynthetic carbon acquisition mechanism (see “Inorganic carbon” section), granted the PAR measured at the nearby (10 km distant) meteorological station with correction for shading by river banks and reflection at the water surface and an assumed thallus PAR absorptance of 0.5 (MacFarlane and Raven 1990; see also Raven et al. 1992). This energetic constraint might help to account for why the alga uses the low and variable (<10 μM) concentration of NH₄⁺ rather than the abundant (400 μM) NO₃[−] from agricultural run-off in the habitat (MacFarlane and Raven 1990).

Photoinhibition by PAR and photodamage by UV

Barry Osmond made important contributions to studies of photosynthesis and photoacclimation in the green marine macroalga *Ulva* (Franklin et al. 1992; Osmond et al. 1993), including the effects of N limitation on photoacclimation (Henley et al. 1991).

Photoinhibition by PAR is predicted to be greatest for organisms with large PSII unit sizes; for macroalgae this means the red algae, where the occurrence of large PSII units involves especially effective transfer of excitation

energy within the units (Chen et al. 2012). Rhodophytes lack either of the ‘classic’ xanthophyll cycles (Goss and Jakob 2010; Schubert et al. 2011; Table 1), but some red algae grow well in the high intertidal (e.g. *Stictosiphonia* in New Zealand). Other mechanisms of excitation energy dissipation presumably occur (Schubert et al. 2011). The results of Schubert et al. (2011; see Schubert et al. 2006; Schubert and García-Mendoza 2008) suggest a diversity of photoacclimation and photoprotection mechanisms in red algae which is related to the kinds of carotenoids present. Turning to the growth of algae at very low PAR, it would be predicted that the xanthophyll cycle components (in brown and green algae) would be less abundant, by adaptation or acclimation, in low than in high irradiances; this has been demonstrated for the deep-water *Laminaria abyssalis* compared to the shallow-water *L. digitalis* (Rodríguez et al. 2002). As there may still be some expression of xanthophyll cycles in brown and green algae growing at very low PARs, it is possible that the absence of xanthophyll cycles in red algae decreases the energy cost of growth in red algae at low PARs. Raven (2011a) has calculated the costs of producing and operating the xanthophyll cycles, but was not able to calculate the cost of producing and operating alternative responses to photoinhibition. At very low PAR, the main costs would be those of production rather than operation.

UVR, damaging (among other cellular constituents) PSII and other photosynthetic components, as a determinant of zonation is championed by Bischof et al. (2006; see also Franklin and Forster 1997), with some success. There is a need for study in macroalgae paralleling the study from Badger’s group emphasising the dominant role (on an incident photon basis) of UVR in the solar spectrum in damaging PSII in *Arabidopsis* (Takahashi et al. 2010), with due attention paid changes to the spectrum with depth in given coastal water type. It must be remembered that damage by UVR is largely a function of UVB (380–320 nm); UVA (320–400 nm) can, through chlorophyll and carotenoid absorption, energize photosynthesis, although photon absorption by proteins and other components decreases the photosynthetic photon yield with decreasing UVA wavelengths (Haldall 1964).

Effects of pigment types for elemental requirements

There are implications of pigment types for elemental requirements. It is predicted that there are higher N (as well as energy) costs for phycobilin-containing algae (other than in phytochrome), as a result of the higher protein content per unit chromophore of pigment complexes. Data on elemental composition show higher C:N ratios in brown than in red algae, as predicted, but the lower C:N in green algae is not in agreement, probably because the C:N ratio is more

strongly influenced by life-forms of the algae than by their phylogeny and hence pigmentation (Atkinson and Smith 1983; Weykam et al. 1995). This argument can be extended to P, as a greater allocation of cellular protein synthesis to photosynthetic structures and catalysts implies a greater allocation of RNA, and hence P, to photosynthesis-related syntheses. Raven (2011a) has extended the argument about RNA and hence P, to the repair of photodamage to photosystem II in photoinhibition, through the effect is relatively small. Again, data on C:N:P (Atkinson and Smith 1983) give very limited support to the prediction.

An argument can also be made for variations in Fe requirement. There is a sixfold greater Fe content in each PSI unit than in each PSII unit, and the higher PSI:PSII in red algae than in green or brown algae (Raven et al. 1999; Falkowski and Raven 2007), suggests that they might have a greater Fe requirement. Suzuki et al. (1995) suggested a lower Fe requirement for a crustose coralline red alga than for two brown algae based on growth enhancement upon Fe addition to very Fe-poor seawater. However, it is difficult to compare the growth rates (linear extension for the brown algae, increase in area for the red alga) in the data set (Suzuki et al. 1995) and, for example, a threefold higher specific growth rate of a brown than a red alga would more than offset a twofold higher PSI:PSII ratio in the red than the brown alga, assuming optimal allocation of Fe in both cases (see Cooke et al. 2004).

Inorganic carbon

Mechanisms of carbon uptake

The biochemistry of photosynthesis in macroalgae seems to be almost always C₃ based on the kinetics of ¹⁴C inorganic C assimilation in the light into identified organic compounds, although studies at times shorter than the shortest time usually employed (10 s) would be desirable (Johnston 1991). The exceptions are C₄-like photosynthesis in the tropical marine acellular ulvophycean green macroalga *Udotea flabellum* (Reiskind and Bowes 1991) and, at some times of year, possible also in the brown temperate marine macroalga *Ascophyllum* (Johnston 1991; see Raven 1997; Hillrichs and Schmid 2001; Cock et al. 2010; Gravit et al. 2010). Raven (2010) considered a claim that, based on genomic (expressed sequence tag) studies, the bangiophycean red alga *Porphyra haitanensis* might have C₄ photosynthesis (Fan et al. 2007), and concluded that there was no good evidence for C₄ photosynthesis. Any contribution of CAM or a related process to C gain in macroalgae is limited to a few percent in some members of the Fucales (Raven et al. 1985, 1989, 1995, 1996; Johnston and Raven 1986b; Raven and Samuelsson 1988; Surif and Raven

1989b; Raven and Osmond 1992; Keeley 1998; Cock et al. 2010; Gravot et al. 2010).

The mechanism of inorganic C flux from the bulk medium to the site of the initial carboxylation [usually by Rubisco (Form IB in green algae, Form ID in brown and red (and chrysophycean and tribophycean): Table 1)], occasionally phosphoenolpyruvate carboxylase (PEPc) or phosphoenolpyruvate carboxykinase (PEPck) (Johnston 1991; Reiskind and Bowes 1991; Raven 1997; Giordano et al. 2005; Falkowski and Raven 2007) is a matter of some controversy. The mechanism by which inorganic C species cross the plasmalemma in freshwater red macroalgae, some marine red macroalgae, a few marine green macroalgae and (probably, allowing for diatoms embedded in the gelatinous matrix) the freshwater chrysophycean macroalga *Hydrurus foetidus*, is apparently solely CO₂ by a diffusive process which is driven by the drawdown of inorganic C inside the cell by photosynthetic assimilation: this maintains the concentration gradient between the medium and the active site of Rubisco (Raven and Beardall 1981b; Raven et al. 1982, 2005; MacFarlane and Raven 1985, 1989, 1990; Maberly 1990; Johnston et al. 1992; Maberly et al. 1992, 2009; Kevekordes et al. 2006; Hepburn et al. 2011; Marconi et al. 2011; Moulin et al. 2011; cf. Middelboe and Hansen 2007a, b). Even here, though, facilitation of the inorganic C flux by CO₂-transporting protein channels in the plasmalemma and probably at the plastid envelope too, and often by CAs from the bulk external phase to the plasmalemma and between internal membranes, may be the rule (Raven et al. 2005). This represents C₃ physiology paralleling C₃ biochemistry, although the mechanism of inorganic C entry in the C₄-like metabolism in *U. flabellum* (Reiskind and Bowes 1991), which seems to act as a CCM, is not known.

Quantitative modelling of the CO₂ fluxes based on measurements of the external boundary layer thickness (discussed in more detail later), estimates of the conductance of the membrane and aqueous phases between the inside of the cell wall and Rubisco, the measured kinetics of Rubisco, and the ¹³C:¹²C of organic matter in the algae relative to that in the medium, account quantitatively for the physiological properties of inorganic C assimilation in the freshwater red macroalga *Lemanea* (MacFarlane and Raven 1985, 1989, 1990; Raven 1992; Raven et al. 2005). It would be of interest to examine the inorganic C acquisition physiology of freshwater red algae which have independently evolved a *Lemanea*-like morphology and which live in similar habitats, i.e. *Psilosiphon* (Entwistle 1989) and *Petrohua* (Vis et al. 2008).

The natural abundance of stable carbon isotopes has also been used as an indicator of C₃ biochemistry plus diffusive CO₂ entry; a low (negative) value for δ¹³C (lower than −30 ‰ for source dissolved CO₂ in equilibrium with the

present atmosphere, corrected for any variations in source δ¹³CO₂) parallels C₃ physiology (Raven et al. 1982, 2002a, b, 2005; MacFarlane and Raven 1985, 1989, 1990; Johnston et al. 1992; Maberly et al. 1992; Kevekordes et al. 2006; Hepburn et al. 2011; Marconi et al. 2011; Moulin et al. 2011). An assumption made in the use of C stable isotope natural abundance is that Form IB (green algae) and Form ID (brown, red algae) Rubisco have identical selectivities for ¹²CO₂ over ¹³CO₂; however, recent study on the in vitro C isotope discrimination of the Form ID Rubisco from the haptophytic marine microalga *Emiliania huxleyi* (Boller et al. 2011) shows that not all Form ID Rubiscos have a C isotope discrimination at least as great as that of the Form IB Rubisco from eukaryotes (Tcherkez et al. 2006). It was already known that the cyanobacterial Form IB Rubisco also have smaller C isotope discriminations than those measured for Form IB Rubiscos in eukaryotes (Raven et al. 2002a, b; Falkowski and Raven 2007). Present data on the range of C isotope ratios in macroalgae relative to the relevant values in external CO₂ suggest that the assumption of similar C isotope discriminations by the Form IB Rubiscos for green macroalgae and the Form ID Rubiscos of brown and red macroalgae is valid (Raven et al. 2002a, b; Tcherkez et al. 2006; Falkowski and Raven 2007).

A CCM based on active transport of inorganic C across one or more cell membranes and/or external conversion of HCO₃[−] to CO₂ using carbonic anhydrase and active H⁺ efflux occurs in a majority of marine red macroalgae, almost all marine green algae and marine brown macroalgae, as well as freshwater green algae (Maberly 1990; Johnston et al. 1992; Maberly et al. 1992; Beer 1996; Larsson and Axelsson 1999; Sherlock and Raven 2001; Axelsson et al. 2002; Raven et al. 2002a, b, 2005; Kevekordes et al. 2006). There always seems to be a contribution from active influx of HCO₃[−] across the plasmalemma, probably with a contribution from active CO₂ entry at the plasmalemma as well (Raven 1997). The suggestion that a CCM is involved is based on the kinetics of inorganic C uptake from the medium of inorganic C and the known dependence of the appropriate form of Rubisco on the CO₂ concentration; the steady-state inorganic C concentration the cells is less commonly measured, and often yields equivocal results.

There is a well-supported mechanism proposed for the CCM in ecorticate characeans with well-defined acid and alkaline bands on the giant internodal cells, and a similar CCM based on abaxial acidification and adaxial alkalization in leaves of some freshwater flowering plants (Arens 1939; Lucas and Smith 1973; Bisson and Walker 1980; Smith and Walker 1980, 1983, 1985; Walker et al. 1980; Price and Badger 1985; Price et al. 1985; Walker 1985; Staal et al. 1989; Ray et al. 2003; cf. Brechignac and

Lucas 1987; Lucas et al. 1983, 1989). The acid zones provide CO_2 from HCO_3^- diffusing in from the bulk medium, based on the higher the equilibrium concentration ratio $\text{CO}_2:\text{HCO}_3^-$ and the faster HCO_3^- to CO_2 conversion at lower pH values, although typically there is also a requirement for extracellular CA which further increases the rate of conversion. The alkaline zones are required for intracellular charge and acid–bases balance (Raven 1984b).

A similar mechanism has been proposed for seagrasses (Hellblom et al. 2001; Beer et al. 2002; Uku et al. 2005; cf. Beer 1996), and subsequently for many of the marine macroalgae thought to have CCMs (Mercado et al. 2006; Zou and Gao 2010; Moulin et al. 2011). The conclusion about the involvement of acid and alkaline zones in marine macroalgae is based on the inhibition of HCO_3^- use by inhibition of CAs and of membrane transporters involved in active H^+ efflux and of the energy metabolism which ultimately power the H^+ efflux, and on the use of membrane-impermeant buffers to decrease or eliminate pH differences among acid and alkaline zones and the bulk medium (Mercado et al. 2006; Zou and Gao 2010; Moulin et al. 2011).

However, there has been no direct visualisation of the acid and alkaline zones in the boundary layer which are (implicitly or explicitly) assumed to be individually smaller than, but each occupying a similar, i.e. approximately equal, fraction of the plasmalemma area as, the acid and alkaline zones in freshwater organisms. The minimum size of the acid and alkaline zones is presumably set by the lateral surface area over which H^+ fluxes can occur between acid and alkaline zones per area of plasmalemma in the zone over which transmembrane H^+ occur in generating the acid and alkaline zones: the smaller the area of plasmalemma per zone, the greater the potential for equilibration of acid and alkaline zones by lateral H^+ diffusion within the boundary layer. An additional means of H^+ equilibration which also becomes increasingly important with decreasing sizes of acid and alkaline patches is H^+ movement along the outer surface of the plasmalemma (Prats et al. 1986; Gabriel and Teissié 1996; Medvedev and Stucebrukhov 2011). Both the radial and lateral loss of H^+ from the acid zones is presumably restricted, as far as use of H^+ in conversion of HCO_3^- to CO_2 is concerned, by the presence of extracellular CAs.

Ideally the mechanism involving acid and alkaline surface zones would occur at the individual cell level, i.e. with (an) acid and an alkaline zone(s) on each cell in contact with medium. The argument here is that, at least in red algae, there are no intercellular connections (pit connections) laterally between epidermal cells, as opposed to through the pit connections formed developmentally at cell divisions in radial files of cells giving rise to the epidermal cell layer (van den Hoek et al. 1995; Graham et al. 2009).

This means that it would be difficult to transfer inorganic C concentrated in a ‘acidifying’ epidermal cell to the laterally neighbouring ‘alkalinising’ epidermal cell. Even when several acid and alkaline bands form on one giant cell in the Characeae, the photochemical quenching, including the photochemistry involved in CO_2 assimilation, is greater in the (stationary) chloroplasts under acid bands than under alkaline bands (Bulychev et al. 2001), despite the rapid (up to 100 μm per second) cytoplasmic streaming in these cells which would help equilibrate inorganic carbon through the cytoplasmic layer (Raven and Smith 1978; Raven 2003b). A mechanism for inorganic C assimilation involving acid and alkaline zones on single epidermal cells has been proposed for the submerged freshwater flowering plant *Ranunculus penicillatus* ssp. *pseudofluitans*, although without direct visualisation of cell surface pH within the transfer cell-like invaginations (Newman and Raven 1993, 1999). Study on other aquatic *Ranunculus* species emphasises the possible role of the transfer cell-like invaginations (Prins and Elzenga 1989; Rascio et al. 1999; Maberly and Madsen 2002).

In this hypothesised mechanism, the main plasmalemma energization process related to the CCM is a primary active electrogenic H^+ extrusion pump such as has been characterised in the freshwater characean macroalgae and flowering plants as well as the seagrass *Zostera* (García-Sánchez et al. 2000; Rubio et al. 2005), but not explicitly in the marine macroalgae where H^+ is probably close to electrochemical equilibrium at the plasmalemma, except in *Acetabularia* with its active electrogenic Cl^- influx which operates in the light (Raven 1976, 2011b; Smith et al. 2011; Suffrian et al. 2011; Taylor et al. 2011). Crucially, attempts are needed to use confocal microscopy with fluorescent pH indicators used at as low concentrations as possible as weak electrolyte pH indicators also act as pH buffers.

The uptake of inorganic carbon as HCO_3^- can also occur in macroalgae. Most of the evidence comes from the use of substituted stilbene inhibitors (e.g. DIDS) of anion exchangers. It should be remembered that there could be DIDS- and SITS-insensitive HCO_3^- transporters, and that the substituted stilbenes are inactivated in long-term (several hours) exposure to PAR (Herfort et al. 2002). The latter point is not relevant to the study of Larsson and Axelsson (1999) where DIDS-sensitive and DIDS-insensitive inorganic carbon acquisition by algae was found under the same experimental conditions. Larsson and Axelsson (1999) examined 11 green, 5 red and 11 brown algae; DIDS sensitivity was found in some of the green algae (species of *Chaetomorpha*, *Monostroma* and *Ulva* *senses lato*, i.e. including *Enteromorpha*) but not in other green algae or in any of the red or brown algae tested. DIDS sensitivity of photosynthesis has been shown for the red alga *Eucheuma denticulate* (Granbom and Pedersén

1999). Earlier study not involving DIDS suggested a major role for HCO_3^- uptake in the red alga *Chondrus crispus* (Brechignac et al. 1986), although other study on this alga gave different findings (Smith and Bidwell 1989).

Regardless of the detailed mechanism, there are phenotypic (acclimatory) interactions of CCM expression in macroalgae with the availability of inorganic carbon, PAR, UVR and P (the only three resources tested). Increased inorganic C supply decreases the affinity for inorganic C (increases the half-saturation concentration of inorganic C). This does not imply a graduated replacement of the CCM by diffusive CO_2 entry, as the driving force on CO_2 movement from the site of Rubisco activity is directed outwards until the external CO_2 concentration exceeds that produced at the site of Rubisco activity by the CCM (Raven et al. 2012). P limitation decreases the inorganic C affinity of the CCM in a red alga (Xu et al. 2010), and light limitation decreases inorganic C affinity of the CCM in red macroalgae (e.g. Kübler and Raven 1994, 1995; Zou and Gao 2009), although the light effect is reversed in a brown macroalga (Zou and Gao 2010). No data seem to be available for N or Fe deficiency effects on the CCM affinity. UVR increases inorganic C affinity in the non-calcified red alga *Gracilaria lemaneiformis* under both P-limiting and P-replete conditions (Xu and Gao 2009). UVR inhibits photosynthesis to a greater extent under high (above ambient) CO_2 growth conditions in a coralline red alga, perhaps as a result of decreased calcification (Gao and Zheng 2010). Genotypically, the fraction of red algae with diffusive CO_2 entry is higher in habitats with lower PARs, though such algae also occur in high PAR habitats (e.g. *Stictosiphonia*) (Maberly 1990; Raven et al. 1992; 2002a, b; 2005; Murru and Sandgren 2004; Giordano et al. 2005; Hepburn et al. 2011; Marconi et al. 2011; Moulin et al. 2011).

Ectocarpus (Phaeophyceae) is the only macroalga to have annotation of the complete genome sequence published. For inorganic C assimilation, the genome annotation and associated diel metabolomic analysis are models of the critical approach required. An example is the conclusion that, on present evidence, not all of the genes needed for the photorespiratory carbon oxidation cycle characterised in flowering plants are yet known in *Ectocarpus* (Gravot et al. 2010).

The inorganic carbon affinity of macroalgae with diffusive CO_2 entry at PAR saturation and pH 8.0–8.2 is generally as expected lower than that for macroalgae with CCMs (Maberly 1990; Johnston et al. 1992; Maberly et al. 1992; Kübler et al. 1999; Raven et al. 2002a, b, 2005; Murru and Sandgren 2004; Hepburn et al. 2011; Marconi et al. 2011; Moulin et al. 2011). Macroalgae with diffusive CO_2 entry often occur in low-light environments, which means a low potential for photosynthesis and hence less

likely to be limited by inorganic C (Maberly 1990; Raven 1997), as mentioned in the context of the lower PAR limit for growth.

Another expectation is that algae with CCMs should have little or no inhibition of photosynthesis or growth by O_2 , while those with diffusive CO_2 entry should have O_2 inhibition competitive with CO_2 . Osmond and coworkers (1976) made an early contribution to this area: before distinction was made between algae with CCMs and those with diffusive entry of CO_2 , it was shown that the O_2 effects differed depending on whether O_2 production (Downton et al. 1976) or ^{14}C inorganic carbon assimilation (Black et al. 1976) was taken as the measure of photosynthesis. Macroalgae with diffusive entry of CO_2 generally show less O_2 inhibition, and less evidence of CO_2/O_2 competition, than predicted from comparison with C_3 land plants, while those with CCMs sometimes show an as yet unexplained O_2 inhibition at inorganic C saturation (Raven 1997; Kübler et al. 1999; Sherlock and Raven 2001; Raven et al. 2005; Maberly et al. 2009). The reasons for these divergences from expectation need further investigation.

A related matter concerns the possibility of thermodynamic O_2 inhibition of the O_2 production mechanism (Clausen and Junge 2004, 2005; Clausen et al. 2005a, b). Raven and Larkum (2007) found no evidence for an ecological role for this inhibition in whole-organism studies, some of which involved macroalgae where the boundary layer O_2 concentration can reach 560 % of the air-equilibrium concentration and concentration at the site of O_2 production in the cells must be even higher as O_2 loss from their plastids is by diffusion down a concentration gradient. Recent study on the effect of O_2 on O_2 production in more resolved systems found no evidence for the proposed thermodynamic inhibition (Kolling et al. 2009; Shevela et al. 2011).

Ocean acidification (OA)

For marine algae, understanding the mechanisms of carbon acquisition, including the relative ability of different species to utilize bicarbonate versus CO_2 as a substrate for photosynthesis, and H^+ fluxes within diffusion boundary layers (DBL), has become very pertinent as researchers grapple with the potentially wide-ranging effects of OA on marine ecosystems. OA is the term coined to describe the changes to the seawater carbonate system that result from the sustained absorption of anthropogenically released atmospheric CO_2 by the oceans (Caldeira and Wickett 2003; The Royal Society 2005). CO_2 reacts with seawater, and the result is an increase in H^+ (decrease in pH), and a change in the relative proportions of inorganic carbon species. The pH of surface ocean waters is thought to have declined by 0.1 U as the start of the industrial revolution,

equivalent to a 30 % increase in H^+ . By 2250, a worst-case-scenario prediction is a further 0.6 U decline (Caldeira and Wickett 2003). The consequence to inorganic carbon availability is that by 2250, CO_2 is set to increase by a further 194 %, HCO_3^- by 14 % and carbonate ion decrease by 56 % (The Royal Society 2005). Most OA research on algae has focussed on the possible detrimental effects on calcifiers (e.g. Kuffner et al. 2008; Langer et al. 2009; Raven 2011b), but the increases in CO_2 and HCO_3^- concentrations could affect all algae (Hurd et al. 2009).

In today's oceans, concentrations of bicarbonate are $\sim 2,200 \mu M$ and dissolved $CO_2 \sim 10 \mu M$. Many seaweeds can assimilate bicarbonate (see above) but the predicted 194 % increase in dissolved CO_2 due to OA has implications for the competitive abilities of seaweeds based on their carbon uptake strategies (Hurd et al. 2009). Seaweeds such as *Lomentaria articulata* that rely on the diffusive supply of CO_2 are likely to benefit by the increase in CO_2 concentration as they are limited at current oceanic concentrations (Kübler et al. 1999). Bicarbonate-users may also benefit, if they can down-regulate bicarbonate use and increase the relative proportion of inorganic C entering as CO_2 (Cornwall et al. 2012). However, active CO_2 uptake does not necessarily involve an energy saving relative to active HCO_3^- uptake coupled to OH^- efflux which gives the same steady-state CO_2 concentration inside the cells (Raven et al. 2005), and replacement of the CCM by diffusive CO_2 entry requires an external CO_2 concentration in excess of what is achieved internally by the CCM (Hepburn et al. 2011; Raven et al. 2012). Kübler and Raven (1994) showed that bicarbonate use by *Palmaria palmata* is facultative, and when grown in low light ($25 \mu mol \text{ photons m}^{-2} \text{ s}^{-1}$) the proportion of CO_2 increased relative to bicarbonate, whereas in the high light treatment ($75 \mu mol \text{ photons m}^{-2} \text{ s}^{-1}$) bicarbonate was preferred. Nevertheless, despite the increased use of CO_2 which may involve lower energy input (see above), the growth rate of *P. palmata* in the low-light treatment ($3.7 \% \text{ day}^{-1}$) was about half that of the high light treatment. In contrast, *L. articulata* uses only CO_2 and the same light treatments had no effect on growth rate; their growth rate of $2.0\text{--}3.2 \% \text{ day}^{-1}$ was similar to that of the low-light *P. palmata*. A community-wide survey of carbon-use strategies by seaweeds in Southern New Zealand revealed a greater proportion of CO_2 -only users low-light sites (up to 8.9 % cover) than in shallow sites, and their competitive ability is predicted to increase with OA as CO_2 becomes more available, whereas coralline seaweeds that occupy 80 % cover are predicted to decline as calcification becomes more difficult at lower pH (Hepburn et al. 2011).

A cautionary note is that most of the study on the effects of OA on macroalgae is predicated on an inorganic carbon system in the natural waters around the algae being close to

at or close to air equilibrium. However, it is clear that the concentration of CO_2 in the light in macroalgal beds (Middelboe and Hansen 2007a, b), and especially in high intertidal rock pools (Bjork et al. 2004), can be well below air equilibrium. Nevertheless, increasing atmospheric CO_2 will bring about an increase in CO_2 and a decrease in pH superimposed on these biologically induced effects.

Carbon acquisition in air versus water

For intertidal algae with a capacity to assimilate atmospheric CO_2 at low tide in the light while the thallus is hydrated adds to the mismatch between acquisition of inorganic C and assimilation of N and P. What evidence is available for *Chara* and a few acellular green marine rhizophytes suggests that inorganic C acquisition from the sediment by rhizoids is minimal, in contrast to their capacity for acquisition of N and P, and in contrast to the major role in inorganic C acquisition played by roots in submerged and amphibious vascular plants of the isoetid life form.

Intertidal macroalgae can assimilate atmospheric CO_2 during emersion, with decreasing rates with increasing water loss. Johnson et al. (1974) showed that two low intertidal macroalgae had lower rates of photosynthesis when emersed at optimal hydration than when they were submersed, while three middle and high intertidal algae had higher photosynthetic rates when emersed at optimal hydration than when submersed. Johnston and Raven (1986a) and Surif and Raven (1989a, 1990) found that the photosynthetic rate of various intertidal and subtidal brown macroalgae during emersion in present day air and before desiccation were a substantial fraction of the rates when submersed in air-equilibrated seawater. Maberly and Madsen (1990) found that 25 % of the daily C assimilation by the higher intertidal *Fucus spiralis* occurred during emersion in spring, while Williams and Dethier (2005) find much lower contributions during emersion than during submersion for the intertidal *F. gardneri*. Matta and Chapman (1991) make the implicit assumption that emersed and submersed photosynthesis are identical in their analyses of daily C balances of the brown alga *Colpomenia peregrina*. These rather variable results certainly do not support the suggestions that essentially all of the C assimilated by intertidal macroalgae comes from the atmosphere, or alternatively that all of the inorganic C comes from seawater during submersion.

The extent of atmospheric input of inorganic C to algae has implications beyond coastal biogeochemistry and ecology, and has implications for the use of intertidal seaweeds found in archaeological sites in ^{14}C dating. Dillehay et al. (2008; see Erlandson et al. 2008) suggest a predominantly atmospheric input of C to their intertidal

seaweeds, and so use a similar approach to that used for samples derived from terrestrial plant photosynthesis, and employing a correction based on the algal organic matter $\delta^{13}\text{C}$ to predict the ^{14}C : ^{12}C ratio assimilated into organic C when the seaweeds were photosynthesising. Dillehay et al. (2008) list, as well as direct use of atmospheric CO_2 when emersed, atmospheric CO_2 supply to the surface layer of seawater (unlikely to be quantitatively important), and freshwater input in run-off, as influences on the C sources for seaweed photosynthesis in addition to seawater with a low mean ^{14}C : ^{12}C as a result of isolation from atmospheric exchange and resupply with atmospheric ^{14}C . While the assumptions made by Dillehay et al. (2008) as to the ^{14}C : ^{12}C assimilated by the algae may be correct, granted the low algal $\delta^{13}\text{C}$ of the algal samples, the greater freshwater input from glacial melting in the past, and the salinity to extant seawater in the area being <36 ‰ it would be helpful to have more precise accounting of the inorganic C sources. A significant role for low- ^{14}C seawater as C source for the algae would make the ^{14}C -derived dates older than is really the case.

DBLs, morphology and resource acquisition

The DBL, already mentioned in different contexts, is crucial in understanding inorganic carbon assimilation in macroalgae. It at once imposes a constraint on diffusive fluxes of solutes between the bulk medium and the plasmalemma, and provides a (leaky) compartment in which chemical reactions can be catalysed by enzymes (e.g. CAs, phosphatases) and also have their rate constants and equilibrium constants altered by the local chemical (e.g. pH) environment (Smith and Walker 1980; Walker et al. 1980). DBL thickness is a function of organism size and shape (thicker boundary layers round larger and more crowded structures) and slower water flow rates over the organism. In early study, DBL thicknesses around marine macroalgae were estimated using Fick's first law of diffusion (e.g. Wheeler 1980; Hurd et al. 1996) or Sherwood numbers (Gonen et al. 1993). More recently, they have been measured directly using O_2 and/or pH (H^+) microprobes (Table 2). For *M. pyrifera* estimated values are in good agreement with direct measurements, but using probes has the advantage of being able to determine morphologically induced, small-scale variations in DBL thickness (Hurd and Pilditch 2011).

As water velocity increases, DBL thickness decreases and rates of photosynthesis increase (Wheeler 1980; Gonen et al. 1995; Enríquez and Rodríguez-Román 2006). The reason for this increase is often attributed to the increased flux of inorganic carbon across DBLs, but it is also possible that in slow flows O_2 accumulation at the seaweed surface

results in higher rates of photorespiration, and thus lower rates of photosynthesis (Mass et al. 2010). There is evidence that this occurs for *G. cornea* (Mass et al. 2010) although Gonen et al. (1995) found no effect of O_2 concentration on photosynthesis in *G. conferta*; they suggested that the increased rate of removal of OH^- from the seaweed surface causes enhanced photosynthesis at higher velocities. Kübler et al. (1999) also saw no such effect of high O_2 concentrations on photosynthesis for *L. articulata*. The effects of the metabolically induced H^+ and OH^- fluctuations near the seaweed surface on seaweed photosynthetic physiology is an area that requires further research.

The pH at the surface of an alga can be very different to that of the mainstream seawater. Photosynthesis causes pH within the DBL to increase, while respiration and (for calcifiers) calcification cause pH to decrease (de Beer and Larkum 2001; see Hurd et al. 2011). The range of pH experienced at the surface of calcifying seaweeds has implications for their relative ability to acclimate and/or adapt to OA. For the coralline seaweed *Sporolithon durum*, the pH at the surface over 2 h in the light then dark was ~ 0.85 U (at mainstream flows of 1.5 cm s^{-1}), a range that spans that of pre-industrial seawater pH to that predicted for 2145. At a mainstream flow of 6.3 cm s^{-1} , the pH range in the light and dark was reduced to 0.15 U as the DBL thickness was reduced (Hurd et al. 2011). In a future ocean, an ability to raise pH above that of seawater may be advantageous as it could reduce dissolution and, for algae with external calcification, promote calcium carbonate precipitation (Ries et al. 2009; Hurd et al. 2011). Also, seaweeds that experience slow flows and can form thick DBLs may be better equipped for survival in future OA conditions than those whose DBLs are persistently eroded by water motion and therefore experience the pH of the mainstream seawater (Hurd et al. 2011).

Flow rate can also modify organism shape in the short term, where a faster flow can stretch (smaller cross-section and longer than when in still water) and cause clumping of segments of many algal thalli, particularly those without calcification (e.g. the freshwater *Lemanea* which lives in continuous water flow speeds in excess of a metre per second). There are also acclimation effects, where growth of a given genotype of alga in a faster flow regime involves the development of a more compact thallus. While faster flow can decrease diffusive restrictions on solute exchange between the bulk phase and the plasmalemma and hence increase the rate of acquisition of chemical resources, there is likely to be resource costs of building a more robust structure in the faster flow regime of 120 mm s^{-1} .

The surface topography of the blades of the laminarian brown alga *M. pyrifera* affects the local DBL thickness (Table 2). Within the edge undulations of the smooth-

Table 2 Summary of studies in which the DBL thickness at the surface of a seaweed or seaweed assemblage has been measured (in the light and at ambient seawater pH), using pH or O₂ microprobes

Seaweed	Minimum bulk seawater velocity (cm s ⁻¹)	Maximum bulk seawater velocity (cm s ⁻¹)	DBL thickness (mm) at minimum velocity used in experiment	DBL thickness (mm) at maximum velocity used in experiment	References
<i>Halimeda discoidea</i>	0	–	0.5	–	de Beer and Larkum (2001)
<i>M. pyrifera</i> —inside undulation of wave-sheltered blade morphology	0.8	2.1		0.73	Hurd and Pilditch (2011)
<i>M. pyrifera</i> —inside corrugation of wave-exposed blade morphology	0.8	4.5	0.80	0.67	Hurd and Pilditch (2011)
<i>F. serratus</i>	0	4.6	1.0–1.5	0.4	Irwin and Davenport (2002)
<i>F. vesiculosus</i> —glabrous blade	–	1.5	–	0.5	Spilling et al. (2010)
<i>F. vesiculosus</i> —pilose cryptostomata	–	1.5	–	0.8	Spilling et al. (2010)
<i>Feldmannia caespitula</i>	0	–	1.3	–	Pöhn et al. (2001)
<i>S. durum</i> , within crenulation	0	10	10.2	0.4	Hurd et al. (2011)
<i>S. durum</i> , apex crenulation	0	10	8.80	0.2	Hurd et al. (2011)
<i>Lithothamnion</i> sp.	0	1–3	2.5	0.1–0.2	Kaspar (1992)
Crustose coralline algae	–	8.9	–	0.4	Wangpraseurt et al. (2012)
Algal turf	–	8.9	–	0.4	Wangpraseurt et al. (2012)
Epilithic coral reef algal community	0	8	2	0.18–0.59	Larkum et al. (2003)

The minimum and maximum velocities of the bulk (mainstream) seawater are given, with the corresponding DBL thickness

surfaced wave-sheltered blades, DBLs of 0.73 mm were detected at 0.8 cm s⁻¹ but DBLs were undetectable at 2.1 cm s⁻¹. In contrast, the 1-mm-tall surface corrugations of wave-exposed blades trap fluid, resulting in DBLs that are 0.8-mm thick at 0.8 cm s⁻¹ and 0.67 mm at 4.5 cm s⁻¹. This latter velocity is usually considered sufficient to minimise DBL thickness (Wheeler 1980; Hurd et al. 1996).

Whether maintaining a thick DBL at the blade surface is advantageous to wave-exposed *M. pyrifera* blades is not known, but it is possible that a thick DBL provides a quiescent region in which to deploy external enzymes such as CAs (Hurd and Pilditch 2011) and phosphatases, as well as in maintaining acid and alkaline zones at the algal surface. The carbon isotopic signature of *Ulva pertusa* becomes more negative with increased seawater flow, suggesting increased CO₂ use relative to bicarbonate in faster flows which could be a result of reduced extracellular

CA at higher flows (Cornelisen et al. 2007). For the tropical reef seaweed *Lobophora variegata*, $\Delta F/F_m'$ declined in higher flows, and when a CA inhibitor was added, providing good support for the hypothesis that external CA is washed away at higher flows (Enríquez and Rodríguez-Román 2006).

Other morphology-related influences on photosynthesis concern whether the acquisition of PAR and inorganic C is a major determinant of the total surface area of algal thalli which is exposed to the environment. That photosynthesis is not the sole constraint, which is seen in the significant fraction of haptophytic algae which produce colourless hairs constitutively, seasonally or in response to N or P (or Fe?) deficiency; these structures seem to be involved in acquisition of chemical resources other than inorganic C, and do not seem to act as light guides enhancing PAR supply to the pigmented part of the thallus. One mechanism by which hairs could enhance nutrient uptake is by

increasing the surface area per unit volume but for some seaweeds, such as *Fucus* spp., the hairs can form a very dense coating which is more likely to increase the thickness of the DBL (Hurd et al. 1993). In support of this idea, Spilling et al. (2010) show that the DBL around the cryptostomata (cavities from which hairs arise) is thicker (0.8 mm) than that of a glabrous (no hairs) blade (Table 2). The hairs may provide a motionless region at the blade surface into which external enzymes (alkaline phosphatases) can be deployed and/or which might encourage bacterial growth; alga-produced enzymes and/or bacteria could act upon organic particles trapped by the hairs at the blade surface, thereby supplying a nutrient source other than that of the mainstream seawater (Schaffelke 1999).

The phenotypic plasticity caused by water motion can be so great that morphological variants have been considered separate species: DNA analyses of *Ecklonia brevipes* in the New Zealand Fjords showed that it is, in fact, an extreme variation of *E. radiata* (Wing et al. 2007). Water motion (both magnitude and type—current vs waves) is a key determinant of seaweed gross morphology, with stipes and/or blades forming different morphologies with the mode of water motion (Wernberg and Vanderklift 2010). In general, wave-exposed seaweeds have narrow, thick, strap-like blades compared to wide, thin, undulate blades of wave-sheltered seaweed (Hurd 2000). The seminal studies of Gerard (1987) and Kraemer and Chapman (1991) illustrate that applying a drag force to juvenile kelp results in a wave-exposed morphology and a wave-sheltered morphology forms in the absence of a force. Furthermore, the applied force stimulates carbon uptake, and increases the proportion of carbon allocated to cell walls (Kraemer and Chapman 1991). This study provides a mechanism by which morphological form is triggered, and also explains why wave-exposed sites may be more productive than wave-sheltered sites (Hurd 2000).

Although water motion is a key driver of seaweed morphology, light and nutrient (including carbon) requirements also affect morphology, which is ultimately a trade-off to optimise the acquisition of essential resources in a particular environment. Teasing apart the relative importance of various environmental factors on controlling blade morphology is difficult but the photosynthetic and morphological acclimations of the kelp *E. radiata* in Australasia have been particularly well studied (e.g. Wernberg et al. 2003; Fairhead and Cheshire 2004; Wing et al. 2007). The Fjords of Southern New Zealand provide a natural laboratory in which to study acclimations to strong gradients of light and water motion. The morphology of *E. radiata* varies along these gradients, and at the high light, wave-exposed sites blades are thick and narrow (strap-like) while the low-light, wave-sheltered blades are wide with undulate edges and much thinner (Miller et al. 2006; Wing

et al. 2007; Miller et al. 2011). Pigment content and photosynthetic parameters co-vary with morphology. The thin, wide blades of the wave-sheltered morphologies have higher concentrations of Chl *a* per g tissue, and a higher α (initial slope of the P vs E curve) and lower E_k compared to wave-exposed morphologies, while P_{max} were similar, suggesting more efficient light harvesting for the wave-sheltered morphology (Miller et al. 2006; Wing et al. 2007). For these Fjord populations, water motion and underwater light climate interact to affect the overall morphology of *E. radiata* (Wing et al. 2007). In Western Australia, however, blade dimensions (width and thickness) of *E. radiata* varied little with water motion, whereas stipe dimensions did (longer, thicker stipes in more wave-exposed sites); the morphological responses of the *E. radiata* stipes are likely to be acclimations to withstanding wave-action (Wernberg and Vanderklift 2010), and the lack of morphological change in the blades suggests that light and/or nutrient availability are not the limiting resources in these sites.

Phenotypic variation in blade morphology under different flow regimes has also been studied for kelp with respect to carbon and nitrogen acquisition in slow flows, where DBLs can be thick (see above). The hypothesis is that the wide, undulate blades typical of many wave-sheltered seaweeds are adaptations to increase turbulence and thereby increase the transport of carbon (Wheeler 1980) and/or nitrogen (Hurd et al. 1996; Roberson and Coyer 2004; Hurd and Pilditch 2011) across the DBL. However, evidence to support this hypothesis is weak because the level of turbulence generated by wave-sheltered and wave-exposed morphologies of *Macrocystis pyrifera* is similar (Hurd and Pilditch 2011), and there is no difference in rates of inorganic nitrogen uptake by these different blade morphologies (Hurd et al. 1996). It seems more likely that the wave-sheltered blade morphology has a role in enhancing light harvesting, with the undulations causing blades to flap at low velocities (Koehl and Alberte 1988; Koehl et al. 2008) thereby generating a more dynamic light field which could increase photosynthesis in the same way that wave-induced light-flecks often do (Greene and Gerard 1990; Wing and Patterson 1993; Wing et al. 1993; Kübler and Raven 1996a, b). Blade flapping, in combination with blade thinness, may allow light to be transmitted to underlying blades; flapping could also enhance carbon and nutrient supply via periodic stripping of the DBL.

A further point about DBLs is the influence of epiphytic organisms. Macroalgae often have epiphytes on longer lived structures; these epiphytes include a variety of smaller seaweeds, and also benthic microalgae such as diatoms, and sessile multicellular animals such as hydroids and ectoprocts. Epiphytes fundamentally alter the interface between the seaweed basiphyte and the external environment, and

create greater heterogeneity at the seaweed surface (Wahl 2008). Larger epiphytic algae and animals may project beyond the DBL, although they could act to extend the DBL because seawater velocity within the ‘epiphyte canopy’ will be reduced and a canopy DBL will form. Smaller epiphytes, including crustose seaweeds, spirorbid worms and colonial bryozoans are small enough to lie within the DBL, but could also extend it depending on their morphology. The epiphytes pose additional barriers to the flux of substances to and from the seaweed surface, and for photosynthetic epiphytes, compete with the basiphyte for light. Sand-Jensen (1977) examined this competition for epiphytes on the seagrass *Zostera marina*, and showed that the inorganic carbon affinity for light-saturated photosynthesis was decreased by the presence of epiphytes. Shading by the photosynthetic epiphytes also decreased light-limited photosynthesis of the basiphyte (Sand-Jensen 1977). Study of this kind is needed for macroalgae, where what evidence is available shows that whatever the negative effects of shading and nutrient pre-emption by photosynthetic epiphytes on the photosynthesis of the basiphyte, the epiphyte does not acquire photosynthates from the basiphyte (Raven et al. 1995, 2001; Raven 2003a, and references therein).

The animal epiphytes can also shade the basiphyte, but in some cases ectoprocts can increase basiphyte photosynthesis, presumably by provision of CO₂ from respiration of particulate organic matter acquired by the animal; Raven (2003a; see also Schaffelke 1999) reviews earlier study. Subsequent study by Hepburn and Hurd (2005) and Hepburn et al. (2006) found more evidence for mutualistic interactions between *Macrocyctis* and hydroids, mainly via nitrogen supply, than between *Macrocyctis* and ectoprocts. The negative impacts of epiphytes on the basiphytes (competition for light and nutrients; increased drag) have been associated with processes minimizing the occurrence of epiphytes, e.g. shedding the outer wall layers of the basiphyte. Perhaps the most extreme response is that of coenocytic green marine algae where all the protoplasm from an epiphytised blade may be removed (‘blade abandonment’) and redeployed to new blades (Littler and Littler 1999).

Prospects for future study and the impact of environmental change on macroalgae

Much remains to be done to relate the structure of macroalgae, the mechanisms of photosynthesis which they inherited from the unicellular ancestors, and the functional changes in their evolution as macroalgae, to their environment.

There has been a resurgence of interest in carbon physiology of macroalgae in response to OA, i.e. the predicted changes in the proportions of dissolved inorganic carbon species (CO₂, bicarbonate and carbonate) and increases in [H⁺]. Investigation of the physiological effects of increased

H⁺ concentration as a result of OA is required, particularly what happens within the DBL of seaweeds. We also need to know if increased CO₂ concentrations will affect the competitive ability of CO₂-using seaweeds compared to bicarbonate-users, and if bicarbonate-users will down-regulate CCMs in a higher CO₂ ocean. The competitive interactions between calcifying and non-calcifying seaweeds also requires further study, as do the interactions between carbon and nitrogen and phosphorus metabolism because nitrogen (as nitrate) and phosphate supply is predicted to decline due to shoaling of the thermocline (Steinacher et al. 2010), although other nitrogen and phosphorus sources might increase due to eutrophication, and both these processes have consequences to the C:N:P balance of growing tissues, and their food value to herbivores.

The relative effects of changes in inorganic carbon, nitrogen and phosphorus supply to growth, but also resource allocation and reproductive fitness are also pertinent to predicted environmental changes. For the one nutrient examined (P), the inorganic C affinity of the CCM will decrease, i.e. a change in the same direction as the response to increasing CO₂. Acquisition of carbon and nitrogen depend on light availability as well as, of course, does growth, and investigation is needed that how shoaling of the thermocline will influence distribution of benthic macroalgae. A shallower upper mixed layer will not directly effect the supply of PAR (and UV), but the change in the variation in temperature with depth, could alter species distribution, and changes in phytoplankton assemblages related to decreased nutrient input from deeper waters local increases in terrestrial supplies of nutrients, and higher mean PAR and UVB, could alter phytoplankton–macroalgae competition.

In addition to investigation of the interactive effects of the different environmental change factors on macroalgal performance, i.e. acclimation, it would be very useful to have information on the effects of these factors on (genetic) adaptation, i.e. evolution, in macroalgae. However, repetition on macroalgae of the studies on increased CO₂ (Collins and Bell 2004, 2006; Lohbeck et al. 2012) and temperature (Huertas et al. 2011) on adaptation on microalgae will be difficult in view of the large number of generations needed for this study and the longer generation times of macroalgae, although seaweeds with relatively short generations times, that are easily grown in small-scale laboratory culture and whose physiology is well studied, e.g. *Ectocarpus* (Charrier et al. 2008; Cock et al. 2010; Gravot et al. 2010) would be a useful starting point.

Conclusions

Macroalgae have been neglected in photosynthetic studies relative to flowering plants and microalgae; although they

contribute of less than 1 % to global primary productivity, their area-based primary productivity is higher than that of phytoplankton and is similar to that of land plants, and the diversity of their photosynthetic machinery (antenna pigments, xanthophyll cycles if present) and Rubisco form are more diverse than in embryophytes.

Attempts have been made to relate the depth (negatively correlated with irradiance) distribution of the three main higher taxa of marine macroalgae to their photosynthetic light use through their pigmentation in relation to variations in spectral quality of PAR with depth (CCA), and also to their optical thickness and hence the extent of the package effect. These attempts have been relatively unsuccessful, to some extent because of other factors (e.g. water movement). The presence (Chlorophyta, Phaeophyceae) or absence (Rhodophyta) of xanthophyll cycles involved in excitation energy dissipation is also not well correlated with depth distribution of marine macroalgae.

Photosynthetic inorganic carbon acquisition in some red and a few green macroalgae involves entry of CO_2 by diffusion. Other red and green macroalgae, and brown macroalgae, have CCMs. These CCMs frequently involve acid and alkaline zones on the surface of the alga with CO_2 (produced from HCO_3^-) entering in the acid zones, while some macroalgae also, or alternatively, have CCMs based on active influx of HCO_3^- . These various mechanisms have different responses to the thickness of the DBL. In addition to implications of DBL thickness for inorganic carbon acquisition, the water movements which partially determine DBL thickness also cause, in the case of waves, periodic variations in PAR within an algal canopy which can alter productivity.

Energetic predictions that macroalgae growing at or near the lower limit of PAR for growth should rely on diffusive CO_2 entry without acid and alkaline zones, and on NH_4^+ rather than NO_3^- as nitrogen source, are partially borne out by observation.

The impact of global environmental change on marine macroalgae mainly relates to OA and warming, leading to a shoaling of the thermocline and a decreased nutrient flux to the upper mixed layer. Predictions of the impact on macroalgae requires further experiments on interactions among increased inorganic carbon, increased temperature and decreased nitrogen and phosphorus supply. Studies of genetic adaptation to environmental change are also desirable, but it is difficult to perform experiments over hundreds of generations with organisms with generation times significantly longer than those of microalgae.

While this paper has emphasised the role of photosynthesis in the biology and evolution of algae, as befits the remit of Photosynthesis Research and the interests of Barry Osmond, it must be remembered that many other factors,

e.g. interactions with grazers, should also be considered in providing a more complete account of macroalgae.

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