

Review

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The role of macroalgal habitats as ocean acidification refugia within coastal seascapes

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Abstract

Ocean acidification (OA) refers to a global decline in the average pH of seawater driven by the absorption of atmospheric carbon dioxide (CO₂). Marine macroalgae, while affected by this pH change, are also able to modify seawater pH through their own interaction with inorganic carbon in the carbonate system. Through this action, macroalgae-dominated habitats are potential refugia from OA for associated marine species. This review summarises the most prominent literature on the role of macroalgae in OA mitigation and the potential of macroalgal habitats to serve as OA refugia. It includes a brief overview of macroalgal distribution in an effort to illustrate where such refugia might be most prevalent. Macroalgae influence seawater carbonate chemistry through the absorption of CO₂ and HCO₃⁻ during photosynthesis, raising surrounding seawater pH in the process. This transient effect on seawater chemistry could provide some respite from the negative effects of OA for many marine species. This refuge role varies over a range of scales along with macroalgal architecture, which varies in size from low-growing turfs to large canopy-forming stands. The associated pH changes can range over various temporal (daily and seasonal) and spatial (from centimetre to kilometre) scales. Areas of high macroalgal biomass are likely to play an important role as significant OA refugia. Such communities are distributed widely throughout the globe. Large brown macroalgae (Laminariales) dominated communities are common in temperate regions, while members of the Fucales are responsible for substantial macroalgal stands in warmer tropical regions. These marine fields and forests have great potential to serve as localised refuges from OA. While more work needs to be done to clarify the effect of macroalgal communities on seawater pH on a large scale, such refuge areas could become important considerations for the management of marine resources and in protected area selection.

Impact statement

Ocean acidification (OA) is recognised as a significant aspect of global change that will have widespread impacts on marine ecosystems. There has been a recent increase in published research that acknowledges the potential for marine vegetation, such as macroalgae, to modulate local pH conditions through biotic processes and thereby serve as OA refugia for marine organisms. However, the specific role that macroalgae play in the carbonate chemistry dynamics of shallow coastal marine environments has not yet been reviewed in detail. This review assesses the available literature documenting the distribution patterns and structural complexities of macroalgae and how this informs their role in pH modulation over various temporal and spatial extents. A wholistic understanding on the role of macroalgal marine vegetation as OA refugia can facilitate improved local OA management and protected area management to benefit impacted coastal marine species.

Introduction

In the marine environment, ocean acidification (OA) refugia refers to locations where naturally higher pH levels are observed, through biotic or physical drivers, providing periodic or sustained relief from global OA for marine organisms (Kapsenberg and Cyronak, 2019). OA is a consequence of increasing anthropogenic emissions of carbon dioxide (CO₂) into the earth's atmosphere (Caldeira and Wickett, 2003; Sabine et al., 2004; Doney et al., 2009). This global process results from increased absorption of atmospheric CO₂ by the oceans, which ultimately shifts the carbonate chemistry equilibrium of seawater resulting in a decline in average seawater pH (Doney et al., 2009; Dickson, 2010). Concurrent changes in carbonate chemistry associated with a decline in pH include changes to the concentrations of inorganic carbon, such as an increase in dissolved CO₂ and bicarbonate (HCO₃⁻) and a decrease in carbonate ions (CO₃²⁻) (Feely et al., 2004; Dickson, 2010).

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 Cambridge Prisms

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In addition to OA, other natural and anthropogenic processes (e.g., pollution, mariculture, aquaculture, upwelling and freshwater inputs) can result in intensified acidification, resulting in even more complex carbon system dynamics, especially in coastal areas (termed coastal acidification; e.g., Wallace et al., 2014; Doney et al., 2020; Isah et al., 2022; Savoie et al., 2022). These changes in ocean chemistry have implications for marine organisms and ecosystems by reducing carbonate ion availability for calcification (Hofmann et al., 2010) and disrupting key biological processes through changes in pH (e.g., organism physiology and behaviour; Pörtner, 2008; Heuer and Grosell, 2014; Clements and Hunt, 2015; Nagelkerken and Munday, 2016).

While lowered seawater pH caused by OA can have substantial impacts on coastal vegetation (Koch et al., 2013; Narvarte et al., 2020), these species can in turn also affect seawater pH. For example, seagrass and macroalgae can raise pH on a local scale by taking up carbon through photosynthesis (Krause-Jensen et al., 2015). The role of coastal vegetated habitats, such as seagrass, mangroves, salt marshes and macroalgae as carbon sinks is widely acknowledged (e.g., Bouillon et al., 2008; Duarte et al., 2010; Alongi, 2012; Fourqurean et al., 2012; Chmura, 2013; Krause-Jensen and Duarte, 2016). However, the role that coastal vegetated habitats play in influencing localised carbonate chemistry and pH of surrounding seawater, particularly in the context of OA, has only come to the forefront more recently, consequent to the increased attention given to coastal acidification.

Macroalgal vegetation can play a significant role in influencing the carbonate chemistry of seawater over various spatial and temporal scales (Middelboe and Hansen, 2007; Wahl et al., 2018; McNicholl et al., 2019) through autotrophic, calcification and respiration processes (Middelboe and Hansen, 2007; Krause-Jensen and Duarte, 2016). These localised zones of elevated pH associated with macroalgal beds could potentially serve as OA refugia (Noisette and Hurd, 2018). For example, Wahl et al. (2018) found that dense beds of brown algae and seagrass in the Western Baltic increased the overall mean pH of the surrounding water by as much as 0.3 units relative to other similar habitats with no macrophytes and also imposed strong diurnal pH fluctuations (due to photosynthetic activity). This allowed mussels (*Mytilus edulis*) to maintain calcification even under acidified conditions and suggests that seagrass and macroalgae may mitigate the impact of OA on organisms living in these habitats.

Macroalgal physiology and carbon use strategies

Photosynthesis and respiration

The process of photosynthesis (which occurs only during the day) in macroalgae requires the uptake of dissolved inorganic carbon (DIC), which is ultimately required in the form of CO_2 , together with water and light, to produce glucose and oxygen (Hanelt et al., 2003). In aquatic and marine environments, DIC exists in different forms: CO_2 , HCO_3^- and CO_3^{2-} (Cornwall et al., 2015; Stepien et al., 2016). In seawater, DIC predominantly occurs in the form of HCO_3^- (~90%) and not as dissolved CO_2 gas (<1%) due to the rapid dissociation of CO_2 in seawater (Park, 1969). As such, most macroalgae have evolved carbon concentrating mechanisms (CCMs), which facilitate the active uptake of DIC in the form of HCO_3^- using various energy-driven mechanisms, such as external conversion of HCO_3^- to CO_2 catalysed by the enzyme carbonic anhydrase (common in red, green and brown seaweeds; e.g., Flores-Moya and Fernández, 1998; Axelsson et al., 1999; Mercado

et al., 1999) or through the uptake of HCO_3^- directly in this form via anion exchange proteins or proton pumps (Fernández et al., 2014). Once taken up into the cells, the enzyme carbonic anhydrase facilitates the interconversion of DIC to make it available for photosynthesis (Raven, 1995). In many macroalgal species, CCMs are used in addition to passive CO_2 diffusion (Maberly, 1990; Raven, 2003; Giordano et al., 2005; Cornwall et al., 2015; Stepien et al., 2016) depending on the availability and forms of DIC in surrounding seawater. Very few macroalgal species rely on passive CO_2 diffusion alone for DIC uptake (Raven, 2003; Giordano et al., 2005; Raven and Hurd, 2012; Stepien et al., 2016).

The DIC acquisition strategies employed vary among macroalgal species and taxonomic groups (Maberly, 1990; Raven, 1997). Green algae, like *Ulva*, for example, can efficiently use both CO_2 and HCO_3^- as inorganic carbon sources (Beer and Eshel, 1983; Rautenberger et al., 2015). Brown algae species rely almost exclusively on the uptake of DIC in the form of HCO_3^- (Surif and Raven, 1989; Zou and Gao, 2010; Fernández et al., 2014). The red algae are also primarily HCO_3^- users, with some exceptions, like *Lomentaria articulata* and *Delesseria sanguinea*, which lack this ability and rely on CO_2 as a DIC source (Johnston et al., 1992; Kubler and Raven, 1994). The ability and efficiency with which different DIC sources are used by macroalgal species appears to be related to habitat rather than specific to particular taxonomic groups (Maberly, 1990; Kubler and Raven, 1994; Murru and Sandgren, 2004).

During periods when photosynthesis is not occurring or limited (e.g., at night or under reduced light availability), there is a net release of CO_2 gas into surrounding seawater through respiration (Duarte et al., 2005; Middelboe and Hansen, 2007; Semesi et al., 2009). This process also influences the carbonate chemistry and forces the equilibrium to a state that decreases pH (Middelboe and Hansen, 2007; Saderne et al., 2013; Wahl et al., 2018). The influence of photosynthesis and respiration on seawater carbonate chemistry is most significant over larger spatial scales when macroalgal growth and density is high. Since the carbonate chemistry equilibrium of seawater is dynamic, the periodic uptake of DIC for photosynthesis by macroalgae acts to increase pH, and CO_2 released by respiration, conversely, decreases pH often resulting in diurnal pH cycles. Despite these complex and ongoing changes to this equilibrium, which result in highly variable conditions in these habitats, there is evidence to suggest that macroalgae raise the overall average pH in surrounding seawater, which can have temporary or long-term benefits for the organisms that live in these habitats (Krause-Jensen and Duarte, 2016; Kowek et al., 2018; Wahl et al., 2018).

Calcification

In addition to photosynthetic needs, some macroalgal species rely on DIC in the form of CO_3^{2-} , HCO_3^- or CO_2 to build and maintain calcium carbonate structures through the precipitation of CaCO_3 (Roleda et al., 2012a; Hofmann and Bischof, 2014). This process may also modulate the carbonate chemistry equilibrium of surrounding seawater through both the absorption of DIC and the release of CO_2 (Kalokora et al., 2020). As such, the role that calcifying species have on carbon dynamics of surrounding seawater is complex, as processes of photosynthesis, calcification and respiration simultaneously influence the carbon system, and ultimately pH, in counteracting ways (Kalokora et al., 2020).

The best-known calcifying group of algae are the order of red algae, the coralline algae, that form crustose or articulated

structures by depositing CaCO_3 extracellularly (Hofmann and Bischof, 2014; McCoy and Kamenos, 2015). These algae can form large aggregations spanning several square kilometres or also occur as smaller crusts or as epiphytes on other living organisms (McCoy and Kamenos, 2015). Although calcification in this group is considered to be sensitive to OA, as CO_3^{2-} is less available in seawater under acidic conditions (Feely et al., 2004; Fabry et al., 2008; Raven, 2011; Stepien et al., 2016), the fact that many calcifying macroalgae utilise HCO_3^- or CO_2 as substrate for calcification, and not carbonate may limit this sensitivity (Roleda et al., 2012a). Furthermore, carbonate concentrations can be increased by these algae through alteration of pH of water in close association with the thallus (e.g., intercellular spaces) during photosynthetic use of CO_2 and/or HCO_3^- (Digby, 1977; Borowitzka and Larkum, 1987), reducing reliance on elevated ambient carbonate ion concentrations. In fact, dissolution of calcified structures because of OA might be a greater problem than reduced calcification rates (Doney et al., 2009; Hofmann and Todgham, 2010).

Through these interactions with the carbonate system of seawater, macroalgae influence the carbon equilibrium of surrounding seawater over various scales. However, for macroalgal vegetation to play a meaningful role as OA refugia for other marine organisms, the density of these primary producers needs to be high enough. Macroalgal vegetation is not evenly distributed with respect to species and biomass and certain regions would be of greater significance in their effect on local seawater carbon fluxes and pH. The greatest potential for OA mitigation is likely to be in coastal areas with large, dense and complex macroalgal communities or seaweed farms (Chung et al., 2013; Zacharia et al., 2015; Fernández et al., 2019; Xiao et al., 2021).

Macroalgal distribution patterns

Globally, macroalgal distribution is determined by seawater surface temperature, while local scale distribution is established in response to substrate properties and depth. Lüning (1991) described

macroalgal floras of the world in detail and the regions identified based on macroalgal vegetation closely resemble the seven temperature zones adopted by Briggs (1995) (Figure 1).

Marine forests

Canopy-forming macroalgae occur along various coastlines and include large brown species, such as large Laminarian kelps and smaller Fucalean genera, which dominate marine benthic communities known as marine forests. Large robust canopy-forming brown algae are recognised habitat engineers known for their ability to alter physical conditions in the surrounding benthos (Steneck et al., 2002; Schiel and Foster, 2015; Teagle et al., 2017; Wernberg et al., 2019). These subtidal brown algae are the most important macroalgal primary producers based on area cover and net primary production (Duarte et al., 2022). Kelp forest communities include a variety of canopy-forming species that differ widely in stature. Steneck et al. (2002) recognised at least three different groups of large forms that represent the kelp-component in kelp forests. The floating canopy kelps (e.g., *Macrocystis*) that grow up to 45 m in length, smaller canopy kelps like *Ecklonia* and *Nereocystis* (<10 m); and kelps that are held upright by rigid stipes (*Laminaria* and *Ecklonia radiata*) (<5 m). These ecosystem engineers create forest-like marine vegetation types that have complex three-dimensional structures. Like terrestrial forests, kelp communities have associated understory algal communities (Leliaert et al., 2000; Bennett and Wernberg, 2014; Leclerc et al., 2016; Smale et al., 2020).

The smaller canopy-forming algae are from the Fucales, of which *Sargassum* and *Cystoseira* species are the most widespread (Nizamuddin, 1970). *Sargassum* is more common in the warm-temperate, subtropical and tropical coasts (Yip et al., 2020), while *Cystoseira* is most diverse in the Mediterranean (Nizamuddin, 1970). This pattern of canopy-forming algal distribution is reflected in the mapped brown algal marine forests, which show strong representation in cool- to cold-temperate regions, but also in some

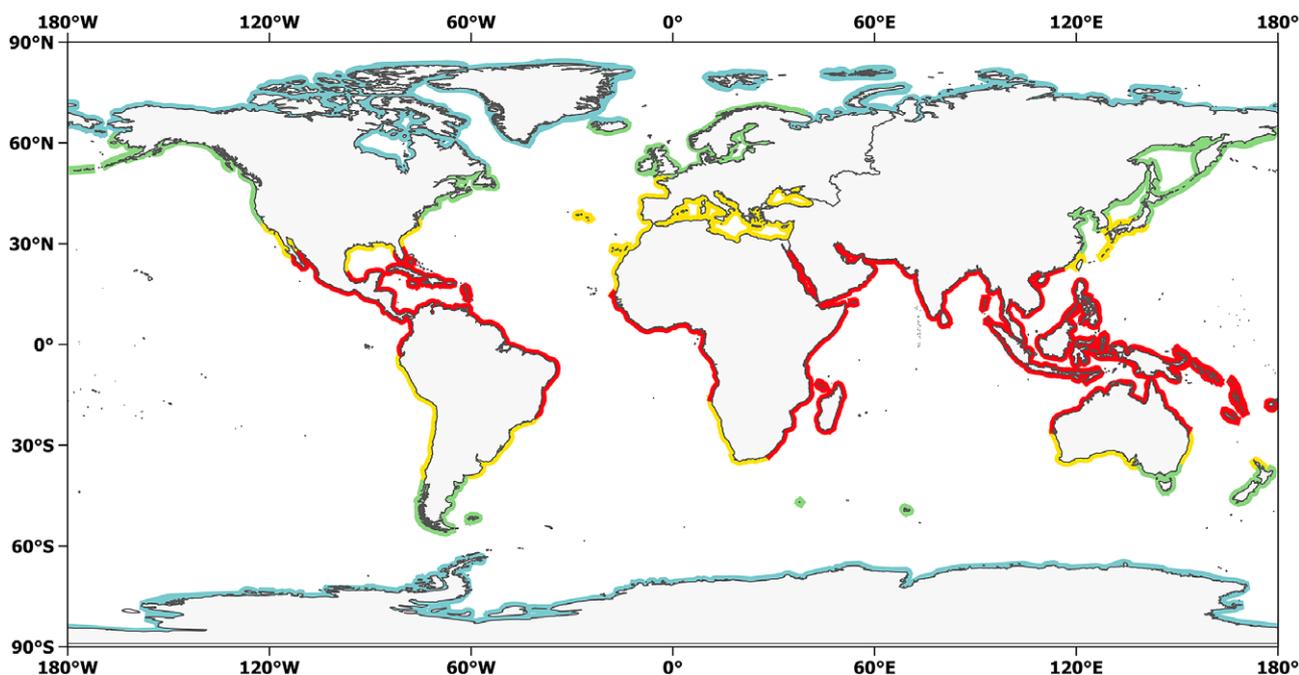


Figure 1. Distribution of coastal temperature zones based on Briggs, 1995 (reproduced from Bartsch et al., 2012). Blue, polar regions; green, cool temperate; yellow, warm temperate; red, tropical.

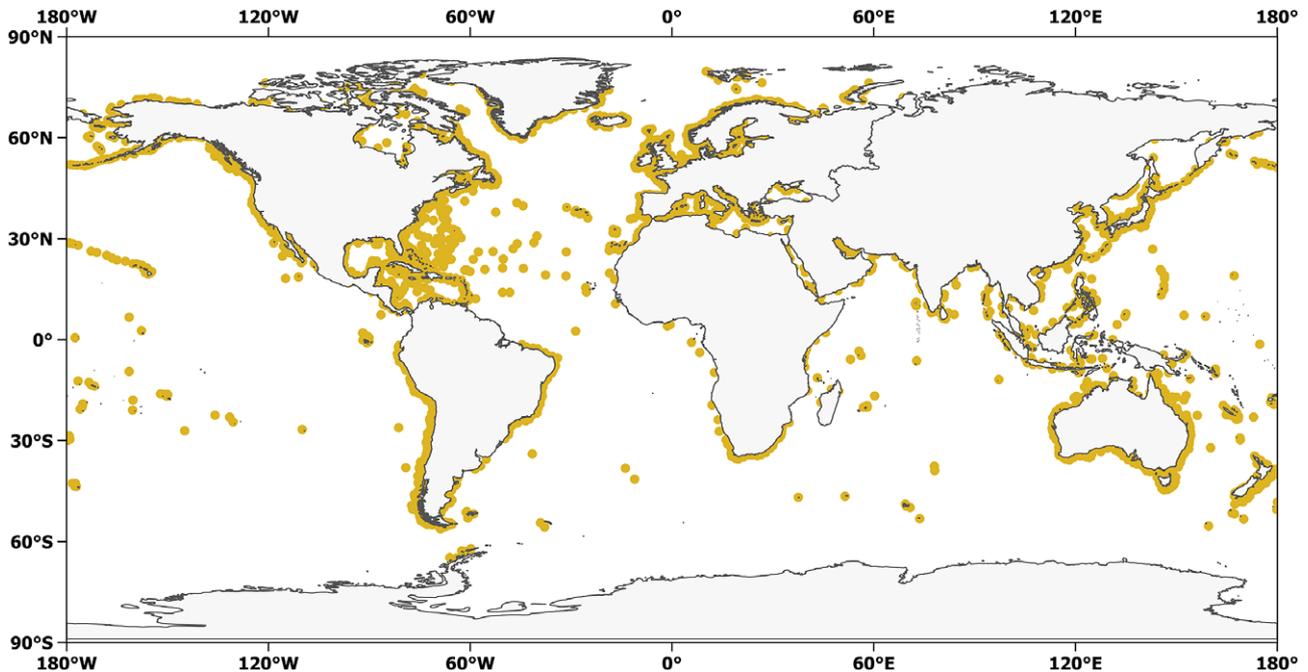


Figure 2. Modelled distribution of brown forest forming macroalgal species (after Assis et al., 2020).

warmer tropical coasts such as the Caribbean and Indo-China (Figure 2) (Assis et al., 2020).

Lower canopy-forming algae like *Gelidium corneum* are also considered foundational, or habitat forming species (Quintano et al., 2017; Borja et al., 2018; Muguerza et al., 2022), particularly on some European coasts, with *Gelidium canariense* representing an important canopy-forming species on Macronesian islands (Alfonso et al., 2017; Hernández, 2021). While these algae are not as tall as the kelps, the canopies formed are similar in height (20–30 cm) to some of the fuclean-dominated communities (Robertson, 1987; Quintano et al., 2018; Alfonso et al., 2021; Hernández, 2021). Smaller brown and red foliose species are usually important components of the under-story vegetation and occur both under canopies of larger brown algae as well as in the gaps between stands of taller algae. However, temperate *G. corneum* (Quintano et al., 2017, 2018; Casado-Amezúa et al., 2019) and *Gelidium canariense* (Alfonso et al., 2021; Hernández, 2021) are both recognised as short canopy-forming species in their own right.

Polar macroalgae

The polar macroalgae flora is confined predominantly to the subtidal zone due to seasonal ice scour, which abrades rock surfaces on the intertidal reefs (Zacher et al., 2009). Light limitation during winter months limits the poleward distribution of kelps that form such extensive forests in temperate regions (Steneck et al., 2002). However, a few Laminarian species do occur in these cold polar regions (Filbee-Dexter et al., 2019), with macroalgal communities in cold polar waters generally comprised of a canopy of large brown algae, with an under-story community of foliose and coralline macroalgae (Brouwer et al., 1995; Wiencke and Amsler, 2012). Although the Arctic has limited potential for substantial macroalgae communities, since only 35% of the benthos in this region has hard substrate that can support large attached macroalgae like kelp forests (Filbee-Dexter et al., 2019), subtidal macroalgae communities can reach biomass values comparable to temperate kelp communities (Wiencke and Amsler, 2012).

Temperate algal vegetation

In cold- and warm-temperate regions, the large brown algae also dominate the subtidal zone (Flores-Moya, 2012; Huovinen and Gómez, 2012). The most prominent group in this regard are the kelps (Laminariales), which attain the largest size of these brown canopy-forming algae (Steneck et al., 2002). These are common in cooler regions (warm and cold temperate) but relatively rare along warmer coastlines (Bolton, 2010). Dense beds of smaller macroalgal groups are also common in temperate areas (Lüning, 1991; Shepherd and Edgar, 2013). Estimates based on habitat availability models show that, while these smaller algae potentially cover a substantial area, they make a limited contribution to primary production (Duarte et al., 2022).

Tropical algal vegetation

Subtidal algal vegetation in tropical regions usually forms a mosaic with coral reefs. These metazoan colonies share space with both turf and foliose macroalgae communities, the relative abundance of which is dependent on the interplay between herbivory, nutrients and light availability (Hurd et al., 2014). Foliose algae are usually rare in coral reef systems, unless there is reduction in herbivory or an increase in nutrients (Lobban and Harrison, 1994). These algae are often fucoids like *Cystoseira*, *Turbinaria* and *Sargassum* (Mejia et al., 2012). Foliose algae, along with some coralline algae, usually form communities on the shallow shoreward reef flats of coral atolls, while the seaward slopes are usually occupied by corals, coralline algae and calcified macroalgae such as *Halimeda* (Littler and Littler, 1994). One of the reasons for this is the availability of hard substrate on a relatively flat surface to which they can attach (Fong and Paul, 2011). Extensive macroalgal communities are not common in tropical regions, however, Wilson et al. (2010) and Evans et al. (2014) report substantial algal meadows off the coast of Australia.

Based on macroalgal distribution models, there appears to be great potential for OA mitigation in algal beds, both in temperate

and tropical regions. However, the greatest opportunities for larger scale OA refuge would lie within the high biomass areas offered by temperate marine forests. High biomass can also be created through coastal seaweed aquaculture initiatives, which may alleviate OA stresses in shallow coastal areas.

Trends in ocean acidification refuge provision by macroalgae

Temporal trends

Refuge from OA provided by macroalgae can be temporally consistent or cyclical, depending on several factors such as seasonal productivity (Middelboe and Hansen, 2007), photosynthetic state (diurnal cycles), water retention time and mixing (Middelboe and Hansen, 2007; Buapet et al., 2013; Koch et al., 2013) and nutrient availability (Gao and McKinley, 1994; Celis-Pla et al., 2015).

Macroalgae are subject to seasonal differences in productivity and photosynthetic rates, like many other plant species, related to temperature preferences, irradiance and nutrient availability (Takahashi et al., 2002; Saderne et al., 2013; Attard et al., 2019; Kapsenberg and Cyronak, 2019). This means that their provision as OA refuges may vary with seasonal differences in productivity (Li et al., 2022). Studies have found that in most regions macroalgal productivity is typically higher in summer and spring months. For example, Middelboe and Hansen (2007) identified seasonal pH variability associated with macroalgal productivity (*Fucus vesiculosus*, *F. serratus*, *Ceramium rubrum* and *Ulva* spp.) on the northeast coast of Zealand (Denmark), evidenced by higher average pH in summer and lower pH in winter, which they attributed mostly to seasonal differences in irradiance. These findings are similar to other studies that also found higher average pH and higher variability in carbonate parameters ($p\text{CO}_2$ and DIC) in productive summer months, for example, Krause-Jensen et al. (2015) in a subarctic fjord in Greenland and Delille et al. (2009) in a Southern Ocean Archipelago. As such, macroalgal-dominated habitats may provide seasonal relief for marine organisms from OA during periods of higher productivity.

Many studies have identified diurnal cycles in seawater pH adjacent to macroalgal vegetation, with the common pattern being higher pH during the day (driven by photosynthesis) and lower pH at night (driven by respiration; e.g., Middelboe and Hansen, 2007; Semesi et al., 2009; Frieder et al., 2012; Cornwall et al., 2013; Krause-Jensen et al., 2015; Wahl et al., 2018). These patterns occur in response to daylight availability for photosynthesis. In some cases, diurnal variability in pH can be as high as 1.2–1.5 units depending on the density of macroalgal growth and resultant levels of productivity (Krause-Jensen et al., 2015; Wahl et al., 2015). The extent of diurnal variability can also be influenced by physical factors, such as tidal processes or seawater exchange. Shallow areas with less mixing and higher water retention times usually experience high diurnal pH variability (Middelboe and Hansen, 2007; Hurd, 2015). Diurnal fluctuations in pH can benefit associated organisms by providing cyclical or periodic relief from OA. Wahl et al. (2018) found that the brown algae *F. vesiculosus* in the Kiel Fjord increased overall mean pH of seawater by 0.01–0.2 units, with diurnal variability of 1.2 units. Mussels (*Mytilus edulis*) benefited from this autotrophic pH modulation as they were able to maintain calcification rates even at low pH levels (7.7–8.1 depending on algal density) by shifting their calcification process to daytime periods to fall in with the periods of higher pH provided by the vegetation (Wahl et al.,

2018). Other studies have found similar benefits for growth, development and physiology in other bivalve species (summarised in Table 1) (Frieder et al., 2014; Young and Gobler, 2018; Jiang et al., 2022; Young et al., 2022). However, there is also evidence to suggest that not all species are capable of adapting their calcification process to benefit from diurnal pH variability (Cornwall et al., 2013) and, as such, may still be negatively affected by corrosive conditions at night.

Spatial trends

Macroalgae can serve as OA refugia over a range of spatial scales as they can form habitats ranging in size from large stands and canopies to low-level algal crusts (Hepburn et al., 2011). Macroalgae also occur at a vast range of locations, such as in shallow coastal areas, rock pools, estuaries or deeper subtidal locations (Layton et al., 2020; Falkenberg et al., 2021). The distribution and structure of macroalgal growth will offer refuge from OA at different spatial extents. On a small scale, pH fluctuation related to biological activity can occur at spatial scales as small as centimetres, for example, in the diffusive boundary layer at the thalli surface (Noisette and Hurd, 2018; Guy-Haim et al., 2020). Conversely, in large- and dense-algal aggregations, biological activity can have an influence at an extent of metres to kilometres (Krause-Jensen et al., 2015).

On a micro-scale (centimetres) macroalgal metabolism can create favourable micro-zones of higher pH within their diffusive boundary layer (Noisette and Hurd, 2018; Guy-Haim et al., 2020), where pH can be up to 1–3 units higher than surrounding seawater (Wahl et al., 2015). Marine organisms that live on the surface of macroalgae can benefit from this chemical refuge, especially during the daytime when photosynthetic activity is highest (Noisette and Hurd, 2018) (Table 1). For example, Saderne and Wahl (2013) found that both calcifying (*Electra pilosa*) and non-calcifying (*Alcyonidium hirsutum*) Bryozoan species were tolerant of high $p\text{CO}_2$ levels ($1,193 \pm 166 \mu\text{atm}$) associated with upwelling events in the Western Baltic Sea, and they attributed this tolerance to the potential periodic relief from OA provided by the brown macroalgal species *Fucus serratus* on which these species live. Similarly, Doo et al. (2020) found that an epiphytic foraminifera, *Marginopora vertebralis*, showed higher tolerance to end-of-the-century temperature ($\pm 3 \text{ }^\circ\text{C}$) and $p\text{CO}_2$ ($\sim 1,000 \mu\text{atm}$) when kept experimentally under these treatments with its red macroalgal host, *Laurencia intricata*. Similar beneficial symbiotic relationships that facilitate micro-refugia from OA exist between calcifying and non-calcifying algae. For example, Guy-Haim et al. (2020) and Short et al. (2014) found that the coralline algae *Ellisolandia elongata* and *Hydrolithoideae* spp. are less susceptible to the effects of OA, evidenced by higher calcification rates at low pH (7.8 and 7.7, respectively), when associated with non-calcifying epiphytic algae. There are also examples of species, such as urchin larvae (*Pseudechinus huttoni*) that are well adapted to pH variability and therefore show no positive or negative response to the variable pH in their settlement habitats (Houlihan et al., 2020).

The effect of photosynthesis on surrounding seawater carbonate chemistry can extend further than the immediate vicinity of the algal growth. Macroalgal assemblages that form complex communities can provide refuge from OA over much larger spatial scales from metres (e.g., in rock pools or within canopies) to kilometres (e.g., extensive algal beds in temperate areas) due to higher and more concentrated levels of metabolic activity (Björk

Table 1. Examples of studies assessing the ocean acidification (OA) refuge provision by macroalgal species for various coastal organisms

	References	Macroalgal species	Refuge function	Refuge provision
Phaeophyceae (brown)	Frieder et al., 2014	Simulations based the La Jolla Kelp Forest (not species specific)	Bivalve (<i>Mytilus californianus</i> and <i>Mytilus galloprovincialis</i>) developmental delays associated with OA mitigated under variable pH conditions simulating kelp forest conditions.	✓
	Wahl et al., 2018	<i>Fucus vesiculosus</i>	Bivalve (mussel <i>Mytilus edulis</i>) calcification impacts associated with OA mitigated in the presence of macroalgae (<i>F. vesiculosus</i>).	✓
	Young et al., 2022	<i>Saccharina latissima</i>	Bivalves (<i>Mercenaria mercenaria</i> , <i>Crassostrea virginica</i> and <i>M. edulis</i>) showed higher growth rates at low pH in the presence of macroalgae (<i>Saccharina latissima</i>).	✓
	Jiang et al., 2022	<i>Saccharina japonica</i>	Bivalve (Pacific oyster, <i>Crassostrea gigas</i>) showed higher scope for growth, clearance rate and decreased respiration rate and excretion rate at low pH in the presence of macroalgae (<i>Saccharina japonica</i>).	✓
	Cornwall et al., 2014	pH simulations for a kelp forest (not species specific)	Coralline algae (<i>Arthrocardia corymbosa</i>) showed further reduced growth rates under variable OA treatments.	×
	Saderne and Wahl, 2013	<i>Fucus serratus</i>	Bryozoan species (calcifying <i>Electra pilosa</i> and non-calcifying <i>Alcyonidium hirsutum</i>) showed higher tolerance to OA (high pCO_2) due to the periodic relief from OA provided by macroalgae (<i>F. serratus</i>).	✓
Rhodophyceae (red)	Pettit et al., 2015	<i>Padina pavonica</i>	Negative effect of OA on Foraminifera community composition was not mitigated by macroalgae (<i>Padina pavonica</i>)	×
	Doo et al., 2020	<i>Laurencia intricata</i>	Effect of low pH in Foraminifera (<i>Marginopora vertebralis</i>) growth and calcification mitigated in the presence of macroalgae (<i>L. intricata</i>)	✓
	Guy-Haim et al., 2020	<i>Polysiphonia</i> sp., <i>Ceramium</i> sp., <i>Rhodomenia</i> sp., <i>Ectocarpus</i> sp. and <i>Chondracanthus</i> sp.	Coralline algae <i>Ellisolandia elongata</i> is less susceptible to OA when colonised with non-calcifying macroalgal epiphytes.	✓
	Houlihan et al., 2020	CCA encrusted cobbles (not species specific)	Urchin (<i>Pseudoechinus huttoni</i>) settlement and post settlement growth unaffected by pH variability associated with the CCA encrusted cobbles.	—
Chlorophyceae (green)	Young and Gobler, 2018	<i>Ulva</i> sp.	Juvenile North Atlantic bivalves (<i>M. mercenaria</i> , <i>C. virginica</i> , and <i>Argopecten irradians</i> , <i>M. edulis</i>) showed higher growth rates under OA conditions when in the presence of <i>Ulva</i> .	✓

et al., 2004; Middelboe and Hansen, 2007; Duarte et al., 2013; Krause-Jensen et al., 2015). The refuge potential is especially significant in macroalgal assemblages with dense growth and complex canopy structure with the additional benefit of reduced seawater flow, which increases water residence time (Hendriks et al., 2014; Hurd, 2015).

Macroalgae have been reported to increase the average pH (to levels >8.5 pH units) in rock pools (Björk et al., 2004), lagoons (Menéndez et al., 2001) and bays (Buapet et al., 2013). For example, Krause-Jensen et al. (2015) found pH variability of 0.1–0.3 units occurs within the scale of 1 m² in response to location within the canopy of a large kelp forest in the Kobbefjord in southwest Greenland. At a slightly larger scale, Buapet et al. (2013) compared the pH conditions in different vegetation types (mixed macroalgae and seagrass beds) to non-vegetated areas in six shallow coastal bays in temperate Sweden. Their results showed that vegetation can influence the conditions at the scale of an entire bay as evidenced by higher pH and lower DIC concentrations relative to the adjacent seawater outside the

bay, even in areas of the bay where vegetation did not occur (Buapet et al., 2013).

Impacts of ocean acidification on macroalgae

It is important to consider the potential negative impacts that OA may have on macroalgae in order to determine their provision as OA refugia under future acidified conditions. Most studies that have assessed the response of macroalgae to changes in seawater carbonate chemistry associated with OA have shown that macroalgal species from all algal groups (red, brown and green) are generally physiologically tolerant to predicted OA and even show enhanced growth under these conditions (see reviews by Porzio et al., 2011 and Koch et al., 2013). This tolerance is attributed to the ability of most macroalgal species to efficiently assimilate DIC in various forms for photosynthesis thus allowing them to benefit from increased availability of DIC under acidified conditions (Fernández et al., 2015; Cornwall and Hurd, 2019). Of course, there

are exceptions with some species sensitive to OA, with sensitivity likely linked to mechanisms of carbon uptake and calcification (Cornwall et al., 2012; Hofmann and Bischof, 2014) as well as the scale of exposure (e.g., extreme low pH conditions associated with coastal acidification induced by mariculture activities as shown by Narvarte et al., 2020). Of all the algal groups, sensitivity to OA is most often reported for calcifying species (see the section “Calcification”), with this group facing the threat of being outcompeted by the more tolerant non-calcifying algae (Hofmann and Bischof, 2014).

Considering that some macroalgal species have heteromorphic life cycles (e.g., many kelp species), it is also important to consider the impact of OA on the different stages, where the early life stages (unicellular and microscopic stages) are usually deemed more sensitive to environmental change (Roleda et al., 2007). Although the early life stages of some macroalgal species have been shown to be more sensitive to other environmental factors (e.g., UV radiation; Roleda et al., 2007), there is evidence to suggest that early life stages are not affected by OA conditions (Roleda et al., 2012b, 2015; Leal et al., 2017). This provides positive evidence for the persistence of macroalgal habitats in future.

Conclusion and relevance

Macroalgae form important components of shallow coastal marine ecosystems and have been identified as potentially beneficial habitats for coastal species facing ongoing OA by provision of higher average pH conditions (Kapsenberg and Cyronak, 2019). Being a dynamic process, autotrophic pH modulation exposes organisms to higher variability in pH in space and time, and therefore alternating periods of stress and recovery (Wahl et al., 2018). As such, the species that occur in vegetated environments, like macroalgal ecosystems, although benefitting from periodic relief from the physiological stress incurred by OA, still require the physiological capacity to withstand high pH variability (Falkenberg et al., 2021). Despite short-term fluctuations in pH conditions, autotrophic biological activity likely provides associated organisms with long-term relief from ongoing OA (Hurd, 2015; Koweeck et al., 2018; Pacella et al., 2018). Considering the apparent tolerance of most photosynthetic macroalgae to future OA conditions, and particularly those taxa that are known to form large stands and aggregations, it is likely these habitats will continue to provide an important refuge for the many marine species associated with them.

The research highlighted in this review provides important evidence for the potential OA refuge function of brown, red and green macroalgae by mitigating the negative effects of OA on growth and calcification of mainly bivalves but also bryozoans, foraminifera and coralline algae (Table 1). However, research conducted over large spatial scales, across biogeographic regions, and for many macroalgae-associated species (such as other calcifying organisms and fish) is lacking and needs to be addressed in future research. The role of macroalgal habitats as refugia should be considered for local OA management and protected area management for conservation efforts (Morelli et al., 2016; Kapsenberg and Cyronak, 2019), especially in productive coastal marine environments where these habitats already provide important nursery areas for many marine species (James and Whitfield, 2022).

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