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22

Seagrasses and Macroalgae: Importance, Vulnerability and Impacts

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22.1 Introduction

Seagrasses and macroalgae are often grouped together for the reason that they are marine plants that provide many similar ecosystem services (e.g., nutrient cycling, fish habitat), but there are important differences between them. Seagrasses are vascular plants, meaning that they contain vascular tissues that allow them to distribute resources throughout the plant and grow to larger sizes than non-vascular plants. Although this latter feature becomes less important in the oceans, where gravity is less influential on body size than it is in air. Seagrasses are the sole entirely marine representative of the flowering plants (Angiosperms). Despite their name, they are not true grasses (Poaceae), although many seagrass species do superficially resemble grasslands in that they grow in large, leafy meadows (Figure 22.1a). Macroalgae, or seaweeds, resemble vascular plants in many ways, but they are actually protists – a group of eukaryotes that also includes fungi, protozoans, sponges and microalgae. Macroalgae are distinguished from their microscopic cousins – the “phytoplankton” and other single-celled algae – in that they are multicellular and generally reach much larger sizes (Figure 22.1b). Both seagrasses and macroalgae have the potential to be “ecosystem engineers” because they *create* habitat, providing organisms (e.g., marine mammals, fish and invertebrates) with a source of food and shelter, and change the abiotic and biotic environment (Jones *et al.*, 1994, 1997; Bos *et al.*, 2007). They oxygenate the water, recycle nutrients, trap and stabilize sediments, and provide a nursery ground for many marine organisms, particularly fishes. Indeed, seagrasses and macroalgae form the basis of the world’s primary fishing grounds.

22.1.1 Basic Biology and Ecology

Seagrasses

Seagrasses are aquatic angiosperms found in the marine environment. They occur along all continents except for Antarctica (Green & Short 2003; Short *et al.*, 2007) in areas ranging from intertidal coastal habitats to depths up to 61 m in offshore meadows (den Hartog 1970; Coles

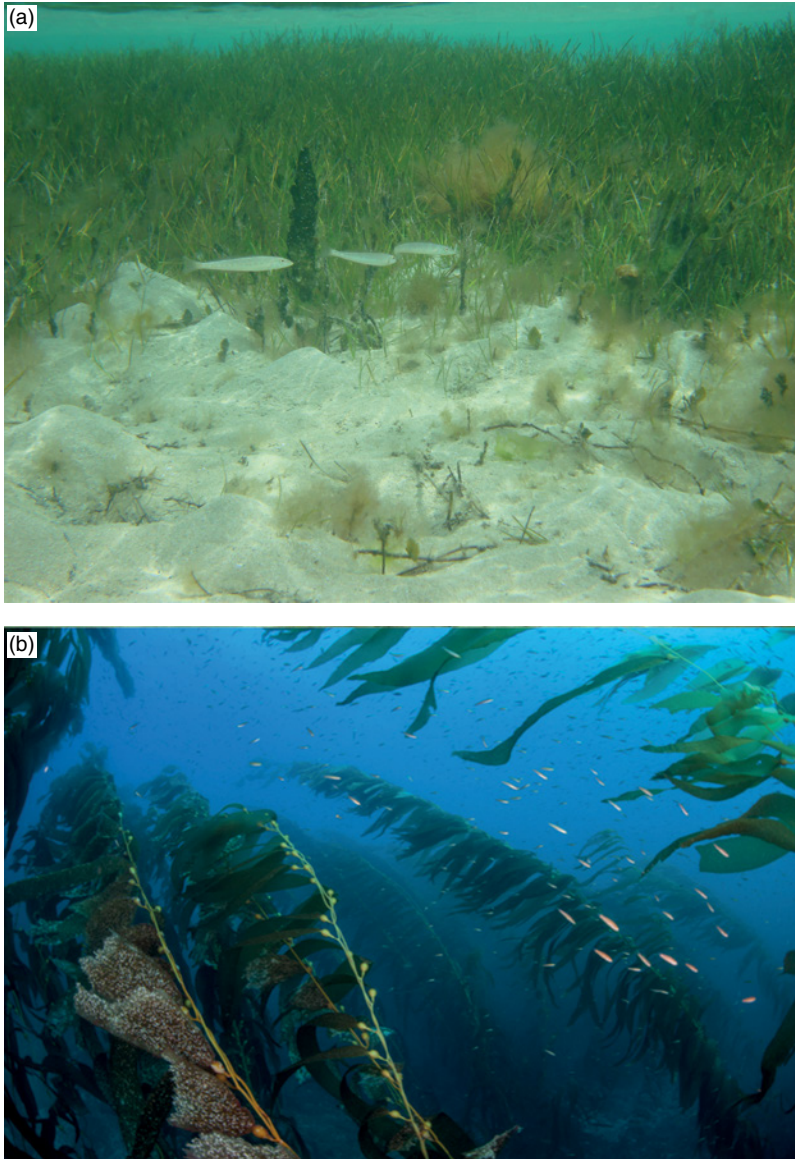


Figure 22.1 Fish use (a) seagrass meadows (photo credit: Peter Macreadie) and (b) kelp forests as a nursery grounds (photo credit: Shutterstock).

et al., 2009). The term seagrass represents an ecological rather than a taxonomic grouping and comes from the saline habitat in which these plants are found, the herbaceous growth form of the individual shoots and the formation of extensive meadows (den Hartog & Kuo, 2006). To be considered a seagrass marine plants must (i) be adapted to life in a saline medium; (ii) be able to grow when fully submerged; (iii) have a secure anchoring system; (iv) have a hydrophilous, or water mediated abiotic, pollination mechanism; and (v) compete successfully with other organisms in the marine environment (den Hartog & Kuo, 2006). To be able to survive, grow and reproduce in the marine environment seagrasses have developed flexible tissues with little to no lignin allowing for a more hydrodynamic design (Kuo & den Hartog, 2006), a lacunar

system to efficiently exchange gases between the below ground and above ground portions of the plant (Roberts *et al.*, 1984; Roberts & Moriarty, 1987), extreme reduction of the cuticle and loss of stomata allowing for gas and nutrient exchange directly between the leaves and the surrounding water column (Tomlinson, 1980; Tyerman, 1989) and hydrophilic pollen reducing the need for pollinators (Pettitt & Jermy, 1975; Philbrick & Les, 1996; Ackerman, 2006). Combined, these features have resulted in the successful colonization by seagrasses in coastal marine habitats for over 100 million years (Les *et al.*, 1997).

Seagrass taxonomy is a dynamic field with recent advances in genetic testing of seagrass species resulting in a reorganization of several species (Waycott *et al.*, 2006; Procaccini *et al.*, 2007). The current consensus is that there are fewer than 60 species of seagrass in the marine environment (Short *et al.*, 2007), which is only 0.02% of the estimated greater than 300,000 angiosperms found on the Earth (Les *et al.*, 1997). The relatively low diversity of species is even more surprising given that potential habitats for seagrasses cover up to 18% of the Earth's surface (Les *et al.*, 1997; Dawes, 1998). Seagrasses are classified within the superorder Alismatiflorae (Monocotyledonae) and are therefore not considered to be a true grass (Poaceae) (Les *et al.*, 1997). All species are members of five families: Zosteraceae, Cymodoceaceae, Posidoniaceae, Ruppiaceae and Hydrocharitaceae (den Hartog & Kuo, 2006). Common seagrass genera include *Enhalus*, *Halophila*, *Thalassia*, *Amphibolis*, *Cymodocea*, *Halodule*, *Phyllospadix*, *Posidonia*, *Ruppia*, *Syringodium*, *Thalassodendron* and *Zostera* (Short *et al.*, 2007). Diversity of seagrass meadows is generally greater in tropical compared with temperate systems with the greatest diversity found in the Indo-West Pacific with up to 14 species found in a single meadow.

All seagrasses have the same basic structure consisting of roots/rhizomes, stems/sheaths, and leaves (den Hartog, 1970; Kuo & McComb, 1989). This structure is grouped into three main morphological categories: (i) plants without strap-like leaves but with either a pair of petiolate leaves or leaflets on an erect stem (e.g., *Halophila* species); (ii) plants with strap-shaped leaves found at the top of an erect stem (e.g., *Thalassia*); and (iii) plants with strap-shaped leaves without visible erect stems (e.g., *Posidonia* and *Zostera* species) (Kuo & den Hartog, 2006). Species also differ in size from only a few centimetres tall (e.g., *Halophila*) to several meters long (e.g., *Enhalus*) and in the number of leaves per shoot (den Hartog, 1970; Kuo & den Hartog, 2006). Underground, seagrasses produce a well-developed creeping rhizome which provides stability, absorbs nutrients from sediment porewater, stores energy in the form of soluble carbohydrates and proteins and produces new shoots through clonal elongation (Kuo, 1993; Duarte *et al.*, 1998; Hemminga & Duarte, 2000). Rhizome morphology also differs between species and can be herbaceous to woody, cylindrical to laterally compressed, and monopodially or irregularly branched (Tomlinson, 1969; Roberts *et al.*, 1984; Webster & Stone, 1994; den Hartog & Kuo, 2006).

Seagrasses can reproduce both sexually via flowers and asexually through rhizome elongation and clonal growth. The majority of seagrasses maintain their populations primarily through clonal expansion and vegetative growth (den Hartog, 1970; Tomlinson, 1974; Hemminga & Duarte, 2000; Rasheed, 2004). This can be an efficient method of meadow expansion as seagrass rhizomes extend at rates between 1.2 and 574 cm yr⁻¹ depending upon the species (Marbà & Duarte, 1998). Clonal growth maintains and propagates "good" genotypes through growth and dispersal through fragmentation, removes the needs for the clones of the opposite sex in the dioecious populations, provides multiple versions of the same genotype in the event of mortality (e.g., escape in numbers) and removes the real costs of reproduction (Ackerman, 2006). However, sexual reproduction maintains genetic variation (Waycott *et al.*, 2006), generates new genotypes that can colonize new habitats or niches (Williams, 2001), facilitates dispersal via seeds (Kendrick *et al.*, 2012) and through the production of seeds and seed banks provides a dormant life history stage (e.g., seeds) that affords an escape in time from disturbance (van Lent & Verschuure, 1994; Greve *et al.*, 2005; Jarvis & Moore, 2010). Patterns in reproduction vary with species and are

affected by both biotic (genetics, physiological condition) and abiotic (e.g., light and temperature) factors (Ackerman, 2006).

Growth of seagrasses occurs through leaf elongation or replacement and through the production of new shoots (McRoy & McMillan, 1977). Seagrasses can be broadly characterized into small (cm) ephemeral species like *Halophila* that have high production and turnover rates (days to weeks) but low standing biomass between 2.3 to 104.0 g DW m⁻² or larger slower growing species such as *Amphibolis*, *Phyllospadix* and *Posidonia* with lower overall production and turnover resulting in clones that can be several hundred years old and above ground biomass >500 g DW m⁻² (Duarte & Chiscano, 1999). The rate of growth and relative biomass production are species specific (Duarte & Chiscano, 1999) and directly impacted by both biotic (e.g., competition, grazing) and abiotic factors (e.g., temperature, salinity, light sediment type) (see review in Mateo *et al.*, 2006).

Light is one of the main limiting factors in seagrass growth and survival (Dennison, 1987; Duarte, 1991; Dennison *et al.*, 1993). Compared to macroalgae, which only require between 0.1 to 1% of surface irradiance, seagrasses require 10 to 37% of surface light depending upon the species (Duarte, 1991). Seagrasses also need nutrients to grow, in particular nitrogen, phosphorus and carbon. Due to their reduced cuticle, seagrasses are able to absorb nutrients directly through both their leaves and rhizomes (Iizumi *et al.*, 1982; Short & McRoy, 1984; Stapel *et al.*, 1996; Terrados & Williams, 1997; Lee & Dunton, 1999). This allows seagrasses to become established in low nutrient areas including coral reef flats (Carruthers *et al.*, 2002). In addition, seagrasses have had to develop biochemical mechanisms for enhanced inorganic carbon uptake to ensure photosynthetic carbon demands are met (Mateo *et al.*, 2006). As a result seagrass meadows are a major sink for carbon in the global ocean (Duarte *et al.*, 2005; Fourqurean *et al.*, 2012; Macreadie *et al.*, 2014a).

Herbivores strongly influence the biomass, productivity and community composition of seagrass meadows through both direct and indirect mechanisms (Duffy *et al.*, 2003; Heck & Valentine, 2006; Lewis & Anderson, 2012; Atwood *et al.*, 2015). Vertebrate herbivores (fish, turtles, dugongs, waterfowl) and sea urchins often graze seagrasses directly (Aragones & Marsh, 2000; Rivers & Short, 2007; Hughes *et al.*, 2008). Direct herbivory of seagrass leaves varies widely between species or locations, for example, grazers in *Posidonia oceanica* beds in the Mediterranean consumed between 10 and 70% of above ground biomass (Tomas *et al.*, 2005), while herbivores in *Thalassia testudinum* populations in Bermuda reduced leaf width and length by 70% and 73% respectively (Fourqurean *et al.*, 2010). Smaller mesograzers (crustaceans, gastropods, isopods) indirectly affect seagrass growth by grazing on seagrass epiphytes (Williams & Heck Jr, 2001; Duffy, 2006). Epiphytic algae are regularly consumed by small animals, which serve as a vital food source for upper level consumers that come to the seagrass meadows to forage (Williams & Heck Jr, 2001; Hughes *et al.*, 2008). The control of mesograzers over epiphytic production is a key factor in the balance and transitions between seagrass and algal dominated benthic (seafloor) communities (Duffy, 2006; Reynolds *et al.*, 2014; Atwood *et al.*, 2015; Duffy *et al.*, 2015).

Macroalgae

Macroalgae are the multicellular or siphonocladous representatives from three protistan groups: Rhodophyta (red algae), Chlorophyta (green algae) and the Phaeophyceae (brown algae) within the division (phylum) Heterokontophyta (that also include diatoms, golden algae and oomycete fungi) (van den Hoek *et al.*, 1995). These groups are taxonomically diverse with over 7,000 species within over 700 genera of red algae (primarily multicellular), over 2,000 species from 265 genera of brown algae (entirely multicellular) and over 8,000 species from 500 genera of green algae (of which approximately 1,000 species are multicellular or siphonocladous and marine) (van den Hoek *et al.*, 1995; Guiry, 2012). It is worth noting however, that algal

taxonomy is very dynamic and controversial, with many recent changes being made, particularly with the aid of molecular data. Macroalgae occur in marine, estuarine and freshwater environments but most of the diversity is in marine systems, where algae originated (van den Hoek *et al.*, 1995). In contrast to seagrasses, macroalgal diversity and biomass is often greater in temperate than tropical regions (Phillips, 2001). In particular, the large, brown, macroalgal kelps in the orders Laminariales and Fucales, that often create extensive habitats (e.g., kelp forests and kelp beds) for fish and invertebrates, are generally restricted to waters of $<20^{\circ}\text{C}$. Macroalgae are also found in Antarctica, but in relatively low diversity with approximately 120 species recorded (Clayton, 1994).

With the vast taxonomic diversity of macroalgae there is also diversity in structure, ecophysiology and reproduction. However, in general macroalgae differ from seagrasses in the following key ways: (i) macroalgae lack vascular tissues and therefore the methods by which they transport nutrients and dissolved gases differ as seagrasses transport minerals and nutrients in specialized tissues, while macroalgae rely on diffusion across the cell surface for uptake and transport (Friedlander & Dawes, 1985); (ii) macroalgae generally lack underground tissues and instead attach to hard substrata by a holdfast that is purely an attachment organ and not involved in nutrient and water uptake as the roots of vascular plants are; (iii) there is significant diversity in cell wall structure and biochemistry of macroalgae but generally their cell walls have a fibrillar skeletal framework and extensive polysaccharide matrix (primarily polyanionic over neutral polysaccharides) and lack lignin (Kloareg & Quatrano, 1988; Domozych, 2011); (iv) macroalgae have complex and diverse life cycles and reproduction, but all lack the flowers and seeds common to seagrasses and other angiosperms; (v) macroalgae have five different chlorophyll pigments and a variety of other accessory pigments that harvest light from a range of wavelengths, and all macroalgal tissues are able to photosynthesize (whereas seagrass photosynthesis is limited to cells found in the leaf epidermis) (Zimmerman, 2006; Raven & Hurd, 2012), thus enabling them to grow in a range of light environments with as little as 0.12% of incident light (Markager & Sand-Jensen, 1992), compared to seagrasses that are limited to depths with $\geq 11\%$ of incident light (Duarte, 1991); and (vi) macroalgae have a lower C:N ratio than seagrasses and lack lignocellulose tissue, making them more nutritious and energetically favourable for consumption by herbivores (Enríquez *et al.*, 1993).

The *thallus* (body) of a macroalga consists of a *holdfast* for attachment to hard substrata such as rock or coral, or other organisms (where they may grow epiphytically or epizoically). Some species may then have undifferentiated *fronds* arising from the holdfast, whereas others (particularly large brown algae) have a *stipe* (analogous to the stem of vascular plants) that functions to elevate the *blades* (analogous to leaves) in the water column where light levels are higher. All tissues in the macroalgae contain chloroplasts capable of photosynthesis, although large taxa generally have higher densities of chloroplasts or greater quantities of light-capturing pigments in the blades, which are the primary sites of photosynthesis. Red algal cell walls generally consist of a skeleton of cellulose microfibrils arranged parallel to the cell surface with an entangled network of microfibrils in each layer, and a matrix of sulphated polysaccharides that may be either primarily agarose (regular repetition of β -D-galactosyl (1,4)-3,6-anhydro- α -L-galactose) or carrageenans (primarily κ -carrageenan sulphated on C-4 of 3-linked β -D-galactose and 3,6-anhydro-D-galactose present or λ -carrageenan sulphated on C-2 of 3-linked β -D-galactose), depending on the taxonomic group within the Rhodophyta (McCandless & Craigie, 1979; Kloareg & Quatrano, 1988). Brown algal cell walls also have a skeleton of crystalline cellulose microfibrils in layers, parallel to the cell surface, but without defined orientation in each layer (Kloareg & Quatrano, 1988; Domozych, 2011). The skeletal framework is embedded in a polysaccharide matrix, that may constitute 10–45% dwt of the thallus, that is primarily composed of alginate (linear chains of β -1,4-D-mannuronic acid and α -1,4-L-guluronic acid),

but may also include an abundance of sulfated polysaccharides (fucoidans, ascophyllans), laminarin, mannitol, proteins and phenolics (Kloareg & Quatrano, 1988; Chiovitti *et al.*, 2001). In large brown algae such as the kelps, the matrix components may embed and bond to the cellulose microfibrils resulting in structurally complex cell walls (Kloareg & Quatrano, 1988; Domozych, 2011) that are both strong and flexible to withstand wave forces (Denny & Gaylord, 2002; Martone, 2007; Guenther & Martone, 2014). The green algae have the greatest diversity of cell wall skeletal biochemistry with differences at multiple levels of the taxonomic hierarchy and between life phases within species (Kloareg & Quatrano, 1988; Domozych *et al.*, 2012). Whilst cellulose is generally less abundant in macroalgal cell walls than those of vascular plants such as seagrasses, the cell walls in the green macroalgal orders Siphonocladales, Chlorophorales and Ulvales may contain up to 70% highly crystalline cellulose (Kloareg & Quatrano, 1988), whereas other green algal orders may lack cellulose and instead have a fibrillar skeleton composed of β -1,3-xylans or β -1,4-mannans (Domozych, 2011). Some green (e.g., *Halimeda*) and red (e.g., Corallinales) macroalgae also have calcification of the cell walls (van den Hoek *et al.*, 1995). Cell wall structure is significant in terms of the susceptibility to herbivory, the economic value of polysaccharides extracted from the matrix (e.g., alginates, agar and carrageenan) and the potential contribution different macroalgal taxa may make to blue carbon stores (Hill *et al.*, 2015; Trevathan-Tackett *et al.*, 2015).

Algae have complex and diverse life history strategies, but there some generalizations associated with phylogenetic relationships. Unlike seagrasses, macroalgae do not flower, nor produce seeds. There are three basic life history patterns observed in macroalgae (van den Hoek *et al.*, 1995): (i) *haplontic* algae have one vegetative phase (gametophyte) which is haploid and the zygote is the only diploid cell; (ii) *diplontic* algae also have only one vegetative phase (gametophyte) but in this case it is diploid and the gametes (produced by meiosis) are the only haploid cells; and (iii) *diplohaplontic* algae have a diploid vegetative phase (sporophyte) that alternates with a haploid vegetative phase (gametophyte) (Figure 22.2). The sporophyte and gametophyte of diplohaplonts may be either isomorphic or heteromorphic, in which case either phase may

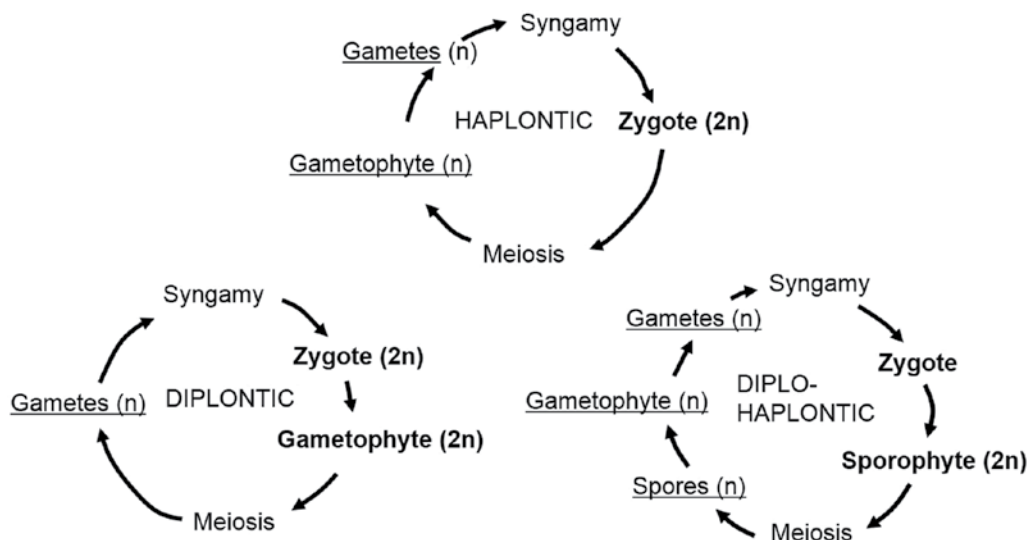


Figure 22.2 Basic life history patterns of macroalgae. Underlined stages are haploid, and bold stages are diploid. Note gametes can be produced by meiosis (diplontic) or mitosis (haplontic and diplohaplontic). Note: syngamy is the fusion of gametes analogous to fertilization. (Source: modified and granted from Clayton (1990)).

dominate. In the major red algal class the Florideophyceae, a special case of a triphasic diplohaplontic life cycle is predominant (van den Hoek *et al.*, 1995). In this case there are two sporophyte stages, where generally a carposporophyte (that usually develops within the female gametangia from a fertilized egg and is parasitic on the gametophyte) produces carpospores that germinate to form a second sporophyte stage that is free-living known as a tetrasporophyte. The tetrasporophyte produces tetraspores that germinate to form gametophytes. Within all life cycles, the gametophytes may be either dioecious (with separate male and female thalli) or monoecious (essentially hermaphroditic).

The propagules (spores, gametes and zygotes) of macroalgae are theoretically capable of planktonic dispersal, enabling both gene flow between populations and colonization of new habitats. However, while there is evidence that some macroalgae may be capable of long-distance dispersal by floating fertile fragments (van den Hoek, 1987; Macaya *et al.*, 2005; McKenzie & Bellgrove, 2008; Macreadie *et al.*, 2011; Fraser *et al.*, 2013), most macroalgal taxa are thought to have relatively limited dispersal of planktonic propagules (Santelices, 1990). Understanding the dispersal capacity, genetic diversity and potential for adaptation in a changing climate is currently an active area of phyiological research.

Macroalgae are photoautotrophs, often with very high rates of primary productivity that make significant contributions to carbon capture (Hill *et al.*, 2015), nutrient cycling and global oxygen production. With few exceptions, energy used in the metabolism of all living organisms comes from the fixation of sunlight in the process of photosynthesis. This process is carried out by both aquatic and terrestrial autotrophs (chlorophyll-containing plants), which convert inorganic carbon in the form of carbon dioxide or carbonates from their environment into organic compounds. Whilst light reaching the earth's surface is scattered and absorbed by particles in the atmosphere, the degree of scattering and absorption is significantly greater under water. This means that the challenge of capturing light to drive photosynthesis is greater for aquatic plants than terrestrial ones. As solar energy penetrates the oceans it is altered in both quality and quantity through attenuation with depth, and varies in both space and time. Thus the penetration of different wavelengths of light is not equal. Generally infrared and far red (above 700 nm) and UV (below 400 nm) spectra are absorbed in surface waters and only the visible spectrum penetrates to depth. Red light (620–700 nm) is more rapidly attenuated than light in the blue – green (approximately 450–575 nm) part of the visible spectrum, which penetrates the deepest.

Algae are able to capture photosynthetically active radiation (PAR; light in the range 400–700 nm) because they possess chlorophyll-*a* and a range of additional accessory pigments that capture light at different wavelengths. The light energy is passed either directly from the chlorophyll-*a*, or from accessory pigments to chlorophyll-*a*, and then onto the reaction centres of photosystems I and II, where electron transport occurs and ATP and NADPH are generated. The Calvin Cycle then uses the chemical energy of ATP and NADPH to reduce CO₂ to sugar.

Different lineages of algae have resolved different solutions to the challenges of capturing light at depth, and consequently there is significant diversity of accessory pigments amongst algal lineages (van den Hoek *et al.*, 1995). The three macroalgal groups differ in their photosynthetic physiology and therefore their capacity to photosynthesize in different light environments. Indeed the red, green and brown colouration of the three macroalgal divisions is attributable to the different combinations of photosynthetic pigments. There are also differences in the structure of the chloroplasts amongst lineages (related to the endosymbiotic origins of the plastids). The green macroalgae have similar photophysiology to that of seagrasses and land plants with chloroplasts bound by a double membrane and thylakoids stacked into grana, chlorophylls *a* & *b* and carotenenes as the primary photosynthetic pigments, and starch as the storage product (van den Hoek *et al.*, 1995). Because the key absorption peaks of chlorophyll are in the red end of the spectrum (Table 22.1) and red light attenuates fastest, green

Table 22.1 Absorption peaks (in nm) for major algal photosynthetic pigments in organic solvents (from Jeffrey & Humphrey, 1975; Evans, 1988; Tandeau de Marsac & Houmard, 1988).

Pigment	Wavelength (nm)
Chlorophyll <i>a</i>	420, 662
Chlorophyll <i>b</i>	455, 644
Chlorophyll <i>c</i>	444, 626
β -carotene	425, 450, 480
Fucoxanthin	425, 450, 475 (in hexane)
Phycoerythrin	495, 545, 564 (main)
Phycocyanin (PC)	618
Allophycocyanin (APC)	650

macroalgae (as with seagrasses) are generally restricted to shallow waters. The red macroalgal chloroplasts have single thylakoid lamellae that are unstacked and run parallel to long axis of the chloroplast, contain chlorophyll-*a* only and phycoerythrin, phycocyanin, allophycocyanin and carotenoids as the key accessory pigments, and store excess photosynthates as floridean starch (α (1–4) glucan) (van den Hoek *et al.*, 1995). This combination of accessory pigments allow red macroalgae to harvest light at a range of wavelengths, including the blue-green light (Table 22.1), and thus red algae are often found at the greatest depths. The brown macroalgae have chloroplasts surrounded by four membranes including the endoplasmic reticulum, three thylakoid lamellae and a girdle lamella, contain chlorophylls *a*, *c1*, *c2* & *c3*, β -carotene, and fucoxanthin as the primary photosynthetic pigments and store their energy reserves as chrysolaminarian (β (1–3) glucan) or mannitol (van den Hoek *et al.*, 1995). The photosynthetic pigments are associated with the thylakoid membranes of the chloroplasts. Most chloroplast pigments, including chlorophylls, carotenoids and xanthophylls are integrated into the thylakoid membranes (Hurd *et al.*, 2014). In contrast the phycobiliproteins of the Rhodophyta are formed in phycobilisomes on the surfaces of thylakoid membranes (Hurd *et al.*, 2014).

As with seagrasses, herbivores can also strongly influence the biomass, productivity and community composition of macroalgal assemblages through both direct and indirect mechanisms. Studies have shown that in addition to macrograzers (>2.5 mm) such as molluscs, fish and sea urchins (Paine & Vadas, 1969; Underwood, 1980; Andrew & Underwood, 1993; Hixon & Brostoff, 1996; Bennett & Bellwood, 2011), mesograzers (500 μ m – 2.5 mm) such as amphipods and small herbivorous snails (Brawley, 1992; Duffy & Hay, 2000; Bellgrove *et al.*, 2014) and micrograzers (<500 μ m) such as copepods (Bellgrove *et al.*, 2014) can influence the structure of macroalgal assemblages. For example, amphipods are known to decrease macroalgal and microalgal abundances (Brawley & Adey, 1981; Brawley & Fei, 1987; Brawley, 1992; Poore, 1994; Duffy & Hay, 2000; but see Poore *et al.*, 2009) and aid propagule dispersal (Buschmann & Bravo, 1990; Brawley, 1992). Through consumption of mature algal thalli and/or microscopic propagules, different intertidal and subtidal herbivores can affect chemical defences and successional pathways, determining algal species composition and abundance (Duffy & Hay, 1994; Dunmore & Schiel, 2003; Burkepile & Hay, 2010; Bellgrove *et al.*, 2014). The transition from algal canopies to more simplified, coralline algal assemblages has been described thoroughly in intertidal and shallow sublittoral temperate (Livore & Connell, 2012) and tropical marine ecosystems (McClanahan & Kurtis, 1991; Andrew & Underwood, 1993; O’Leary & McClanahan,

2010). Dramatic changes to the abundances of kelps and their associated communities have been associated with trophic cascades from the removal of keystone predators (Estes & Palmisano, 1974) and, more recently, interactions between climate change and overfishing (Johnson *et al.*, 2011; Atwood *et al.*, 2015). The impacts of these habitat losses on commercially important fisheries stock has also been recognized (Johnson *et al.*, 2011).

22.1.2 Distribution and Habitat

Seagrasses grow on every continent, with the exception Antarctica (Larkum *et al.*, 2006). Their distributional patterns are often defined according to mean water temperature for the warmest month: tropical – 25°C; subtropical – 20°C; temperate – 15°C; and cold temperate – 10°C (Larkum *et al.*, 2006). The main habitats are estuaries, coasts (including gulfs and bays), and deep water. Macroalgae are found on all coastlines, including Antarctica (Clayton, 1994), but their distributional patterns have been influenced by biogeographical, ecological and phylogenetic processes over millennia and have less distinct latitudinal gradients linked to temperature (Clayton, 1994; Phillips, 2001) than are apparent for seagrasses.

With few exceptions, seagrasses tend to grow in soft sediments (sand and mud), where they use roots to maintain their position, whereas macroalgae, grow on hard substrates (e.g., dead coral, rock) or epiphytically and epizoically on other organisms, and use holdfasts to anchor themselves (Figure 22.3). Therefore, macroalgae and seagrasses tend to be benthic plants. Both grow intertidally and subtidally, with their depth limit determined by light levels (necessary for photosynthesis) and their capacity to harvest different wavelengths of light (Table 22.1) – e.g., in clear waters they can grow deeper than in murky waters. Seagrasses have a depth limit of 90 m (Duarte, 1991), whereas macroalgae have been reported at depths of more than 200 m (Raven & Hurd, 2012). Differences in nutrient uptake rates and light requirements account for which autotroph dominates benthic habitats; where seagrasses and macroalgae co-occur seagrasses out-compete macroalgae only under high-light, low-nutrient conditions (Valiela *et al.*, 1997; Thomson *et al.*, 2012).

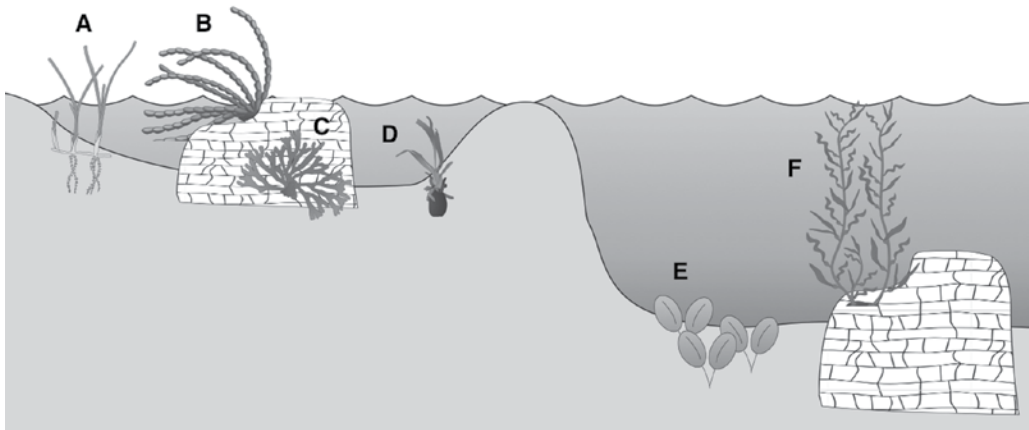


Figure 22.3 Macroalgae (B, C, F) tend to grow on hard substrates, whereas seagrasses (A, D, E) tend to grow on soft sediments. Examples of common macroalgal and seagrass species: (A) *Halodule wrightii* (shoalweed), (B) *Hormosira banksii* (Neptune's necklace), (C) *Codium fragile* (Dead man's fingers), (D) *Posidonia oceanica*, (E) *Halophila ovalis*, and (F) *Macrocystis pyrifera* (giant kelp). Figure created by Peter Macreadie using the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

22.2 Importance for Fisheries and Aquaculture

22.2.1 Use of Seagrass and Macroalgae by Fish and Crustaceans

Seagrasses and macroalgae are often important foundation species in coastal habitats (Dawes, 1998; Hemminga & Duarte, 2000; Orth *et al.*, 2006a). Their structure in the water column and along the substrate creates a potential habitat and foraging area for a diverse faunal community including many types of fish, octopuses, squids, snails, oysters, sponges, shrimps, worms, urchins, anemones, crabs, polychaetes, and clams (Hemminga & Duarte, 2000; Heck & Valentine, 2006; Hughes *et al.*, 2008). Fauna that utilize these habitats are categorized into resident or transient species (Jackson *et al.*, 2001). Resident species are those organisms that inhabit the beds all year round throughout their entire lives, while transient species may use the seagrass meadow or macroalgal bed seasonally or for only a portion of their life-cycle.

Within marine plant communities it is difficult to discern between resident and transient species due to the large sampling requirements both in type of data (e.g., length-frequency distributions, age classes) and frequency of sampling required to make this distinction (Moser *et al.*, 1998; Jackson *et al.*, 2001). In addition, marine macroalgae are not always attached to the substrate and can travel over long distances in the open ocean complicating observations of fauna utilization (Kingsford & Choat, 1985; Coston-Clements & Center, 1991; Wells & Rooker, 2004). Current studies show that resident seagrass and macroalgal species are typically smaller cryptic species with minimal value as commercial or recreational fisheries species (Kikuchi, 1974; Fedoryako, 1989; Kingsford, 1993; Edgar & Shaw, 1995; Jackson *et al.*, 2001). A large portion of those economically important fisheries species utilize seagrass meadows and macroalgal beds or rafts on a transient basis (Jackson *et al.*, 2001; Wells & Rooker, 2004; Macreadie *et al.*, 2011). These species are primarily utilizing these areas either as a foraging habitat, as protection from predation or as a temporary nursery area for juvenile development (Pollard, 1984; Ebeling *et al.*, 1985; Carr, 1991, 1994; Edgar & Shaw, 1995; Guidetti, 2000; Macreadie *et al.*, 2009).

Foragers are attracted to marine plant habitats due to the abundance and diversity of potential faunal prey (Bell & Pollard, 1989; Webb, 1991; Tupper & Boutillier, 1995; Jackson *et al.*, 2001; Macreadie *et al.*, 2010a, b; Jenkins *et al.*, 2011). Seagrass meadows are able to support diverse food webs based on primary production derived from seagrasses, epiphytic algae growing on seagrass leaves and benthic microalgae from the sediment surface (Hemminga & Duarte, 2000; Heck & Valentine, 2006). Most of the primary production transferred to higher trophic levels within seagrass meadows is due to the consumption of fast growing epiphytes by mesograzers including small crustaceans and gastropods (Klumpp *et al.*, 1992; Jernakoff & Nielsen, 1997) rather than by direct grazing of seagrass leaves. These mesograzers are the key prey items for many commercial and recreational fisheries linking seagrass meadows to upper trophic levels (Jordan *et al.*, 1997). Marine macroalgal communities also support large populations of mesograzers as well as herbivorous fish and invertebrates (Davenport & Anderson, 2007). However, unlike seagrass meadows many grazers within macroalgal beds are feeding directly on the macroalgae rather than epiphytic material (Steneck *et al.*, 2002). Grazing is higher in macroalgae compared to seagrasses due in part to the greater nutritional values of macroalgae (Duarte, 1990; Pillans *et al.*, 2004; Raubenheimer *et al.*, 2005) and plant defences within seagrasses such as toughness and secondary metabolites (e.g., Paul & Hay, 1986; Targett & Targett, 1990; Meyer *et al.*, 1994) resulting in an overall greater palatability and ease in digestion of macroalgae compared to many seagrass species.

Seagrass meadows and macroalgal beds or rafts also function as vital nursery grounds for many marine fisheries species (Carr, 1991, 1994; Jackson *et al.*, 2001; Heck *et al.*, 2003; Guido *et al.*, 2004; Unsworth *et al.*, 2008). For example, recent surveys in the Mediterranean have shown that between 30–40% of the value of commercial and approximately 29% of recreational

landings were of fish species that predominantly rely on seagrass habitats during their juvenile stages (Jackson *et al.*, 2015). For a habitat to serve as a productive nursery, juveniles within that habitat must reach maturity in order to contribute to future generations (Beck *et al.*, 2001). Structurally, seagrasses and large macroalgae such as kelp provide substrate for direct spawning (Polte & Asmus, 2006), alter local hydrodynamic conditions promoting planktonic larval settlement (Jackson *et al.*, 2001; Plaza *et al.*, 2010), and reduce predation pressure (Orth *et al.*, 1984; Main, 1987; Rooker *et al.*, 1998; Hindell *et al.*, 2000; Steneck *et al.*, 2002), thereby increasing the chances of juvenile survival. This makes marine macrophyte habitats essential to the continued successful management of coastal fisheries species.

22.2.2 Abundance, Diversity, Growth, and Survival of Fish in Seagrass and Macroalgae as Compared with other Nearshore Habitats

Compared to unstructured nearshore habitats (e.g., sandy substrate, mud flats), marine macrophyte communities, in general, support greater abundance, diversity, growth and survival of commercial and recreational fisheries species (Orth *et al.*, 1984; Kingsford & Choat, 1985; Main, 1987; Rooker *et al.*, 1998; Hindell *et al.*, 2000; Nagelkerken *et al.*, 2002; Steneck *et al.*, 2002). As a result both seagrass meadows and selected macroalgal communities (including rafting *Sargassum*) were designated as essential Fish Habitat for several coastal migratory species enhancing the protection of these populations in the United States under The Magnuson-Stevens Fishery Conservation and Management Act (Administration, 1996). The enhanced fisheries production is primarily attributed to the structure provided by marine macrophytes as both survival and growth are similar or enhanced between seagrass meadows and other structured habitats including macroalgal beds, oyster reefs, mangroves or salt marshes (Beck *et al.*, 2001; Nagelkerken *et al.*, 2002; Heck *et al.*, 2003; Hosack *et al.*, 2006). Lower predation pressure results in less time and energy spent on evading capture or hiding and more time spent on foraging (Fraser & Gilliam, 1987; Bax, 1998). The energy not utilized in avoiding predators is applied to faster growth rates resulting in greater survival rates (Orth *et al.*, 1984; Kingsford & Choat, 1985; Rooker *et al.*, 1998; Nagelkerken *et al.*, 2002).

However, it is important to note that the complexity of the structure, not just its presence, is important as habitats with greater space-size heterogeneity (greater variation in gap size and shape between structures) support higher diversity compared to more homogeneous structured habitats (Hori *et al.*, 2009; St. Pierre & Kovalenko, 2014). Within seagrass and macroalgal beds, homogenous structure (dense high cover areas) is beneficial to smaller fish in the form of refuge from predators. Therefore, successful evasion is also detrimental to visual predators, which are often the more economically valuable fisheries species (e.g., red drum; Holt *et al.*, 1983), due to greater number of hiding places for prey in high density habitats (Kingsford, 1993; Edgar & Shaw, 1995; Hovel & Lipcius, 2002). For habitats with greater space-size heterogeneity, the combination of open space and patchy structure may provide benefits for both smaller fish hiding from predators and for visual predators hunting for prey. This pattern was observed in both Caribbean and Indonesian juvenile reef fish communities where greater species richness was documented in areas that seagrass beds were adjacent to mangrove habitats. The combined habitat had a greater space-size heterogeneity and greater species richness compared to either habitat alone (Nagelkerken *et al.*, 2002; Unsworth *et al.*, 2008).

22.2.3 Spatial Scales at which Fish and Crustaceans Use Seagrass and Macroalgal Habitat

Fish and invertebrate communities are affected by factors across a continuum of scales ranging from patch ($<10\text{ m}^{-2}$) to ecotone (100s m) levels (Jordan *et al.*, 2012). Understanding the scales

that affect fish and crustacean abundance, species richness, survival and growth are important for fisheries modeling, conservation and protection of habitat, and marine park zonation. Such information allows questions to be answered such as: “How will increasing fragmentation of seagrass meadows and macroalgal beds affect fish and crustacean populations?,” “What is an appropriate boundary for a Marine Protected Area to protect important fish and crustacean source populations?,” and “How will changing water temperatures and increasing storminess in the coastal zone affect habitat use by fisheries species?”

At small spatial scales ($<10 \text{ m}^{-2}$) communities of fishes and invertebrates utilizing seagrass meadows and macroalgae are significantly affected by habitat characteristics such as shoot density, canopy height, and patchiness. Gratwicke & Speight (2005) developed a simple habitat assessment score (HAS) to assess the importance of complexity at small spatial scales on species richness and total fish abundance for shallow tropical marine habitats, including sandy patches, algal beds, seagrass meadows, and reefs. According to multiple regression models, they found that HAS variables – including rugosity, variety of growth forms, height (vertical relief), refuge size, and percent cover of plants and reef – accounted for 71 and 22% of the variation in observed species richness and total fish abundance respectively. Rugosity and the variety of habitat-forming growth forms were the main predictors of species richness, whereas vertical relief was the main predictor of total fish abundance. Habitat complexity is therefore likely to be the most important predictor of fish crustacean use of seagrass and macroalgal habitats at small spatial scales.

At broad scales (100s m) habitat heterogeneity significantly affects species abundance and community composition through the modification of ecosystem functions such as predator–prey interactions (e.g., lower predation rates on fish moving between structured habitats than fish moving across unstructured habitats; Irlandi, 1996; Sheaves, 2005; St. Pierre & Kovalenko, 2014). Inter-habitat interactions may result in greater abundance and more diverse fish communities than either habitat alone indicating an enhanced performance of ecosystem function resulting in higher catch rates and underscore the need to consider coastal vegetated environments as mosaics of interconnected habitats that interact dynamically (Baillie *et al.*, 2015). At intermediate to large spatial scales, fish and crustaceans inhabiting seagrass and macroalgal-dominated environments are predominately affected by abiotic factors (e.g., water temperature, salinity, wave exposure) over multiple temporal scales (tidal, diel, seasonal) and adjacent habitat type (Heck & Orth, 1980; Bell & Westoby, 1986; Grabowski *et al.*, 2005; Macreadie *et al.*, 2010; Baillie *et al.*, 2015). Advances in remote sensing and ecosystem-based models designed to link fisheries species to habitat have increased dramatically in the past decade. Significant outcomes of such work include the identification of changing use of seagrass and macroalgal habitat corresponding with abiotic changes (e.g., water temperature) associated with climate change (Booth *et al.*, 2011), which will be discussed in further detail in subsequent sections.

22.2.4 Habitat Value

Currently 28.8% of global fish stocks are estimated to be overfished or fished at a biologically unsustainable level (FAO, 2014a). In addition, 61.3% of stocks are considered to be fully fished with no room to increase harvest without overfishing the stock. To meet the demands for fish in an ever growing human population, aquaculture efforts have risen over the last 30 years and now account for nearly 50% of the world's fish used as food (FAO, 2014a). Aquaculture production increased 6.2% between 2000 and 2012 resulting in an all-time high global aquaculture production of 90.4 million tonnes in 2012 (US\$144.4 billion); (FAO, 2014a). In conjunction with the benefits from increased aquaculture, issues associated with aquaculture including

eutrophication of adjacent coastal waters attributed to fish and shrimp farming and the leasing of benthic habitat as space for shellfish aquaculture has also increased (Handy & Poxton, 1993; Delgado *et al.*, 1997; Bouwman *et al.*, 2013).

Impacts of aquaculture on seagrass growth and survival depends upon the methods used and the species being cultivated. One of the primary issues associated with fish farms, and shrimp and fish ponds in coastal marine habitats is the accompanying increase in eutrophication due to high nutrient outputs from fish farm wastes (Holmer & Kristensen, 1992; Burford *et al.*, 2003; Herbeck *et al.*, 2013). High nutrient loads stimulate growth of epiphytes, macroalgae and phytoplankton reducing light availability for seagrasses resulting in possible declines (Hauxwell *et al.*, 2001; McGlathery, 2001; Burkholder *et al.*, 2007). In addition, top-down control of herbivores on epiphytes is also reduced due to overfishing of herbivorous fishes resulting in greater epiphyte growth and reduced seagrass growth (Neckles *et al.*, 1993; Heck *et al.*, 2000; Reynolds *et al.*, 2014). In areas where floating fish farms are located seagrass disappears directly underneath the cage in the surrounding areas shoot mortality increases while biomass, shoot density and rhizome growth decrease (Holmer *et al.*, 2003; Pergent-Martini *et al.*, 2006; Holmer *et al.*, 2008).

Shellfish aquaculture has been shown to negatively affect seagrass habitats due to direct competition for space (Wagner *et al.*, 2012; Skinner *et al.*, 2014). Research on oyster aquaculture in Willapa Bay, Washington on the US west coast suggests that this interaction is nonlinear and thresholds occur above which shoot density of native seagrasses (*Zostera marina*) declines markedly (Wagner *et al.*, 2012). This threshold value may be affected by the method in which the oysters are grown. For example, oysters grown on structures can have additional physical effects, including shading and sediment erosion around the structure resulting in a loss in seagrass cover of up to 75% for oyster stake culture and up to 100% loss of eelgrass under oyster racks (Everett *et al.*, 1995). However, oysters grown on longlines, in suspended bags and hanging culture of floating oyster bags and have been documented to cause little reduction in eelgrass density and cover (Wisehart *et al.*, 2007; Tallis *et al.*, 2009; Skinner *et al.*, 2014). Harvesting methods can also have varying effects on seagrass growth and survival (Wisehart *et al.*, 2007; Tallis *et al.*, 2009). Mechanical shellfish harvest practices directly removed plants and generally caused more disturbance than hand harvest or off-bottom longline oyster culture techniques in Willapa Bay (Wisehart *et al.*, 2007; Tallis *et al.*, 2009; Dumbauld & McCoy, 2015). Further research into the best practices for shellfish aquaculture in seagrass habitats is required for more efficient management of this industry.

To a lesser extent than shellfish or finfish aquaculture, seagrass meadows also compete for space with "seaweed" farms (Eklöf *et al.*, 2005; Ehre & Meeuwig, 2015). As with finfish and shellfish aquaculture, seaweed aquaculture has also increased dramatically from <1 million wet tonnes in 2000 to 23.8 million wet tonnes in 2010 (FAO, 2014b). Open-water seaweed farming was first introduced to Unguja Island (Zanzibar, Tanzania) around 1990 and was quickly established in and around seagrass meadows (Pettersson-Löfquist, 1995; Msuya *et al.*, 2014). Two species of red algae, *Eucheuma denticulatum* and *Kappaphycus alvarezii* are primarily grown and harvested by hand for extraction of hydrocolloid carrageenans (Pettersson-Löfquist, 1995). Seaweed farming does not require any inputs of fertilizers or pesticides (Johnstone & Olafsson, 1995; Bryceson, 2002) and utilizes pet and line or off-bottom methodologies (Msuya *et al.*, 2014). However, recent studies indicate that seagrass beds underneath seaweed farms generally had less seagrass, finer sediment, lower sediment organic matter content and a macrofauna, community that was more similar to a sand bank compared to local seagrass beds without seaweed farms (Eklöf *et al.*, 2006). While negative effects of seaweed farming are observed in seagrass beds they are much more localized compared to finfish or shellfish aquaculture.

22.2.5 Biogeochemical Cycling

Seagrass and macroalgae habitats are highly productive and through photosynthesis produce 1.5 and 1.05 g C m⁻² hr⁻¹ (median values), respectively (Duarte & Chiscano, 1999). Much of this carbon sustains the food web in coastal ecosystems, whereby, on average, 19% of seagrass production and 34% of macroalgae production is consumed by grazers (Duarte & Chiscano, 1999). For seagrasses, only 19% of the carbon supports the food web by direct grazing, while more than half of the carbon produced enters the detrital cycle (50%) or is exported outside the coastal habitat (24%) (Cebrián *et al.*, 1997; Duarte & Chiscano, 1999). Conversely, macroalgae are more nutritious and so are subject to greater grazing, especially in temperate regions, as their tropical counterparts tend to contain more anti-herbivory compounds (Bolser & Hay, 1996). Approximately 38% of carbon produced by macroalgae enters the detrital cycle (Duarte & Chiscano, 1999). Once the remaining macrophyte biomass enters the detrital cycle, both microbes and infauna breakdown or remineralize the macrophyte carbon into CO₂ convert or incorporated into new biomass. Again, as macroalgae are more nutritious, decomposition rates are typically faster than seagrasses (Enríquez *et al.*, 1993; Cebrián, 1999). The greater resistance to decay for seagrasses also makes them more apt to contribute to long-term sediment carbon stock, e.g., refractory carbon not fully decomposed will accumulate in the sediments (Cebrián, 1999; Trevathan-Tackett *et al.*, 2015). Seagrasses and macroalgae also provide one more pool of carbon to the food webs via the excretion from leaf or root tissues (Haas *et al.*, 2013). While this pool of carbon is sometimes less of a focus for biogeochemical cycling, the dissolved organic carbon produced can support a diverse number of bacteria, fungi, protists and algae. The released exudates are transferred between leaf/blade and epiphytes or microbes (Ziegler & Benner, 1999; Haas *et al.*, 2013), and between seagrass root and rhizosphere-associated microbes (Moriarty *et al.*, 1986). The epiphytic and microbial growth benefiting from exudate production will provide carbon to grazing invertebrates and fish or other microbes, which can then be transferred up the food chain.

In addition to exudate carbon, seagrass roots produce a layer of oxygen around the root tip (a by-product of photosynthesis and oxygen diffusion into the leaf transferred from the leaf to the root by internal airways called *aerenchyma*) (Borum *et al.*, 2006). The oxygen release from the roots not only help the seagrass avoid the diffusion of toxic hydrogen sulphide into it tissues (Borum *et al.*, 2005), but the oxygen also supports aerobic microbes in an otherwise highly anoxic environment (Donnelly & Herbert, 1998). There is also evidence that the oxygenated rhizosphere also supports fungal growth (Kuo *et al.*, 1981). There is still forthcoming research on the roles of fungi in seagrass systems as to their function in nutrient cycling, e.g., mycorrhizal fungi (Shoemaker & Wyllie-Echeverria, 2013; Vohník *et al.*, 2015).

Nitrogen and phosphorus availability is an important factor in influencing the production of seagrass and macroalgae ecosystems. Seagrasses and macroalgae obtain nutrients from water column, in addition to the sediment porewater for seagrasses. Seagrasses and large, long-living algae like fucoids have lower nutrient needs than ephemeral macroalgae by allocating nutrients where they are needed (Pedersen & Borum, 1996). In oligotrophic, or nutrient-poor, systems, seagrass growth is limited by phosphorus in carbonate sediments, which are low in usable phosphorus, while seagrasses growth is limited by nitrogen availability in sandy and terrigenous sediments (Touchette & Burkholder, 2000). Nutrient additions often elicit growth of seagrasses (reviewed in Touchette & Burkholder, 2000). For example, a long-term fertilization programme using perches to encourage bird droppings within seagrass meadows enhanced seagrass abundance in the phosphorus-limited Florida Bay (Fourqurean *et al.*, 1995; Herbert & Fourqurean, 2008). This long-term enrichment also highlighted the variable nutrient needs for different seagrass species, whereby the larger *Thalassia testudinum* benefitted during the first

two years of fertilization followed by domination (97% cover) by smaller, fast-growing *Halodule wrightii* (Fourqurean *et al.*, 1995). Many times nutrient additions are extreme (e.g., eutrophication), promoted by nearby aquaculture, agriculture or industry runoff. Excess nitrogen inputs can lead to deleterious effects for seagrass health, e.g., ammonium toxicity from water column ($3\text{--}220\text{ mM NH}_4^+$) or sediment porewater ($500\text{--}1600\text{ mM NH}_4^+$) (Touchette & Burkholder, 2000). Additionally, under high nutrient conditions, micro- and macroalgae growth can often out-compete the growth of seagrasses due to higher nutrient up-take rates of algae. Extensive and rapid epiphytic algal and macroalgal tuft growth can shade or “smother” seagrasses (McGlathery, 2001). There have been several reported incidences globally where seagrass-dominated ecosystems have declined from nutrient-related algae over-growth (Lapointe *et al.*, 1994; Hauxwell *et al.*, 2001; Short *et al.*, 2006). This shift in primary producers can have large consequences for coastal ecosystems function, including loss of biodiversity and carbon sequestration function as well as shifts in fish nurseries, herbivore/grazer communities and food web structure (Short & Neckles, 1999; Orth *et al.*, 2006a; Burkholder *et al.*, 2007; Macreadie *et al.*, 2012).

22.2.6 Macroalgae as Aquaculture and Wild-Harvested Crops

There has been limited commercial exploitation of seagrasses and no aquaculture production, so our discussion here focuses primarily on the significant global production and application of macroalgae. It is worth mentioning, however, that until the mid-1900s, seagrass live plants and wrack had been frequently harvested in various parts of the world and used as insulation in housing, for farming and agriculture as well as food (Wyllie-Echeverria & Cox, 1999). Recently, odorous wrack accumulation along beaches has spurred local communities to find creative uses for the dead biomass beyond becoming landfill waste, e.g., coastal habitat fertilizer (Chapman & Roberts, 2004; Cardona & García, 2008; Oldham *et al.*, 2010).

Macroalgae are wild-harvested and cultured for human consumption, animal feed, agricultural fertilizers and for industrial and pharmaceutical applications (McHugh, 2003). Macroalgae are high in protein, dietary fibre, long-chain omega-3 fatty acids and a suite of vitamins, minerals and antioxidants (Fleurence, 1999; Dawczynski *et al.*, 2007; Gressler *et al.*, 2010). Regular consumption can reduce obesity and associated illnesses, such as diabetes and heart disease (Mouritsen, 2009; Jung *et al.*, 2012), in addition to other potential health benefits including anti-inflammatory, anti-cancer, anti-viral, anti-oxidant, anti-obesity and anti-diabetic properties (Zubia *et al.*, 2009; Wijesekara *et al.*, 2010; Kim & Pangestuti, 2011; Jung *et al.*, 2012). Macroalgae are increasingly being considered as additives in both terrestrial and aquatic animal feed mixes for the high nutritional and health values (Antaya *et al.*, 2015; Ngo Van, 2015; Shapawi *et al.*, 2015) and to reduce reliance on wild-harvested fish sources of omega-3 fatty acids (Norambuena *et al.*, 2015; Silva *et al.*, 2015; Wilke *et al.*, 2015). Macroalgae have long been used as organic fertilizers, soil conditioners and biostimulants for agricultural crops and have been shown to improve both yield and nutritional value of target crops, with sustained benefits across subsequent crop rotations (Lola-Luz *et al.*, 2014; Illera-Vives *et al.*, 2015; Layek *et al.*, 2015). Moreover, the use of seaweeds for the production of biofuels is a productive area of research (Park *et al.*, 2014; Philippsen *et al.*, 2014), with bioethanol and bio-oils from wet macroalgal biomass looking the most promising (Chen *et al.*, 2015).

The total annual production of macroalgae in 2012 was 23.8 million t live wt valued at US\$ 6.4 billion, with an additional 1.1 million t harvested from wild stocks (FAO, 2014b). Production has increased dramatically in the past decade (FAO, 2014b) with a particular rise in the production of carrageenophytes and agarophytes in southeast Asia. These taxa are principally harvested for their phycocolloids, which have a range of commercial applications, and now account for

47% of the total global yield and 38% of the global value of macroalgae from aquaculture production. Whilst over 10,000 species of macroalgae have been described globally (Guiry, 2012), aquaculture production is concentrated on just eleven taxa that account for 87% of total biomass yield and 81% of value: *Eucheuma/Kappaphycus* spp., *Pyropia* (previously *Porphyra*) spp., *Undaria pinnatifida*, *Gracilaria* spp., *Laminaria/Saccharina* spp., *Sargassum fusiforme*, *Monostroma nitidum*, *Caulerpa* spp., *Ulva* (previously *Enteromorpha*) *clathrata*, *Gelidium amansii* and *Codium fragile* (ranked by decreasing value).

Globally, macroalgal aquaculture is dominated (>99% of total) by seven countries in the Asian Pacific region both in terms of biomass yield (decreasing rank order: China, Indonesia, Philippines, Korea, Japan, Malaysia and Vietnam) and commercial value (decreasing rank order: China, Indonesia, Japan, Korea, Philippines, Vietnam, Malaysia) (FAO, 2014b). Conversely, 96% of wild-harvested macroalgae are from eleven more geographically disparate countries (decreasing rank order: Chile, China, Norway, Japan, France, Ireland, Iceland, South Africa, Canada, Korea and USA) (FAO, 2014b).

22.3 Impact of Climate Change on Seagrass and Macroalgae

The IPCC (2014) identified with very high confidence that coastal systems are particularly sensitive to three key drivers related to climate change: ocean temperature, sea level, and ocean acidity. Here we assess the impacts of these drivers on seagrasses and macroalgae, which are key providers of biogenic habitat in these systems.

22.3.1 Impacts of Ocean Temperature: Thermal Tolerance and the Potential for Range Shifts

“Temperate seagrass and kelp ecosystems will decline with the increased frequency of heat waves and sea temperature extremes as well as through the impact of invasive subtropical species (high confidence)” (IPCC, 2014).

Current and projected changes to mean sea surface temperature (SST) are significant, but for the intertidal, changes to air temperatures at low tide and the frequency and severity of extreme, high-temperature events are likely to be most important. The decrease in the frequency of extreme cold events (Lima & Wetthey, 2012) (likely increasing the number of frost-free days), coinciding with seasonal cycles of morning low tides may also be important for reef-dwelling intertidal organisms. For shallow subtidal systems the influence of extreme weather events should largely be buffered by the water body, such that changes to SST are likely to have the greatest influence on biota (but see Pearce *et al.*, 2011; Smale & Wernberg, 2013). However, the upper subtidal may have greater exposure to increased air temperatures, particularly if extreme weather events coincide with spring tides. Deep subtidal systems are less likely to be affected by increases in SST, although there is currently high uncertainty with regards to how much temperature will increase at depths beyond 20 m.

Intertidal environments are naturally highly variable with respect to temperature (and other physico-chemical parameters) due to tidal cycles of emersion and submersion; with vertical elevation influencing the period of emersion. Thus organisms that inhabit intertidal systems generally have broad temperature tolerances. However, many populations of intertidal organisms, particularly those close to their distributional limits, may already experience their physiological limits under current-day temperature profiles (Stillman & Somero, 2000; Nguyen *et al.*, 2011). Such species are likely to be highly sensitive to further increases in sea and air temperatures and increases in extreme temperature events (Hawkins *et al.*, 2008; Lima &

Wetthey, 2012). The rate of warming can also greatly influence the capacity of intertidal species to tolerate increased temperatures (Nguyen *et al.*, 2011).

Shallow subtidal reefs are often dominated by various species of kelp: large phaeophycean algae in the orders Laminariales and Fucales that can function as autogenic ecosystem engineers (Jones *et al.*, 1994, 1997), providing important habitat (e.g., increased structural complexity) and changing the environment by directly or indirectly modifying the abiotic conditions and/or biotic interactions between species (e.g., reduce light (Reed & Foster, 1984), wave action (Estes & Palmisano, 1974), predation risk (Velimirov & Griffiths, 1979) resulting in unique assemblages associated with the kelps (Smith *et al.*, 1996; Wernberg *et al.*, 2003). Kelps are sensitive to high temperatures, particularly during reproduction and recruitment, such that changes in the composition and/or abundance of kelp stands due to temperature may have significant direct and indirect flow-on effects for the associated assemblages (Wernberg *et al.*, 2011a). An increase in extreme warming events can force step-wise changes in species distributions in marine ecosystems through negative impacts on temperature-sensitive, habitat-forming kelps (Smale & Wernberg, 2013). Furoid and laminarian algae are also sensitive to other anthropogenic stressors such as nutrient inputs and water transparency/quality (Cormaci & Furnari, 1999; Connell *et al.*, 2008). Such sensitivity of native kelps to multiple stressors may open the path for successful invasions by introduced species (Valentine & Johnson, 2003, 2004) with a potentially different suite of consequences for other biota. When considering the sensitivity of kelp-based, shallow-subtidal-reef systems, the influence of changing currents and the potential to transport novel herbivores into temperature-stressed and over-fished assemblages (Ling, 2008; Ling *et al.*, 2009a; Johnson *et al.*, 2011) must not be overlooked.

There is increasing evidence (but see Poloczanska *et al.*, 2011) that species range shifts are already occurring in response to increased SST. While responses can be variable and complex (Stuart-Smith *et al.*, 2015), studies show contractions at species equatorial limits and poleward expansions (Millar, 2007; Ling *et al.*, 2009b; Pitt *et al.*, 2010; Johnson *et al.*, 2011; Last *et al.*, 2011; Wernberg *et al.*, 2011b; Vergés *et al.*, 2014a, b; Heck Jr *et al.*, 2015). Amongst these species, benthic macrophytes are particularly susceptible (Millar, 2007; Johnson *et al.*, 2011; Wernberg *et al.*, 2011b; Vergés *et al.*, 2014a) due to the (i) lack of potential habitat beyond continental borders to which to retreat; (ii) the poor dispersal capacity of many macroalgae or slow vegetative growth of large seagrass species (Santelices, 1990; Marbà & Duarte, 1998; Bellgrove *et al.*, 2004; Coleman *et al.*, 2009, 2011); and (iii) the autogenic engineering role of many vulnerable species (Schiel, 2006, 2011; Wernberg *et al.*, 2011a). For populations that are already at their thermal range edge, episodic heat waves are causing large die-backs or die-offs of local populations (Smale & Wernberg, 2013; Thomson *et al.*, 2015). Additionally, temperate seagrasses and macroalgae are having to cope with the range shifts of fish and the associated grazing pressures (Booth *et al.*, 2011; Vergés *et al.*, 2014a, b). For example, the seagrass populations in northern Gulf of Mexico are not able to expand their ranges due to blockage by land mass (Heck Jr *et al.*, 2015). With the increases in grazing but tropical fish moving into those habitats, there is expected to be a decrease in seagrass biomass as well as a reduction in habitat structure (Heck Jr *et al.*, 2015). If these benthic ecosystem engineers cannot cope with thermal stress, changes in grazing pressure or keep pace with increasing sea temperatures, there will be a threat of significant local and global extinctions within intertidal and shallow subtidal coastal habitats (Schiel *et al.*, 2004; Wernberg *et al.*, 2011b) with inevitable loss of biodiversity.

Increased temperatures (mean and extreme) and advanced seasonal warming are likely to alter both timing of flowering, gamete dispersal and reproduction and recruitment success (due to vulnerability of propagule development (Short & Neckles, 1999; Byrne *et al.*, 2010) of coastal flora and fauna, including economical important species. Increased SST has led to extensive loss of kelp biomass and extent, e.g., in Australia: *Macrocystis pyrifera* in Tasmania

(Johnson *et al.*, 2011) and range contractions at the northern distributional limits of *Durvillaea potatorum*, *Ecklonia radiata*, *Phyllospora comosa* (Millar, 2007).

Changes to the distribution and abundance of autogenic engineers can have cascading effects on the structure, diversity and resilience of associated communities (Schiel, 2006, 2011; Johnson *et al.*, 2011; Schiel & Lilley, 2011; Wernberg *et al.*, 2011b). Understanding the connectivity and genetic diversity (Coleman *et al.*, 2009, 2011), and differences in temperature tolerance (Campbell *et al.*, 2006; Wernberg *et al.*, 2011a) of populations of important intertidal and subtidal habitat-forming species, in the context of their broader geographical distributions, will be important for assessing the capacity of these species (and their associated communities) to adapt to future air and sea temperature scenarios (Macreadie *et al.*, 2014b). Geomorphology and habitat specialization may also be important influences in subtidal systems.

22.3.2 Impacts of Sea Level Rise and Changing Wave Climates

Future sea-level rise and increased storminess will likely lead to greater shoreline protection throughout urbanized and economically important areas of the coast (Thompson *et al.*, 2002). Vertical cliff faces and coastal-protection structures present physical barriers to the shoreward progression of many intertidal species retreating from rising sea level and unable to colonize vertical/high-relief surfaces (Vaselli *et al.*, 2008). Thus intertidal and shallow subtidal macroalgae in the vicinity of coastal-protection structures or vertical cliffs are likely to be highly sensitive to mean sea level (MSL) rise and shore profiles will determine the opportunity for shoreward expansion.

As waves break, they rapidly produce complex, highly-energetic turbulence, with associated rotating, stretching and twisting eddies of propagating bores. The primary forces experienced by an organisms in these conditions are drag and impingement of breaking waves (Gaylord *et al.*, 2008). Such hydrodynamic forces place severe mechanical stress on organisms living in wave-swept environments and can constrain the sizes of intertidal plants and invertebrates (Blanchette, 1997). However, unlike wave-swept invertebrates, algae are typically weak, compliant and easily dislodged (Denny & Gaylord, 2002). Increased wave energy may also disrupt the boundary layer (Denny, 1988) and as such settlement and recruitment phases of macroalgae may be sensitive (Taylor & Schiel, 2003). Increases to wave energy may be expected to increase mixing and may reduce vertical stratification (Levings & Gill, 2010), interacting with temperature and nutrient levels at all depth ranges. Dislodgement of algae can facilitate long-distance dispersal of fertile fronds that remain reproductively viable and disperse propagules (van den Hoek, 1987; Macaya *et al.*, 2005; Stewart, 2006; McKenzie & Bellgrove, 2009); wave-driven increases in the dislodgement of fertile intertidal and subtidal algae thereby has the potential to increase connectivity between populations altering gene flow and the potential for range shifts.

Mosaics of habitat patches on rocky reefs have long been recognized (Sousa, 1984), created and maintained by a number of potential drivers. In temperate, south-western Australia, disturbance by waves has been shown to dislodge significant canopy algae (*Ecklonia radiata* and *Sargassum* spp.) creating open-gap habitats with vastly different assemblage structure (Thomson *et al.*, 2012). It is highly likely that these kelps and others are equally susceptible to wave exposure on Victoria rocky reefs. Thus, we may predict that an increase in the frequency of large wave events and wave heights may result in increased rates of dislodgement of canopy-forming algae and creation of open-gap habitats, with subsequent direct and indirect changes to community structure. Increases in wave energy may also alter the temporal dynamics of algal canopy loss and ultimately reduced species diversity on shallow subtidal reefs (Wernberg & Goldberg, 2008). The scale of canopy loss may be influenced by synergistic effects of temperature and

nutrient sensitivities with wave exposure. Moreover, once created, open-gap patches can persist for decades (Thomson *et al.*, 2012).

The adaptive capacity of canopy-algae-based communities to future wave climates on intertidal and shallow subtidal rocky reefs will be influenced by the (i) algal biomechanics and associated risk of dislodgement (Denny, 1988; Blanchette, 1997; McKenzie & Bellgrove, 2009) and ecomechanics (Denny & Gaylord, 2010) more broadly; (ii) dispersal and recruitment dynamics and capacity to recolonize disturbed areas (van den Hoek, 1987; Santelices, 1990; Bellgrove *et al.*, 2004; Macaya *et al.*, 2005; McKenzie & Bellgrove, 2009); (iii) the influence of existing or new herbivores to the system on canopy algae and persistence of open-gap patches (Ling, 2008; Johnson *et al.*, 2011; Thomson *et al.*, 2012); and (iv) the direct and indirect effects of the presence/loss of an algal canopy on other biota in the system (e.g., Wernberg *et al.*, 2003; Schiel, 2006; Wernberg & Goldberg, 2008; Johnson *et al.*, 2011; Schiel, 2011).

Future changes to the timing, magnitude and duration of storm events are likely to cause intertidal communities to be exposed to large pulse flooding events, which will deliver high concentrations of nutrients and freshwater into the coastal areas. The impacts of the large pulses may override the reductions in annual run-off, but there is high uncertainty in both exposure and sensitivity of biota/ecosystems to such pulses. We would expect to see some changes in intertidal and shallow subtidal algal communities, where evidence has shown greater abundances of opportunistic ephemeral green algae to inhabit areas of high nutrients (Brown *et al.*, 1990; Bellgrove *et al.*, 2010; McKenzie, 2011). High nutrient waters also provide valuable food sources for higher trophic levels of invertebrates and fish, with areas of high runoff contributing to some of the most productive areas of the ocean (Grimes & Kingsford, 1996; Smith & Demaster, 1996; Lohrenz *et al.*, 1999; Dagg & Breed, 2003; Hill *et al.*, 2006, 2008; Schlacher & Connolly, 2009). However, increased run-off could have detrimental effects on the recruitment abilities of fucoid algae such *Hormosira banksii*, as a result of high nutrients and reduced salinities (Doblin & Clayton, 1995; Boyle *et al.*, 2001). Unpredictable periods of high run-off won't only effect macroalgal communities but it may also indirectly affect invertebrate fauna via reduction in suitable habitat (Schiel & Lilley, 2011).

The adaptive capacities of rocky-reef ecosystems to future changes in MSL, astronomical tides and storm surge are likely to be influenced by geomorphology (including spatial extent, geology and vertical profile), the dispersal capacity of associated species relative to the rates of change in the environment, the mobility of organisms, the proximity to coastal-protection structures in the intertidal. It is difficult to predict whether increases in episodic, pulse events will be more important than reductions in annual flow and thus any assessment of adaptive capacity, with respect to rainfall and run-off has high uncertainty. For flora and fauna at all depths, their adaptive capacity with respect to rainfall and run-off will be influenced by (i) their ability to withstand periodic sediment accretion and removal (Santelices *et al.*, 2002); (ii) their ability to withstand periods of low light (influencing photosynthesis, prey capture, mate choice, etc.) associated with plumes; (iii) nutrient limitation (which may interact with temperature and be more severe in the Eastern Region due to the strengthening Eastern Australian Current); and (iv) ability to withstand/benefit from pulses of high nutrients and freshwater in an otherwise low nutrient environment.

22.3.3 Impacts of CO₂ Increases and Ocean Acidification

The oceans have absorbed ~50% of anthropogenically derived carbon dioxide (CO₂) in the past 200 years (Sabine *et al.*, 2004). Atmospheric carbon dioxide is directly related to ocean pH (Caldeira & Wickett, 2003), and pH interacts with carbonate availability (Brierley & Kingsford, 2009). That is, increases in atmospheric CO₂ lead to a simultaneous increase in aqueous CO₂

and a decrease in the concentration of carbonate ions and pH (Orr *et al.*, 2005; Fabry *et al.*, 2008). Many marine organisms from diverse taxa (e.g., molluscs, echinoderms, crustaceans, fish, coralline algae, phytoplankton) have calcified skeletons or other structures that are formed from calcium carbonate derived from primarily (in order of decreasing solubility) magnesium-calcite (Mg-calcite), aragonite, or calcite crystals (Andersson *et al.*, 2008; Fabry *et al.*, 2008). The Southern Ocean is predicted to be undersaturated in aragonite by 2100, and in calcite within a further 50–100 years (Orr *et al.*, 2005). Mg-calcite undersaturation will precede that of aragonite due to higher solubility (Andersson *et al.*, 2008). Thus calcifying reef organisms, particularly those dependent on Mg-calcite or aragonite, may have highest sensitivity (Andersson *et al.*, 2008; Brierley & Kingsford, 2009; Ries *et al.*, 2009) to ocean acidification.

It should also be remembered that the decrease in carbonate availability is matched by an increase dissolved forms of carbon (DIC), including aqueous CO₂, bicarbonate (HCO₃⁻) and carbonate ions (CO₃²⁻) (Orr *et al.*, 2005). Increasing seawater DIC concentration has been shown to increase rates of photosynthesis and growth rates for seagrass and fleshy macroalgae (Beardall *et al.*, 1998; Fabricius *et al.*, 2011; Koch *et al.*, 2013). Longer-term increases in abundance has also been shown for some seagrass species, but primarily for taxa that have dense rhizome/root structures, which store much of the fixed carbon (Russell *et al.*, 2013). Intertidal macroalgae may be least sensitive/responsive to increased CO₂ as most are already at CO₂ saturation (Beardall *et al.*, 1998). However, photosynthesis in many subtidal macroalgae has been shown to be limited by dissolved inorganic carbon (Holbrook *et al.*, 1988), so may be more responsive to elevated CO₂ with enhanced photosynthetic rates (Beardall *et al.*, 1998). However, photosynthesis is unlikely to be greatly enhanced in species with carbon-concentrating mechanism (CCMs) as they largely rely on the ability to use bicarbonate ions which will not change greatly in the future (Beardall *et al.*, 1998; Israel & Hophy, 2002).

Research into the likely impacts of elevated CO₂ and ocean acidification is only in its infancy. Consequently there is a high level of uncertainty, particularly in understanding the indirect community interactions that might flow from direct impacts of elevated CO₂ and ocean acidification on individual species. Most research has focused on the effects of acidification on corals and coccolithophores, with less emphasis on temperate rocky reef biota.

Several studies (Orr *et al.*, 2005; Andersson *et al.*, 2008; Fabry *et al.*, 2008; Brierley & Kingsford, 2009) have suggested that projected decreases in ocean pH will compromise the calcified structures of marine organism due to dissolution of Mg-calcite and aragonite in particular, and disruption of the mineralization process; potentially impacting growth and survival. However, it appears that the story is more complex, with other examples where calcification and growth of organisms were enhanced under acidification scenarios (Doney *et al.*, 2009; Ries *et al.*, 2009). The same has also been seen for the planktonic coccolithophores.

Ocean acidification can negatively affect the early life-history phases of calcifying taxa in complex ways, with direct and indirect effects on multiple processes (e.g., metabolism, fertilization, larval development, growth, settlement) (Fabry *et al.*, 2008; Albright & Langdon, 2011). Molluscs and echinoderms whose larval skeletal structures are composed of highly soluble, unstable, transient, amorphous calcium-carbonate may be particularly vulnerable (Fabry *et al.*, 2008). It is possible (and perhaps likely) that vulnerable early life-history stages of non-calcifying organisms are also affected by acidification through physiological stress and disruption (Fabry *et al.*, 2008). Recruitment limitation and changes in abundance of calcified species may have community and/or ecosystem scale effects (Beardall *et al.*, 1998; Fabry *et al.*, 2008; Ries *et al.*, 2009; Albright & Langdon, 2011) with possible reductions in diversity, structural complexity and resilience of systems (Fabricius *et al.*, 2011).

Fucoid and laminarian kelps are suggested to have functioning CCMs and therefore predicted to show little response to elevated CO₂ (Hepburn *et al.*, 2011). Algal species without

(CCMs) have been suggested to benefit from increased CO₂ (Beardall *et al.*, 1998; Israel & Hophy, 2002; Hepburn *et al.* 2011). Indeed mesocosm experiments on the South Australian coast showed that understorey algal turfs doubled in biomass and quadrupled occupation of space under future CO₂ and temperature scenarios (Russell *et al.*, 2009). Moreover, field manipulations showed that these turfing algae inhibited recruitment of the laminarian kelp, *Ecklonia radiata* (Connell & Russell, 2010).

The adaptive capacity of marine algae to elevated CO₂ and lowered pH may depend on (i) the presence/absence of CCMs (Beardall *et al.*, 1998); (ii) the capacity for positive effects on photosynthesis to counteract negative effects of acidification, particularly for vulnerable early life-history stages (Roleda *et al.*, 2012); and (iii) direct and indirect interactions with other species (Russell *et al.*, 2009). For reef fauna, their capacity to adapt to elevated CO₂ and lowered pH will be largely influenced by (i) their ability to tolerate and/or regulate the physiological stress concomitant with hypercapnia (Fabry *et al.*, 2008); (ii) the carbonate chemistry of any calcified structures (Andersson *et al.*, 2008; Ries *et al.*, 2009); (iii) the level of protection to their outer shell layer afforded by an organic covering (Ries *et al.*, 2009); (iv) synergistic effects of other stressors; and (v) direct and indirect interactions with other species (Doney *et al.*, 2009).

22.3.4 Interactions and Linkages

The climate change projections reviewed above will not happen in isolation. It is generally agreed that it will be the cumulative effects from a range of interacting processes that will have the greatest impacts on existing ecosystems but will also be hardest to predict (Russell *et al.*, 2009, 2012). For example the effects of temperature or salinity on the physiology of organisms will affect their responses to extreme events such as storms, which might include storm surges and flooding and increased turbidity, large run off events with associated water quality changes as well as physical disturbance caused by increased wave action. Similarly the ability to recover or recolonize an area following the combined effects of such climate related events might depend on the delivery of propagules by the prevailing currents, food availability which might be impacted by seasonal changes to upwellings and the effects of ocean acidification on specific larval stages of available organisms.

Climate driven changes also need to be considered in the context of other anthropogenic stressors, such as overfishing (Ling *et al.*, 2009a), invasive species, pollution and urbanization and engineered coastlines (Airolidi *et al.*, 2005). The potential synergies amongst such multiple stressors are only just beginning to be examined. Moreover, it is critical that we have a better understanding of the links between catchments and our coasts in order to understand the downstream effects that may flow from climate driven impacts upstream.

22.4 Climate-Related Loss of Seagrass and Macroalgae and their Potential Links to Fisheries and Aquaculture

The previous sections of this chapter describe multiple ways that seagrass and macroalgal ecosystems are vital to coastal ecosystem function and health. Due to their connections within multiple marine food webs (e.g., primary production, direct food source or habitat for permanent or transient fauna), changes to the presence or function of seagrass and macroalgal communities will ultimately be transferred up the food web. Such changes or shifts may have devastating effects on global fisheries and aquaculture. There is already evidence that the effects of climate change on seagrass and macroalgae are manifesting via changes in primary production and growth, health and resilience and habitat degradation and loss. While more

experimental research is needed to fully understand the bottom–up consequences of ocean acidification, elevated temperature and sea-level rise, we have hypothesized some potential outcomes of these changes on fisheries and aquaculture in Table 22.2. We have briefly

Table 22.2 Effects of climate change on seagrass and macroalgae and how it may affect future fisheries or aquaculture industries.

Effects on seagrass or macroalgae	Climate change-related causes	Potential outcome for fisheries or aquaculture
Increased growth/production	Elevated DIC concentrations via ocean acidification enhancing photosynthetic production and growth rates (Koch <i>et al.</i> , 2013; Russell <i>et al.</i> , 2013).	Increased protection of smaller fish and invertebrates from larger predators → loss of energy further up the food chain. Shift from coral- to macroalgal-dominated tropical reefs will alter the community composition of tropical reef fishes. Increased resources for herbivorous fish → increase in energy further up the food chain.
Change in palatability and nutritional status*	Increased temperatures and ocean acidification as well as changes in solar radiation (UV, range shifts) may alter macroalgae and seagrass anti-herbivory compounds and C:N content (Short & Neckles, 1999; Diaz-Pulido <i>et al.</i> , 2007; Harley <i>et al.</i> , 2012).	Changes in palatability with alter macroalgae function as the base of the food web for fisheries. Changes in primary and secondary metabolites may alter the products from macroalgal aquaculture industry.
Impaired health/sublethal stress or resilience	Changes in ocean circulation alters propagule dispersion and lead to range shifts (Diaz-Pulido <i>et al.</i> , 2007) and increased turbidity (Short & Neckles, 1999). Elevated temperatures may alter flowering and sexual reproduction of seagrass (Short <i>et al.</i> , 2007). Such changes may affect the genetic diversity and fitness of seagrasses (Schlueter & Guttman, 1998; Williams, 2001). Stress related to light reduction, elevated temperatures, salinity changes may decrease growth and production of macrophytes (Davison & Pearson, 1996; Short & Neckles, 1999).	Reductions in macrophyte density, abundance and habitat formation will reduced the fitness and recovery after grazing or episodic loss event, which will negatively affect food web structure. Reduced densities and increases in habitat patchiness will increase the exposure of transient or resident fauna to predation.
Habitat loss	Increased temperatures causing tropicalization of temperate ecosystems can lead to overgrazing, low recovery and loss of ecological function of the macrophyte habitats (Vergés <i>et al.</i> , 2014). Increased runoff and sedimentation from land due to more frequent rain events or poor land practices may lead to habitat loss. This is especially important for seagrasses since high epiphyte loads can cause shading or macroalgae can outcompete under high nutrient conditions (Short & Neckles, 1999; Ralph <i>et al.</i> , 2006).	Habitat loss may result it total food web crash through the loss of major primary production or the loss of nursery or refuge habitat of fauna essential for the survival of fisheries.

*More research is needed to fully understand the broad-scale effects on fisheries and aquaculture.

described two such incidences whereby habitat loss of either macrophyte has resulted in declines in fisheries.

Elgrass and North Atlantic Fisheries. In the 1930, the North Atlantic seagrass *Zostera marina* or eelgrass were afflicted with disease resulting in a die-off that devastated 90% of the populations from Eastern USA to Europe. The cause of the die-off was linked to environmental stresses that reduced the health of the seagrass and increased its susceptibility to wasting disease (Short *et al.*, 1987; Muehlstein *et al.*, 1988). Although not directly linked to climate change, the conditions that induced stress and susceptibility to infection are the same as current climate change impacts (e.g., elevated temperature, low light, changes in salinity) (Short *et al.*, 1988; Giesen *et al.*, 1990). Loss of eelgrass habitat led to the extinction of epifaunal limpet *Lottia alveus*, the first modern extinction of its kind (Carlton *et al.*, 1991). Additionally, the bay scallop, *Argopecten irradians*, fisheries stocks significantly declined along the northern east coast USA (Fonseca & Uhrin, 2009). It took 30–40 years for *Z. marina* to begin recovery, and has continued in many places with the help of restoration efforts, though not in pre-disease abundances (De Jonge & De Jong, 1992; Orth *et al.*, 2006b). Coinciding with seagrass recovery and restoration efforts bay scallops were able to recover in some locations (e.g., Nantucket Harbor) but not others (e.g., Chesapeake Bay) (De Jonge & De Jong, 1992; Orth *et al.*, 2006b; Fonseca & Uhrin, 2009).

Kelp and the Southern Rock Lobster *Macrocystis pyrifera* populations along the Tasmania, Australia coastline declined in the early 1980s and had been linked to warming temperatures and low nutrients from the Eastern Australian Current (Johnson *et al.*, 2011). These habitats are essential to young Southern Rock Lobster (*Jasus edwardsii*) that use these habitats for nocturnal feeding and safety (Booth, 2001; Hinojosa *et al.*, 2014). To further complicate the kelp-lobster relationship, long-spined sea urchin *Centrostephanus rodgersii* distributions have been undergoing range expansion into the area (Johnson *et al.*, 2011). While *J. edwardsii* are predators of the sea urchin, *C. rodgersii* can quickly overgraze kelp beds (Johnson *et al.*, 2004). Overfishing of the rock lobster can enhance these urchin barrens and thus reduce the habitats lobsters use in early life stages (Ling *et al.*, 2009a, b). Such a shift and consequent negative feedback loop is one case that requires urgent management, especially with imminent warming seas (Johnson *et al.*, 2004).

22.5 Conclusions

Seagrasses and macroalgae are among the earth's most productive ecosystems, and play a vital role in supporting fisheries through their provision of habitat. They support both resilient and transient species from a broad variety of harvested taxa, including many types of fish, octopuses, squids, snails, oysters, sponges, shrimps, worms, urchins, anemones, crabs, polychaetes, and clams. Seagrasses and macroalgae occur predominantly in the coastal zone along every continent (with the exception of Antarctica in case of seagrasses) – a zone that is facing a high level of pressure from both climate change and human activities. Already the effects of climate change on these ecosystems, and their concomitant impacts on fisheries, are being seen through multiple pathways. In this chapter we have discussed a handful of examples, which have included bottom-up losses of habitat through ocean acidification, elevated water temperatures, and sea-level rise. The effects of climate change will continue for many decades (and possibly centuries) until the world transitions to a low-carbon economy and finds ways to remove already emitted greenhouse gases from the atmosphere. Predicting and preparing for the flow-on effects of climate change on fisheries species via

their intermediate impacts on seagrass and macroalgal ecosystems remains an important area for research.

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