Chapter 7
Competition, a Major Factor Structuring Seaweed Communities

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7.1 Competition Theory

Competition for shared resources has long been viewed as an important structuring agent in natural communities (Gause 1934; Strong 1980). Generally defined as the simultaneous use of limited resources by two or more organisms, competition can negatively impact population growth rates and influence community-level processes such as predation and/or how species respond to disturbances (Roughgarden 1979). This can occur between individuals of the same species or among individuals of different species. Early mathematical models such as those posed by Lotka (1925) and Volterra (1926) and later demonstrated by Gause (1934) suggest that when competition between two species is asymmetrical, one species will eventually drive the other to local extinction in their "struggle for existence." However, these models do not include the effects of other factors (e.g., predation, herbivory, environmental heterogeneity, or extreme environmental conditions) which often mediate the strength and outcome of competitive interactions (reviewed in Olson and Lubchenco 1990). In fact, even though two species rely on a shared resource, they may not compete if that resource is not limited or if the effects of other factors such as grazing or disturbances are substantially greater. However, when the shared resource is limited and competition for it is strong relative to other factors, the outcome of competition may vary as a function of both inter- and intraspecific interactions (Creese and Underwood 1982), especially as they relate to each species' own carrying capacity. Here, one species may drive

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the other to local extinction if the strength of their competitive abilities is asymmetrical, but they exhibit similar carrying capacities. Conversely, if the carrying capacities of the two species are substantially different, the species with the larger carrying capacity can drive the other species to local extinction even if their competitive abilities are equal.

While numerous examples of competition among individuals and/or species exist, debate over the general importance of competition as a structuring agent in natural communities remains. On the one side, Weins (1977) argues that competition among many species is actually rare in nature and that its importance as an agent of natural selection is therefore minimal. On the other hand, Diamond (1978) supports the view of Darwin (1859), who suggested that competition between closely related species is a deterministic factor in natural selection. In fact, Darwin wrote "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between species of distant genera." In discussing competition among macroalgae specifically, Miller (1967) notes that competition can occur via direct interactions in which one organism and/or species prevents the other from access to a limited resource (interference competition) or via indirect interactions where the species exploit a shared resource but do not directly interact with each other (exploitative competition). However, given that different algal traits such as rapid and/or indeterminate growth, large thallus size, and resistance to unfavorable environmental conditions can be associated with different competitive interactions, it may be difficult to identify if certain interactions are due to interference, exploitation, or a combination of the two (Olson and Lubchenco 1990). This problem can be exacerbated considering that different ecologists will often use different methodologies in their studies of competition and thus the results of their studies may vary simply due to the experimental approached used (e.g., Underwood and Fairweather 1986), and that experiments aimed at identifying the responses to competition may actually reflect only indirect evidence that it has actually occurred (e.g., Connell 1980). Consequently, demonstrating that competition is important to structuring natural communities requires carefully planned combinations of field observations to identify the patterns coupled with directed manipulative experiments to determine the processes behind them. These methods often involve removing one or more (e.g., the competitive dominant) species(s) and monitoring responses in the other species under consideration. In fact, a large number of studies have used these methods in studies of competition within macroalgal communities and have largely demonstrated the importance of both interspecific and intraspecific interactions as structuring agents. In this chapter, we review some of the main developments associated with these concepts and provide examples from case studies that demonstrate their importance. We focus our discussion on competition among benthic macroalgae, although it should be noted that among bloom-forming microalgae, both exploitative (i.e., for shared limited resources) and interference (i.e., via allelopathy) competition can be important in structuring planktonic communities, especially when the blooms are fully developed (e.g., Solé et al. 2005).

7.2 Competition Among Marine Macroalgae

7.2.1 Overview

The distribution of plants is regulated by both physical and biological factors, though the relative importance of these factors is notoriously variable through time and space, and is particularly dependent on the scale at which they are examined (Dayton and Tegner 1984; Edwards 2004). While plant populations may persist within a given ecosystem due to predation on herbivores as postulated by Hairston et al. (1960), in the absence of herbivory, plants would increase in number and ultimately compete among themselves for light, space, and nutrients. In fact, competition has been predicted to be the most important factor regulating the distribution and abundance of plant species in the absence of environmental stressors (Grime 1974, 1977, 1979). It is considered crucial in setting the latitudinal range limits (e.g., Edwards and Hernández-Carmona 2005; see also Chap. 3 by Eggert and Chap. 18 by Bartsch et al.) and tidal distributions (e.g., Hawkings and Hartnoll 1985) of some macroalgae, and regulating patterns of their succession following disturbances in others (e.g., Sousa 1979). However, the mere presence of a competitor may not be sufficient to cause strong competitive effects. Variation in morphology may have variable effects on the availability of and/or access to resources. For example, the exclusion of erect species from the understory within Australian *Ecklonia radiata* kelp forests depends on the morphology of the algae. Shorter and more flexible forms exclude erect taxa by shading and whiplashing the substratum (Connell 2003a; Irving and Connell 2006), whereas longer and more rigid forms do not exclude erect taxa from the understory which is strongly affected by shade (Kennelly 1987a). These differences have profound effects on the understory communities across Australia as 5,000 km of coastline across the Leeuwin Current (west and south coast) are largely structured by the short-flexible forms whereas the east coast (East Australian Current) understory is structured by the long-rigid forms (Connell and Irving 2009). These mechanisms match closely with variation in understory communities across temperate Australia (Irving et al. 2004). Furthermore, interactions among macroalgal holdfasts may result in strong interspecific competition, as seen in some intertidal red algae in Chile, but little-to-no intraspecific competition, as the holdfasts of the same species tend to coalesce (Santelices et al. 2003). What this means for their populations, however, is uncertain. One thing that is clear is that marine macroalgae are susceptible to competition as space, light, and nutrients are often in short supply in coastal ecosystems (reviewed in Carpenter 1990).

7.2.2 Competition for Light

Light is the primary resource requirement for algal growth, reproduction, and survival. Both the quantity (irradiance) and spectral quality (wavelength) are important in determining the distribution of many algal species, especially along depth gradients in the ocean (Kitching 1941; Saffo 1987). For example, Novaczek (1984) observed that the lower depth limit of *Eckonia radiata* off the coast of New Zealand was set by minimum light requirements of ca 40 mol photons m^{-2} d^{-1}. Conversely, Graham (1996) and Fejtek et al. (2011) found that the shallow limits of *Macrocystis pyrifera* and *Pelagophycus porra* (respectively) were set, at least in part, by high irradiance (PAR) effects on their microscopic gametophytes. Further, high UV-B irradiance appears to be especially important in reducing spore survival and consequently inhibiting algal recruitment in shallow water (e.g., Wiencke et al. 2000; Roleda et al. 2005; see also Chap. 1 by Hanelt and Figueroa and Chap. 20 by Bischof and Steinhoff). With regard to spectral quality, Lüning (1981) examined the effects of blue light on sexual reproduction in gametophytes of *Saccharina latissima* near Helgoland (North Sea) and observed that egg release by the gametophytes was reduced by 50% when they were held under only 1.4 μmol photons m^{-2} s^{-1} of blue light ($\lambda = 449$ nm) for 45 min. However, blue light may also have positive effects, such as enhancing nitrate (e.g., Aparicio et al. 1976) and carbon (e.g., Schmid and Dring 1996) uptake and storage as seen in some green and brown algae, respectively. While irradiance and spectral quality may be important in controlling recruitment, growth, survival, and reproduction in many algae, photoperiod may be as important in controlling the timing of their growth and reproduction. For example, Lüning (1986, 1990, 1994) and Lüning and Kadel (1993) observed that new frond formation in several brown algae is regulated by changes in photoperiod, resulting in circannual rhythms and synchronized seasonal growth. Further, Edwards (1998) observed that recruitment in the brown alga *Desmarestia ligulata* in central California, USA, was closely tied to increase in day length during the early spring, but this was limited to areas where the dominant kelp canopies had been removed either experimentally or by winter storms. In summary, light quantity and quality appear important to macroalgal physiology and thus factors that reduce access to light may be integral in establishing spatial and temporal patterns in their distribution and abundance, especially in the ocean where irradiance rapidly diminishes with increasing depth.

In addition to natural attenuation of light in the ocean (e.g., Kirk 1992), light is absorbed and/or scattered by the macroalgae themselves, placing them in both direct and indirect competition with each other. As a result, many species of macroalgae have developed functional morphology forms that allow them to more effectively capture light for photosynthesis in their respective habitats (Vadas and Steneck 1988). These morphologies range from single cells to multicellular parenchymatous thalli with complex tissue differentiation. Within this later group, many species have evolved morphologies that elevate their photosynthetic blades above their competitors. For example, Kitching (1941) observed that on the shores of Carsaig Island, Scotland, the dominant macroalga *Laminaria digitata* possesses erect nonflexible stipes that hold its blades above the substrate in order to more effectively capture light when occurring in the subtidal where light can be limiting, but flexible stipes that allow its blades to lay prostrate in the water when occurring in the intertidal where light was otherwise abundant but desiccation may be an issue. Similarly, many subtidal kelps produce canopies that are either buoyed at the surface by gas-filled pneumatocysts or are supported above the substrate by thick woody stipes (e.g., Abbott and Hollenberg 1976). These canopies place their photosynthetic blades above those of their competitors and enabling them to more effectively capture light before it reaches their competitors (Horn 1971; Hay 1986). This structure results in a rich mosaic of benthic light regimes below the canopies (Gerard 1984) to which macroalgae can "photoadapt" by altering the amount and/or arrangement of their photosynthetic pigments (Ramus 1981; Rosenberg and Ramus 1982). Combined with other factors such as substrate topography, hydrodynamic forces, and grazing, this can result in benthic algal communities being highly variable at a number of spatial scales (Dayton et al. 1984, 1992, 1999; Foster and VanBlaricom 2001; Edwards 2004).

Much in the way competitive dominance by canopy-forming plants plays a structuring role in terrestrial forest communities (e.g., Brokaw and Scheiner 1989; Connell 1989; Spies and Franklin 1989; Hubbell et al. 1999), shading from kelp canopies can be the determining factor in regulating benthic macroalgal populations (Reed and Foster 1984; Kennelly 1989; Edwards 1998; Connell 2003b). For example, it is well understood that in the terrestrial forests, the removal of only a few canopy dominants can prevent the competitive exclusion of many understory species and thereby promote greater diversity (Whitmore 1989; Brokaw and Scheiner 1989). These understory species can be grouped into three general categories based on how they respond to canopy shading. This "ecological response group" approach has been widely used by terrestrial plant ecologists to classify individual species according to how they respond to changes in their light environment and has been very useful in studies on canopy shading (e.g., Collins et al. 1985; Whitmore 1989; Kursar and Coley 1999). The logic behind the response-group approach is straightforward; canopy removal should elicit positive responses in recruitment and/or growth for species that require high irradiances, negative responses for species that require low irradiances, and little-to-no responses for species adapted to a variety of irradiances (Brokaw and Scheiner 1989; Spies and Franklin 1989; Whitmore 1989; Kursar and Coley 1999). Those species, then, that remain rare under dense canopies but rapidly recruit into canopy gaps or following widespread canopy removal have typically been referred to as "light-adapted," "gap-requiring," or "shade-intolerant" and are often considered to represent fugitive species, while those species that occur under forest canopies but do not markedly respond to canopy loss have typically been referred to as "light-flexible" or "shade-tolerant" species and are often considered to represent climax species (Whitmore 1989; Hay 1994; Clark et al. 2004). Whereas light-flexible species are generally numerically more abundant than light-adapted species both under canopies and in canopy gaps, their ability to withstand low light environments may result in a decreased ability to rapidly respond to sudden increases in light (Canham 1989). As a consequence, light-adapted species, through greater recruitment and growth, typically dominate areas following canopy loss.

In temperate marine communities, where shading by thick canopies of kelps and rockweeds (Orders Laminariales and Fucales, respectively) can regulate understory algal abundance in shallow (<30 m) water (Pearse and Hines 1979; Foster 1982;

Reed and Foster 1984; Kennelly 1987a; Harrold et al. 1988; Dayton et al. 1992), the removal of the dominant canopies typically results in increased bottom light and a corresponding increase in the abundance of opportunistic species (Dayton et al. 1984, 1992; Reed and Foster 1984; Kennelly 1987b; Cecchi and Cinelli 1992; Graham 1996; Edwards 1998). In fact, North et al. (1986) conclude that light is the primary factor regulating species abundances within coastal forests, a claim that has been experimentally tested in numerous studies via experimental canopy removal. For example, Ambrose and Nelson (1982) observed that removal of the invasive *Sargassum muticum* at Santa Catalina Island, USA, resulted in reduced recruitment of the giant kelp *Macrocystis pyrifera* by reducing benthic irradiance. Likewise, Reed and Foster (1984) found that removal of the *Macrocystis pyrifera* surface canopy and the subsurface *Pterygophora californica* canopy in a central California, USA, kelp forest resulted in increased recruitment of understory algae, as well as the kelps themselves. Similarly, Clark et al. (2004) replicated Reed and Foster's canopy clearings at three areas in the same central California kelp forest and followed changes to the understory algae for a period of 2 years. Their clearing design (Fig. 7.1) allowed for the simultaneous testing of the individual and combined effects of shading from both surface and subsurface canopies on understory algal assemblages, and from an opportunistic alga, *Desmarestia ligulata*, that recruited into the clearings in very high abundances. Their results indicated that while understory algae did respond to the canopy clearings, the low abundances of individual species and the small magnitude of each species' response compared to their natural temporal and spatial variability made detecting canopy effects difficult. However, when understory species were grouped together in ecological response groups, they were able to detect otherwise cryptic increases in some (i.e., light-adapted) species as much as 1 year earlier than when each species was examined individually. The exception to this was the opportunistic brown alga *Desmarestia ligulata* which showed dramatic rapid increases within the canopy clearings. Edwards (1998) examined this further and found that while *Desmarestia ligulata* remained in low abundances under existing canopies, it recruited in high abundance in the spring and ultimately reached high bottom cover in areas where the canopies were removed (Fig. 7.2). Similar patterns have been observed for *Desmarestia ligulata* in Point Loma, CA, following canopy removal by winter storms (Dayton et al. 1984) and in three central California kelp forests characterized by different hydrodynamic conditions and canopy covers (Foster 1982). Dayton et al.'s work further described that disturbance to the dominant kelp canopies resulted in variation in the benthic light regimes and a corresponding mosaic of understory algal patches. Some of these patches were able to persist for extended periods of time and competitively exclude or delay recovery of the otherwise dominant kelps. The effects of this canopy shading, however, are not limited to interspecific interactions but also impact individuals of their own species via intraspecific interactions. For instance, shading from the dominant *Macrocystis pyrifera* canopies also inhibits recruitment and growth of their own juvenile sporophytes (Anderson and North 1969; Reed and Foster 1984; Dean et al. 1989). Similar negative effects of intraspecific competition were reported by Neushul and

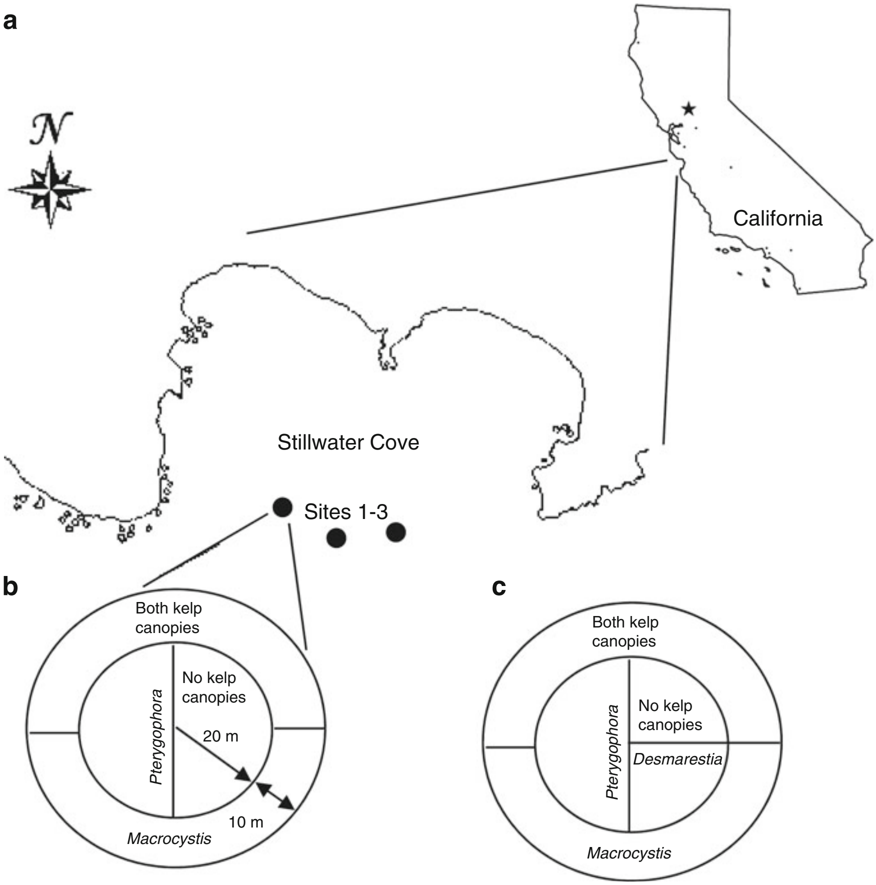

Fig. 7.1 Diagram of kelp canopy clearing experiment used by Clark et al. (2004) showing (**a**) location of the three replicate sites in Stillwater Cove, CA, USA. (**b**) Blocked canopy clearing design showing the 20 m radius inner circles and 10 m radius outer tori from which kelp canopies were removed either individually or in combination. Treatments include "No canopies" = both *Macrocystis* and *Pterygophora* removed, "*Pterygophora* canopy" = *Macrocystis* removed and *Pterygophora* left unmanipulated, "*Macrocystis* canopy" = *Pterygophora* removed and *Macrocystis* left unmanipilated, and "Both canopies" = both kelp species left unmanipulated (also considered as control treatment). (**c**) Canopy clearings showing the placement of the *Desmarestia* removal treatment following dense *Desmarestia* recruitment. Diagram reproduced from Clark et al. (2004)

Harger (1985) and Reed (1987). Consequently, as the dominant kelps begin to recover following a disturbance, they often recruit in much higher densities than can be sustained when they are adults and thus undergo strong intraspecific competition (i.e., density dependence) that results in self-thinning of the population (Fig. 7.3). However, large variability exists in the interpretation of how important density dependence is to algal populations, in part due to differences in the experimental methodologies used to examine it (Flores-Moya et al. 1996; Scrosati 2005).

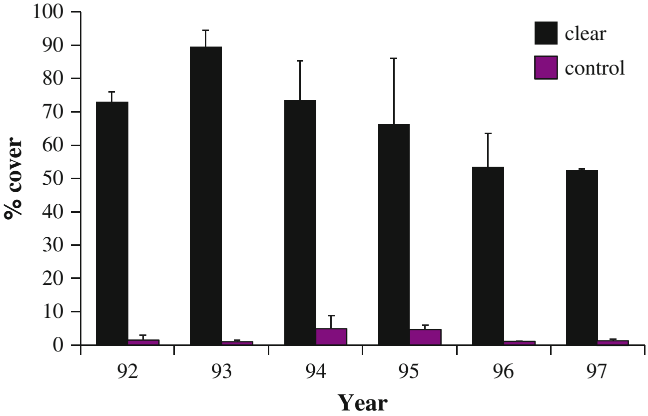

Fig. 7.2 Effects of kelp canopy removal on recruitment (% cover) of *Desmarestia ligulata* sporophytes (means + 1standard error). *Black bars* represent recruitment into areas where kelp canopies had been cleared, and *white bars* represent recruitment into areas where the kelp canopies were unmanipulated (controls) from 1992 to 1997. Reproduced from Edwards (1998)

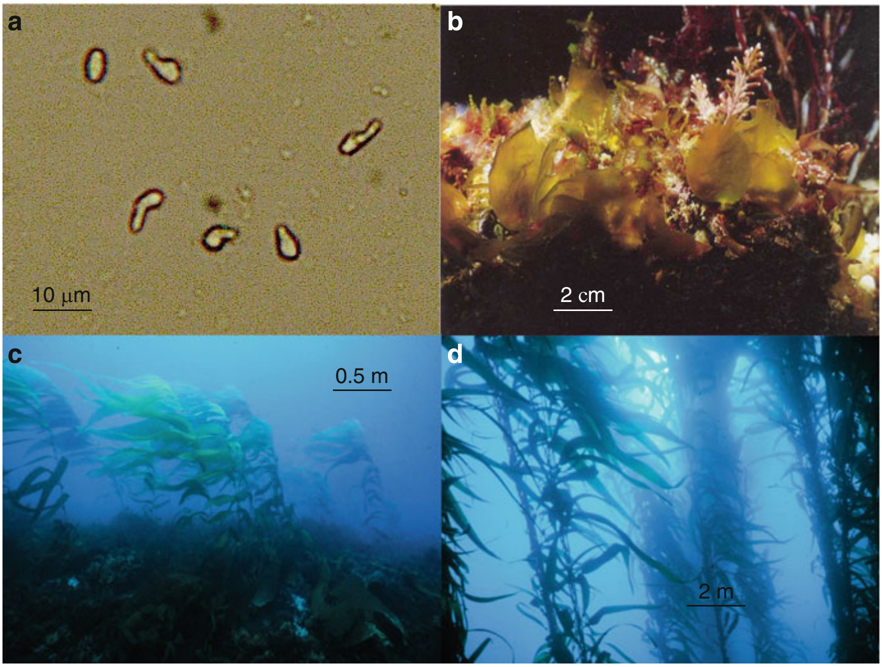

Fig. 7.3 Photographs of giant kelp (*Macrocystis pyrifera*) showing relative densities of different ages as the population self-thins. **a** = young sporophytes (photo taken on a microscope slide), (**b**) recruits, (**c**) juveniles, (**d**) adults. Note the differences in scales showing that younger smaller stages are much more densely packed

Regardless, it is clear that self-thinning is important to many seaweed populations, though this may be more important for unitary species such as *Macrocystis pyrifera* than for clonal species such as *Mastocarpus papillatus* where self-thinning during the growing season is not expected even under high density (Flores-Moya et al. 1996; Scrosati 2006).

While studies along the west coast of North America have shown dramatic responses by the turf-forming algae to kelp canopy clearings, results from other areas of the world are more variable. For example, clearings to the surface and subsurface kelp canopies within *Nereocystis leutkeana* forests in coastal Alaska resulted in complete overgrowth by subsurface kelps within 1 year, while similar clearings within the *Eualaria fistulosa* forest throughout the Aleutian Archipelago resulted in little to no macroalgal recruitment over 1-year period (B. Konar et al. unpublished data). While the reason for this is unclear, we believe it is primarily due to variation in identities and life histories of the species involved (i.e., whether they are annual or perennial), oceanographic conditions (i.e., temperature, nutrient, and wave conditions), grazing pressure, and idiosyncrasies associated with the experiments themselves (i.e., when the clearings were done, how large and thorough they were). However, even with this variability, certain similarities exist among geographic areas. For example, throughout much of Australia, the conditions created by subtidal kelp canopies include reductions in irradiance, sedimentation, and the abundance of turf-forming algae (Kennelly 1987a). Consequently, the kelp canopies maintain encrusting coralline algae from overgrowth by turf-forming algae through shade (Kennelly 1987a; Connell 2003b) and possibly through reduced accumulation of sediments (Melville and Connell 2001). Thus, the clearance of kelp canopies generally leads to the overgrowth of encrusting algae by turf-forming algae, which then trap sediments (Kennelly and Underwood 1993; Connell 2005). Conversely, recovery of the kelp canopies invariably leads to the reverse effect (e.g., Kennelly 1987b), demonstrating that the co-occurrence of canopy and encrusting coralline algae is not just a spatial and temporal coincidence, but rather one driven by the state of the dominant canopy-forming species. Given the strength of association across regions and different taxa in Australia, there appears to be considerable predictive capacity in understanding how the understory macroalgae benefit from the physical light environment created by the canopies (e.g., Bertness and Leonard 1997). These patterns are consistent with the relative abundance of encrusting and turf-forming algae, where the former are relatively abundant in locations of low light and sedimentation (Steneck 1986, 1997), while the latter monopolize locations of high light and high sedimentation (Airoldi 1998).

7.2.3 Competition for Space

On rocky surfaces, access to adequate space is crucial for the attachment and survival of organisms (e.g., Connell 1961). Except for a few examples of free-living algal (e.g., some species in genera *Ulva* (formerly *Enteromorpha*) and

Sargassum, and several species of coralline algae called rhodoliths), most marine macroalgae are attached to rocky reef, other algae, invertebrates, or sediments. This results in their interacting for attachment sites in two dimensions rather than three and thus greatly increases the chances that they will compete for access to the substrate. This will also occur between algae and sessile invertebrates such as is commonly observed on degraded coral reefs where algae are considered competitively dominant to coral larvae and new recruits, but competitively subordinate to coral adults (reviewed in McCook et al. 2001; see also Chap. 16 by Mejia et al. and Chap. 18 by Bartsch et al.). As a consequence, algal proliferation often occurs in areas where coral adults have died, which in turn prevents coral recruitment and slows community recovery (e.g., Kuffner et al. 2006). However, while algal–invertebrate competition is common, we do not address it further here but rather focus our attention to competition between and within algal species.

Although algae may compete strongly for attachment space on the substrate, when examined closely, the actual area of attachment to the substrate is often very small compared to the overall size of the algal thallus. For example, on coral reefs, the actual attachment site of the dominant algae can be as small as 10–100 µm with lots of bare space present between the holdfasts (Hackney et al. 1989). Further, Dayton (1975) found that less than 20% of rocky reef in a subtidal temperate kelp forest was occupied by the kelp holdfasts even though the kelp canopies covered the majority of the reef. Consequently, competition among macroalgae for space, per se, may not be a limiting factor in recruitment in many locations (reviewed in Carpenter 1990). However, given that the thalli of many algae tend to lie prostrate on the substrate or physically abrade the substrate as they move in the waves (Velimirov and Griffiths 1979; Witman 1987; Kennelly 1989), they can prevent settlement and/or growth of other algae on the substrate via interference (abrasion) and exploitative (shading) competition (Duggins and Dethier 1985). Removal of the dominant species, then, generally results in an increase in other macroalgae as observed for intertidal *Hedophyllum sessile* communities in the San Juan Islands, off the coast of Washington State, USA (Duggins and Dethier 1985). Further, some of the strongest competitive interactions in the southern hemisphere tend to be created by large canopy-forming algae (e.g., intertidal *Durvillaea antarctica*; subtidal *Ecklonia radiata*). These individuals exclude many understory species via their fronds which shade or whiplash the substratum (Kennelly 1987b). However, these effects may vary geographically at a number of spatial scales (Connell and Irving 2009) and among different benthic species (Kennelly 1989). Likewise, in the Aleutian Archipelago, physical abrasion from the brown alga *Desmarestia viridis* is an important factor keeping other algae from establishing patches on the tops of pinnacles (Konar and Estes 2003). Physical abrasion by kelp fronds can also prevent recruitment of sessile invertebrates (Connell 2003a) which otherwise monopolize space under lower light and sedimentation such as observed on South Australian coasts (Irving and Connell 2006) or of motile invertebrates that would otherwise graze on the algae (Konar and Estes 2003). Hence, body size often serves as the best measure of the potential for algae and other types of sessile species to exert strong community-wide effects.

Exceptions to the notion that macroalgae do not compete strongly for space have been observed in turf-forming species that can occupy nearly 100% of the substrate in some places and thereby prevent settlement of other algae (e.g., Hruby and Norton 1979), and in areas dominated by encrusting algae which can compete intensely for space (Steneck and Paine 1986). On many temperate coasts, encrusting coralline algae can also occupy up to 80% of hard substrate, dominating space beneath macroalgal canopies (Irving et al. 2004). With the creation of available space (e.g., through storm damage), however, turfs rapidly colonize the space and overgrow the coralline crusts (Russell and Connell 2005; Worm et al. 1999). The morphology of these filamentous turfs allows them to then trap sediment (Airoldi 1998; Gorgula and Connell 2004) and subsequently inhibit the recruitment of canopy-forming species in localities from a diversity of locations around the world (Devinny, 1978; Gorman and Connell 2009). In addition, recruitment of the larger macroalgae can occur on the thalli of the turf algae, though the added hydrodynamic drag on the turf holdfast can result in increased removal rates from waves and thus low survival (Edwards unpublished data). In an example of competition among three species of intertidal crustose and turf algae, Padilla (2003) observed coralline turf algae were better competitors than the upright forms for space, as they were more susceptible to grazing and desiccation. In contrast, two upright forms were inferior competitors for space but were more resistant to grazing and desiccation. Thus, the coralline algae coexisted on the rocky shore, though in different microhabitats. Furthermore, in many temperate systems, if the dominant kelp canopies are excluded from a reef, turf algae may increase in abundance over time and ultimately become the dominant space occupiers, especially in areas where the canopies have been removed (e.g., Edwards 1998; Connell 2003b).

Competition for space itself can be strongly mediated by both physical (disturbance) and biological (competition) factors. For example, Kastendiek (1982) observed three species of algae at Santa Catalina Island, CA, USA, competing strongly with each other but that the nature of this competition differed greatly between species pairs, each of which was influenced by physical disturbances differently. Specifically, the kelp *Eisenia arborea* forms canopies that excludes (or reduces its abundance) the brown alga *Halidrys dioica*, thereby allowing the turf alga *Pterocladia capillacea* to dominate the substrate under the canopy. However, if the *Eisenia arborea* canopy is removed, *Halidrys dioica* recruits in high abundances and dominates the substrate, thus excluding *Pterocladia capillacea* from the area. This switch between competition for light and competition for space appears to be driven by disturbance to the dominant *Eisenia arborea* canopy. Similarly, competition for space may be strongly dependent on species identity and whether the interaction is interspecific or intraspecific. For example, Santelices et al. (2003) observed that in the intertidal region of Chile, when the holdfasts of the intertidal red algae *Mazzaella laminarioides* and *Nothogenia fastigiata* come into contact, one outcompetes the other resulting in its death. However, when the holdfasts of either species come into contact with a member of their own species, the holdfasts coalesce and both individuals survive, suggesting that the populations might be chimeric. Finally, competition for space may be integral in regulating patterns of zonation in the intertidal. Much in the way that Connell (1961) concluded that the upper and lower limits of species distributions in the intertidal may be set by competition and/or predation, Hawkings and Hartnoll (1985) concluded that bands of both dense and sparse macroalgal populations across intertidal shores of the United Kingdom were set by competitive interactions. Specifically, when fronds of the brown algae *Fucus* and *Laminaria* were removed, all other algal species occurring immediately below them were able to colonize further up in the intertidal zone. Similarly, competition may also set the lower limit of those species, as they were also able to colonize the lower parts of the shore following the removal of their competitors.

7.2.4 Competition for Nutrients

Algae require adequate carbon, nitrogen, and phosphorus for growth and survival (see also Chap. 4 by Gordillo), and competition among seaweeds for them has been observed in numerous studies. While the majority of studies on the effects of nutrient limitation have been done for freshwater phytoplankton communities, and have generally reported strong competition for nutrients, their conclusions vary depending on the specific species involved and complex synergies associated with multiple resources (e.g., nitrogen, phosphorus, and silica) that fluctuate independently with one another (e.g., Titman 1976). Unlike freshwater ecosystems, nitrogen (namely nitrate NO_3^-) is the primary limiting nutrient in the ocean, though phosphorus may occasionally be in limited supply. The primary source of nitrogen input into most coastal ecosystems is upwelling of cold nutrient-rich water from below the thermocline, though terrestrial inputs from runoff may also be important in some locations (Gorman et al. 2009). Algae take up the nitrogen directly from the water column via mass transport and thus uptake rates are strongly influenced by thallus morphology ("functional form," surface/volume ratios), tissue and seawater nitrogen content (concentration gradients), and hydrodynamic flow which in turn regulate boundary layer formation around the algal thallus (Hurd et al. 1997). Consequently, during periods of low nutrients and low hydrodynamic flow, algae can compete intensely for nutrients. For example, Dayton and Tegner (1984) report that along southern California, USA, the dominant current flow is caused by longshore currents (see also Winant and Bratovich 1981). While internal waves may be important in cross-shore delivery of nutrients, the longshore currents are the primary source of nutrient delivery into the kelp forest. However, drag imposed on the moving water by the kelp thalli can reduce current speeds within the kelp forest by as much as 33% resulting in reduced nutrient delivery to the inner parts of the forest. Further, the nutrients are taken up by those kelps near the periphery of the forest resulting in further nutrient depletion within the forest. In fact, Jackson and Winant (1983) concluded that nutrient uptake within the Point Loma, CA, USA, kelp forests can be 23% per hour, resulting in the water being nutrient depleted by the time it reaches the interior of the kelp forest, though this may be partially ameliorated by cross-shore delivery of nutrients via internal waves. Consequently, while the individuals near the edge of the forests may be healthy, individuals in the interior can become nutrient stressed and appear less healthy during periods of low nutrient availability, though this varies considerably with forest size (Bernstein and Jung 1979; Dayton et al. 1984). This nutrient limitation may also be important to reproduction in many species. For example, Reed (1990) concluded that both interspecific and intraspecific competition between the microscopic gametophytes of *Macrocystis pyrifera* and *Pterygophora californica* was intense when they settled at high densities but not when they settled at low densities. He attributed this to competition for nutrients even though the culture media was changed regularly. In contrast, Vadas (1972) found no evidence of competition among the gametophytes of *Nereocystis luetkeana*, though this may have been because his overall densities were substantially lower than those used by Reed. Further, Carney and Edwards (2010) observed that delaying development as 1–2 celled gametophytes for 1–3 months can ameliorate the negative effects of intraspecific competition among kelp gametophytes, though she did not test how this impacts eventual sporophyte recruitment.

7.3 Competition in Complex Environments

7.3.1 Synergistic Effects of Different Factors

While it is true that limitation of one or more resources can be important to the recruitment, survival, and reproduction in many macroalgae, synergistic effects among numerous environmental factors may result in substantial variability in how species respond to these limitations. For example, Fujita (1985a, b) reports that when nutrients are plentiful, the green algae *Ulva* spp. (formerly *Enteromorpha*) are able to outcompete the red algae *Gracilaria tikvahiae* for space in the intertidal due to its greater uptake and growth rates. However, *Gracilaria tikvahiae* possesses greater nutrient storage capabilities and therefore outcompetes *Ulva* during periods when nutrients are limited. Likewise, on the New England, USA coast, where the brown alga *Fucus vesiculosus* is the dominant competitor for space over *Ulva* spp. in the absence of grazers, *Ulva* spp. is the competitive dominant species when grazers are present. This occurs because the grazers remove the fast growing young stages of *Ulva* spp., thus allowing the slower growing grazer-resistant *Fucus* to grow. Along the Pacific coast of Baja California, MEX, the giant kelp *Macrocystis pyrifera* forms a surface canopy above the stipitate kelp *Eisenia arborea* and thus outcompetes *Eisenia arborea* for light. However, *Eisenia arborea* is more resistant to low nutrient conditions such as those observed during El Niño Southern Oscillation (ENSO) events (Hernández-Carmona et al. 2001) and thus is able to persist during periods when *Macrocystis pyrifera* dies. Following the ENSO, *Eisenia arborea* is able to form dense subsurface canopies that exclude *Macrocystis pyrifera* recruitment and thus prevent recovery of its populations for several years (Edwards and Hernández-Carmona 2005). Likewise, Dayton et al. (1984) observed similar patterns between *Macrocystis pyrifera* the subsurface kelps *Pterygophora californica* and *Laminaria farlowii* following the 1982–1984 ENSO in a southern California kelp forest. Here, the subsurface kelps were more resistant to the large ocean waves associated with this disturbance and thus exhibited greater survival. Much as with *Eisenia arborea* in Baja California, these kelps were able to delay *Macrocystis pyrifera* recruitment, resulting in longer term changes to the understory algal patch dynamics within the kelp forest. Similar changes to competitive hierarchies have been observed in other areas of the world in response to environmental factors. For example, although *Ecklonia radiata* is generally competitively dominant to turf algae along the South Australia coast, nutrient discharge to the normally oligotrophic waters causes turfs to dominate the space and inhibit recruitment of *Ecklonia radiata* (Gorman and Connell 2009), resulting in a competitive outcome that can persist for several decades (Connell et al. 2008). Finally, Duggins and Dethier (1985) note that while the intertidal kelp *Hedophyllum sessile* outcompetes other algae for space in the intertidal areas of the San Juan Islands, its competitive abilities are regulated by grazing from the chiton *Kathrina tunicata* and by wave exposure, both of which act to remove *Hedophyllum sessile* and create bare space for other algae to recruit. Taken together, it is clear that the competitive abilities of at least some macroalgae can be a trade-off with features that are adapted to the environment. For example, while the giant kelp *Macrocystis pyrifera* develops large canopies above its neighbors and thus outcompetes them for light, its large size and high growth rate make it more susceptible to disturbance from large waves and low nutrients than many of its neighbors (Dayton and Tegner 1984). In their review on competition in seaweeds, Olson and Lubchenco (1990) write, “Because the traits of seaweeds have evolved in a context of multiple selection pressures, the consequences of traits will vary with environmental conditions.” Consequently, a comprehensive investigation of competition in heterogeneous environments requires studying how competition operates under different combinations of environmental conditions.

7.3.2 The Importance of Competition in Maintaining Marine Forests

Marine forests form diverse biological habitats and largely persist by facilitating their own recruitment through the competitive exclusion of opportunistic turf-forming algae (Dayton et al. 1984; Reed and Foster 1984; Connell 2005; Irving and Connell 2006). When kelp canopies are lost, however, turfs rapidly colonize space and inhibit the recruitment of juvenile kelp and reformation of kelp forests (Kennelly 1987a; Gorman and Connell 2009). Under conditions of elevated nutrients, these naturally ephemeral turfs persist in fragmented forests (Airoldi et al. 2008; Gorman et al. 2009) to cause intergenerational decline and collapse of the kelp community (Connell et al. 2008). The competitive dominance of kelps over turfs is a key interaction that enables kelp forests to regenerate and persist, but this dominance may be reversed under conditions that favor the persistence of turfs (Gorman and Connell 2009). As a consequence, it is clear that variation in algal assemblages within and among kelp forests can be attributed partly to differences in the primary canopy-disturbing agents, ocean waves, and temperature (Foster 1975; Cowen et al. 1982; Foster 1982; Dayton et al. 1984, 1992; Seymour et al. 1989; Breda and Foster 1985; Harrold et al. 1988; Graham 1997). This, however, can be highly variable especially on a seasonal scale. For instance, along parts of the west coast of North America, large ocean waves associated with winter storms remove large quantities of kelp canopies, typically resulting in maximum kelp canopies in summer and minimum canopies in winter (Kimura and Foster 1984; Reed and Foster 1984; Dayton et al. 1992). Consequently, competitive interactions between the canopy-forming and understory species can vary temporally, further increasing the overall variation in kelp forest community composition (Pearse and Hines 1979; Gerard 1984; Kennelly 1987a, b; Harrold et al. 1988; Dayton et al. 1999). For example, Edwards and Hernández-Carmona (2005) found that along the coast of Baja California Sur, MEX, the dominant *Macrocystis pyrifera* canopies typically reduce the abundance of the understory *Eisenia arborea* canopies. However, all the *Macrocystis pyrifera* canopies were lost during the 1997–1998 ENSO, resulting in a dramatic increase in *Eisenia arborea* canopies that were able to prevent *Macrocystis pyrifera* recovery at its southern range limit for up to 20 years.

7.3.3 Competition in the Face of Climate Change

The role of global environmental change in driving change to macroalgal communities in marine ecosystems has received heightened attention (e.g., Wernberg et al. 2010, 2011). While range contractions and extensions have been forecast as a function of changing climate (e.g., temperature), the effects on competitive interactions among species are less clear. Unlike kelps, many turf-forming species are ephemeral and require increased resource availability to enable their physiology and life history to be competitively superior to perennial species (Airoldi et al. 2008). Coastal waters that facilitate the expansion of turf-forming algae (e.g., enhanced CO_2, temperature, and nutrients; Gorgula and Connell 2004; Connell and Russell 2010) tend to maintain their dominance of space at the expense of canopy-forming algae (e.g., Gorman and Connell 2009). Much of the global research effort into forecasting the effects of climate change focuses on the direct effects, thereby overlooking indirect effects (e.g., competitive effects). As the name implies, "indirect" effects are not as simple to identify as "direct" effects and can often yield "unexpected results" (Wootton 1994). They are unanticipated because the impact of one species on another (i.e., competitors) requires knowledge of a third species or mediating component is poorly understood. Research into ocean acidification (see Chap. 19 by Roleda and Hurd) is a good case in point. Marine waters absorb approximately 30% of the anthropogenic-derived CO_2 from the earth's atmosphere and the resulting ocean acidification (Feely et al. 2004; Orr et al. 2005) and direct negative effects on calcifying algae. The difficulty is that for noncalcifying algae, elevated inorganic carbon has positive effects on some species and not others, and that these nonuniform effects among alternate species (review by Gao and McKinley 1994) have relatively unexplored consequences to competitive hierarchies, particularly if growth is limited by sources of inorganic carbon.

If competitive interactions are reduced by the increasingly novel conditions brought by human activities, then the persistence of entire biological communities is increasingly likely to be disrupted. Such phase shifts are not uncommon, but anticipating them has been problematic because many involve indirect effects for which the impact of one species (e.g., turfs) on another (e.g., kelp) requires knowledge of a third element that is inadequately understood (e.g., synergies among pollutants). The strength of competition (e.g., dominance of kelp over turfs) is important to understand because it identifies the conditions in which turfs expand. The mere presence of foundation species may not always maintain their competitive strength over turfs. As canopies are thinned, reduced in size, or fragmented, their positive effects are reduced and the associated environmental conditions become more similar to those experienced outside the canopy (Jackson and Winant 1983; Bruno and Bertness 2001). Under these conditions, turfs expand to dominate space and inhibit the recruitment of kelp (Gorman and Connell 2009; Connell and Russell 2010), leading to phase shifts over multiple generations (Connell et al. 2008). Therefore, the maintenance of intact populations of foundation species seems critical to the strength of interaction (i.e., continued dominance over kelp inhibitors) and ensuing maintenance of community structure and function (Bruno and Bertness 2001). The competitive balance between species is often shifted by the abiotic environment which alters the relative abilities of algae to recruit to and retain space. Hence climate change seems set to bring change to competitive processes as we currently understand them.

7.4 Concluding Remarks

In conclusion, competition within and among marine macroalgae is a deterministic influence in establishing patterns of biogeography, regulating growth and reproduction, and in maintaining populations at or below their carrying capacities. It is important to setting species range limits, governing how populations will respond to disturbances, and in structuring coastal ecosystems. However, the direction, strength, and importance of these competitive interactions vary considerably with species identity, the location where these interactions take place, and with changes to the physical and biological environment. Many species have evolved morphologies that enable them to better access the resources, and thus outcompete their neighbors, but these morphologies also may make them more susceptible to environmental stresses, thereby temporarily altering competitive hierarchies and ameliorating the effects of limited resources. Even so, numerous studies have demonstrated that competition can be the most important factor in regulating marine macroalgal population and community dynamics. However, while our understanding of these interactions has grown considerably since Lotka (1925), Volterra (1926), and Gause (1934) wrote their seminal works, information on how these interactions will work in the future remains lacking. Perhaps the most important next step is to assess how these competitive interactions will change under environmental variability, such as predicted with climate change. Understanding this may better inform us of how macroalgal communities will likely be structured in the future.

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