

II. Production of Macrophytes

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Macrophyte Productivity and the Provisioning of Energy and Habitat to Nearshore Systems

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Introduction

Foundation species are disproportionately important to the structure of their associated communities (Dayton 1972, Bruno and Bertness 2001) and are evident in both terrestrial and marine systems (e.g., mangroves, redwood trees, kelps, hermatypic corals). Through the direct provisioning of energy and habitat, foundation species facilitate the maintenance of community structure in different ways than keystone predators (e.g., sea otters, wolves) and ecosystem engineers (e.g., termites, beavers), although these terms are sometimes (and incorrectly) used interchangeably in the literature. Keystone predators actively regulate species interactions (Paine 1969a, Paine 1969b), while ecosystem engineers provide habitat architecture and modify the physical environment (Jones et al. 1994, Hastings et al. 2007). Like these critical species, however, the loss of foundation species from a system generally causes conspicuous declines in local biodiversity, productivity, and ecosystem functioning (Knowlton 2001, Graham 2004, Ellison et al. 2005). The utility of the foundation species concept is that variability in productivity and population dynamics of foundation species may be directly proportional to community characteristics and ecosystem function. Therefore, studies of the ecophysiology of foundation species are critically important for forecasting subsequent variability in associated communities and ecosystems. Because the role of foundation species may be context dependent (Hughes 2010), a

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detailed understanding of how macrophyte foundation species respond to external stressors and environmental conditions is paramount for developing successful management strategies, maintaining key ecosystem services, and promoting natural resilience in marine systems.

Macrophytes clearly play a foundational role in many marine ecosystems, though not all macrophytes can be considered foundation species. In any given system, most macroalgal and seagrass taxa are potential sources of fixed carbon and nutrients for primary consumers (Vadas 1977, Hay et al. 1994, Paine 2002, Sotka and Hay 2002, Amsler et al. 2005, Rasher et al. 2013). The role of marine macrophytes in habitat provisioning, however, is dependent on the size and distribution of the macrophyte relative to the scale of physical structure in the natural environment. The loss of a foliose red alga from offshore pinnacles, for example, may result in a decline in available food for herbivores, but the heterogeneous rocky substrates that remain will continue to serve as critical habitat for associated invertebrates and fishes. Therefore, in this system, the foliose red alga would not be considered a foundation species even though it is consumed as part of the food web. Conversely, large kelps growing on rocky coasts, or even short seagrasses growing on homogenous soft sediments, have a disproportionate effect on the provision of both energy and habitat to their respective systems. The functional importance of macrophytes as foundation species in marine systems is therefore dependent on the simultaneous provisioning of energy and critical habitat, and the magnitude of their relative contributions.

Here, we explore how understanding macrophyte productivity and morphology is useful for studying their role as foundation species in natural systems. Our goal is not to provide an exhaustive review of marine macrophyte productivity rates, nor the physiological and environmental processes that regulate such rates. Instead, our focus is to: (1) identify macrophyte taxa that are clearly disproportionate in their provisioning of energy and habitat to their associated communities; (2) describe some physiological features that facilitate the role of macrophytes as foundation species; and (3) discuss how variability in the productivity of marine macrophyte foundation species may impact their associated communities.

Macrophyte foundation species

The determination of whether a particular macroalgal or seagrass taxon is a foundation species is dependent on the context of the system within which the macrophyte is being studied. As such, it is not possible to provide a simple list of marine macrophyte foundation species, as the same species can function differently across systems. For example, *Laminaria hyperborea* is an important foundation species in rocky subtidal systems of Norway and the Northeast Atlantic, where much of the structure and energy flow of these systems is dependent on this single kelp species (Jupp and Drew 1974, Christie et al. 2003, Norderhaug et al. 2003, Abdullah and Fredriksen 2004, Bartsch et al. 2008). In contrast, there is little evidence for a foundational role of a closely related species *Laminaria farlowii* in California rocky subtidal systems, where high physical heterogeneity and the presence of large, perennial *Macrocystis* forests have been shown to be of overwhelming importance (Dayton 1985, Dayton et al. 1992).

So are kelps of the genus *Laminaria* foundation species or not? The answer depends on the characteristics of the system within which they are present and the scale at which they influence their associated communities. Ultimately, the only true test of a macrophyte's role as a foundation species is to study the structure of the community with and without the macrophyte in question. While an important source of energy and habitat, the loss of a stipitate *Laminaria* species from a California kelp forest is unlikely to fundamentally alter the structure and function of the system, whereas the loss of *Macrocystis* would drive fundamental changes in the community (Graham 2004, Arkema et al. 2009). It is therefore critical to understand the respective roles of macrophytes in different systems and how the role of a single species can change from location to location due to variations in environmental conditions and community structure. While the accurate description of a species as a foundation species can be challenging, it is important to understand which species have the potential to serve as foundation species within an ecological system and which do not.

To date, few studies have examined the effects of the presence/absence of a specific species on community structure to assess whether or not the "foundation species" label is appropriate. For example, Shelton (2010) nicely demonstrated that the surfgrass *Phyllospadix* serves as a foundation species in tidepools by provisioning habitat and modulating environmental conditions. Tidepools in which *Phyllospadix* was present were up to 10°C cooler and had more stable water temperatures, while tidepools that had *Phyllospadix* removed had warmer and more variable temperature, which drove substantial changes in community structure. In most cases, foundation species are identified through natural history observations that suggest particular species are critical to the provisioning of energy and habitat. Other studies have used stable isotopic analysis to quantify the disproportionate importance of a particular species to maintaining energy flow within a system (Duggins et al. 1989, Bustamante et al. 1995, Bustamante and Branch 1996, Miller et al. 2013). Generally, species-removal experiments are aimed at understanding the role of competition in regulating community structure and ecosystem function (Dayton 1975, Santelices and Ojeda 1984a, Clark et al. 2004) and are not always designed to directly address the role of a species as a foundation species. To get at the specific question of habitat provisioning, however, researchers have compared the diversity or community structure of a system with and without the putative foundation species, relying on both experimental and natural removal of key species (Duggins 1980, Connolly 1994, Attrill et al. 2000, Byrnes et al. 2011). Yet, we are unaware of a single study that has directly documented *both* the trophic and habitat consequences of the loss of a foundation species within a system. This is likely due to the large spatial scales over which macrophyte foundation species are distributed and the long timescales within which natural communities respond to physical disturbances or the loss of critical species.

Despite the dearth of experimental studies, it is clear that macrophyte foundation species exist in many systems (Figs. 1 and 2). Temperate coastlines are dominated by kelps and large fucoids that have exceptional biomass, high rates of primary productivity, and provide three dimensional habitat and structure (Steneck et al. 2002, Graham et al. 2007, Bartsch et al. 2008, Bolton 2010). Seagrasses generally grow on soft sediment substrates and provide a fundamental source of resources and shelter to diverse filter feeding invertebrate assemblages within the sediment, and to fish and

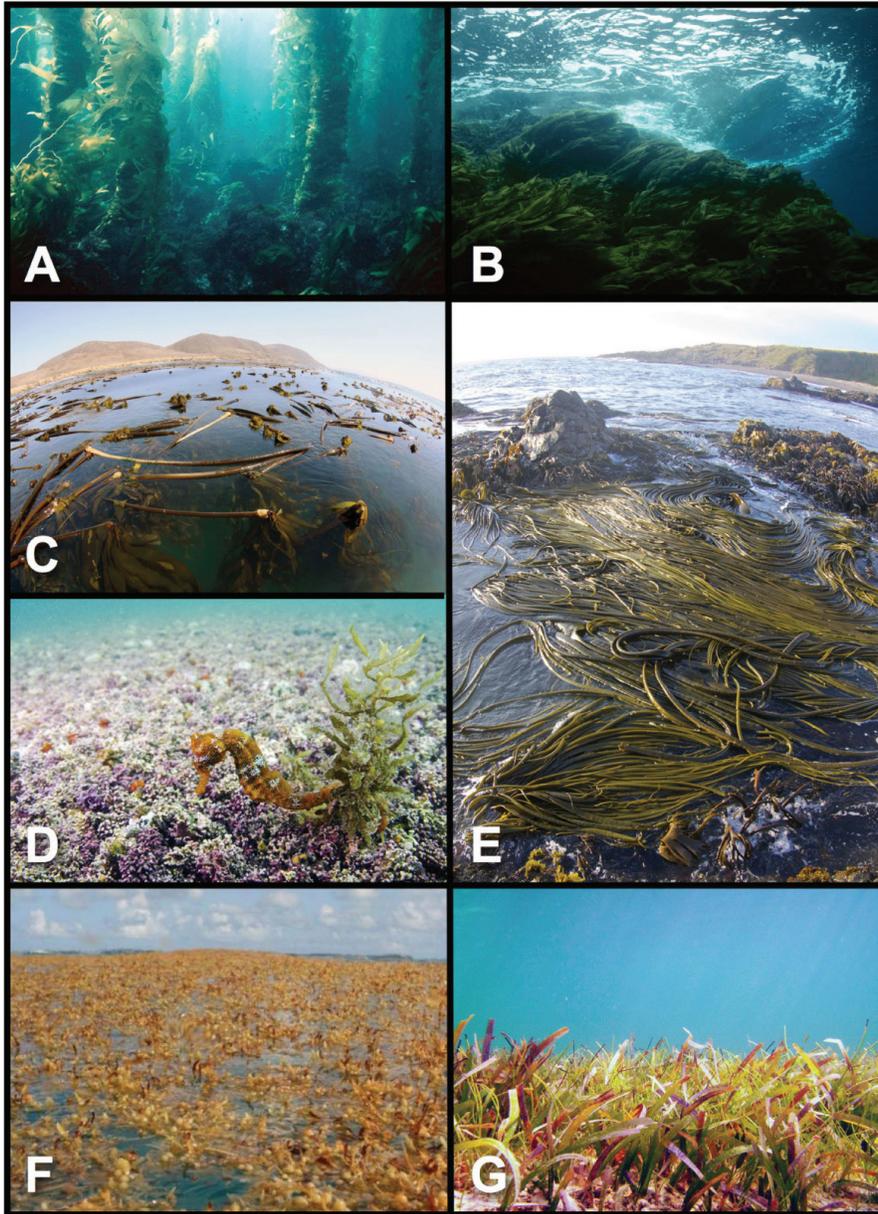


Figure 1. Marine macrophyte foundation species. (A) Subtidal forest of the giant kelp *Macrocystis pyrifera* off San Clemente Island, southern California, USA (photo credit: Enric Sala); (B) Shallow subtidal forest of the *Eisenia arborea* off San Clemente Island, southern California, USA (photo credit: Enric Sala); (C) Subtidal forest of the bull kelp *Nereocystis luetkeana*, central California, USA (photo credit: Scott Gabara); (D) Subtidal rhodolith bed of Santa Catalina Island, southern California, USA (photo credit: Scott Gabara); (E) Intertidal belt of the southern bull kelp *Durvillaea antarctica* off Bahia Mansa, southern Chile (photo credit: Michael Fox); (F) Floating mats of *Sargassum* in the Sargasso Sea, Atlantic Ocean (photo credit: Michael Fox); (G) Subtidal seagrass bed (photo credit: P. Rouja).

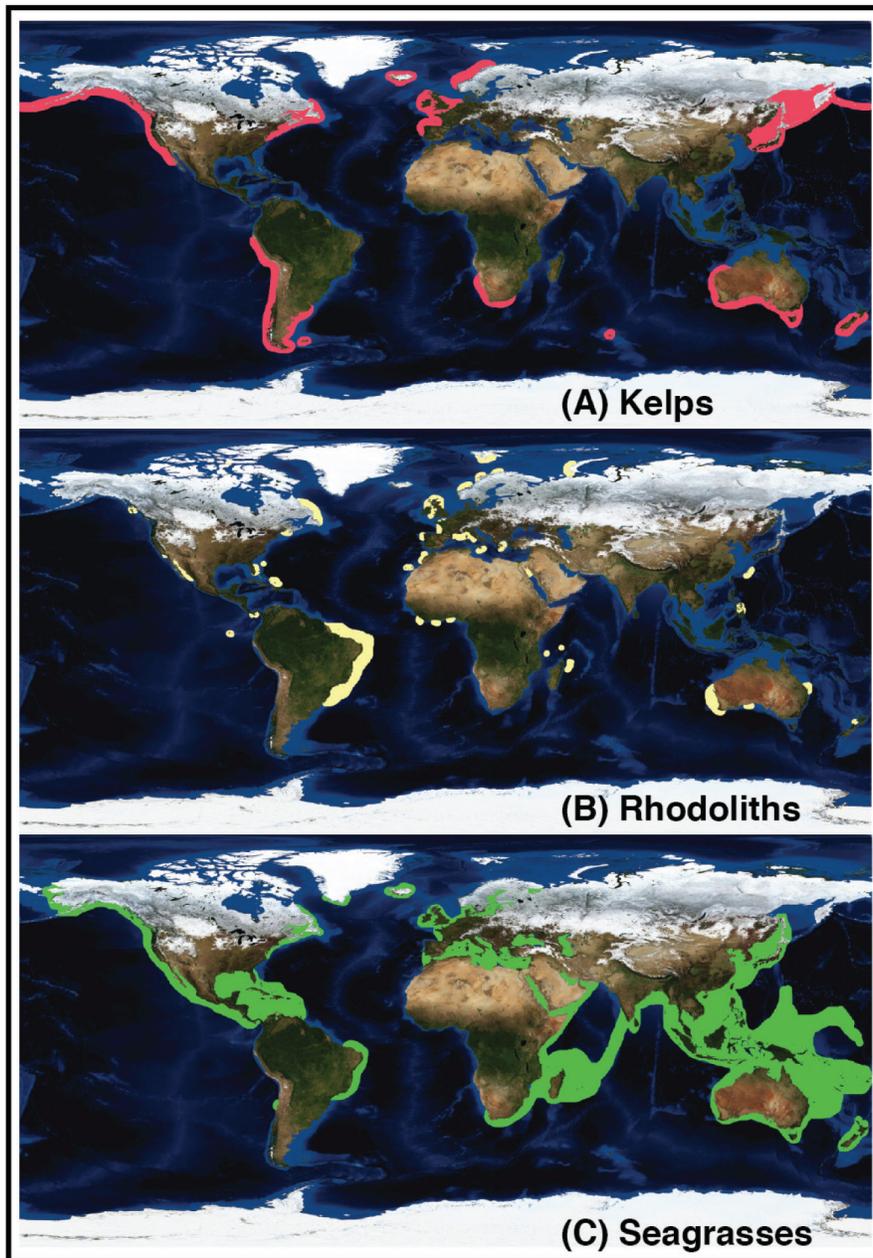


Figure 2. Global distribution of (A) kelps, (B) rhodoliths, and (3) seagrasses. Kelp distribution is not exhaustive for all kelp taxa, but represents areas where *Macrocystis*, *Nereocystis*, *Laminaria*, and *Ecklonia* serve a foundational role (modified from Steneck et al. 2002, Graham et al. 2007). Rhodolith distribution map is modified from Foster (2001). Seagrass distribution map is modified from Short et al. (2007) and represents currently accepted species in the families Hydrocharitaceae, Cymodoceaceae, Posidoniaceae, Zosteraceae, and Ruppiaceae.

invertebrates that live among the seagrass thalli in an otherwise featureless environment (Jackson et al. 2001, Hughes et al. 2008). The Sargasso Sea is a featureless, oligotrophic oceanic environment within which floating mats of *Sargassum natans* and *S. fluitans* provide intricate structure and presumably important energetic resources (Smith et al. 1973, Lapointe 1986). Despite little ecological research in this system, many species appear to have obligate associations with pelagic *Sargassum*, especially for critical early life history stages, which suggests that *Sargassum* likely functions as a foundation species in this system (Dooley 1972, Carr 1987, Moser et al. 1998). Similarly, rhodoliths, free living coralline algal nodules, provide well-documented physical structure to soft-sediment systems (Foster 2001, Steller et al. 2003, Hinojosa-Arango et al. 2014). Although coralline algal productivity rates are inherently low relative to other macroalgae, the tight association with cryptic invertebrates and the complex interstitial matrix of space within the rhodoliths suggests a strong role of rhodoliths as foundation species (Kamenos et al. 2004a,b,c, Steller and Cáceres-Martínez 2009, Hinojosa-Arango et al. 2014). Still, beyond general natural history observations and focused ecological studies, the joint provisioning of energy and habitat to natural systems by marine macrophytes remains poorly studied.

Here, we review the evidence for and identify marine macrophyte foundation species, limiting our discussion to instances in which enough data and information exist to make a strong argument for labeling a particular species using this concept. Many more macrophyte foundation species likely exist and it is important that we begin to document their presence with more experimental rigor than the typical natural history observations employed to date. With the onset of global climate change and the continued degradation of ecosystems through pollution and resource extraction, many macrophyte-based marine systems will face unprecedented challenges (Harley et al. 2012). Rigorous examination of the putative foundation species within a particular system will provide guidance for future ecological studies targeting ecosystem change and for management strategies designed to maintain and prevent future degradation of critical ecosystem services.

Mechanisms for high energy provision

Although direct tests of the disproportionate impact of foundation species on community structure through energy provisioning are not common, enough data exist to recognize the foundational role of certain macrophytes in their respective systems, allowing for a comparison of annual productivity rates among these taxa. We have compiled annual production (g C per m² per year) values for numerous marine macrophyte foundation species from published studies, focusing on those taxa (kelps, fucoids, seagrasses) that have been clearly identified as important to maintaining the structure of their associated communities (Table 1); this compilation is not exhaustive and relies primarily on species that have a clearly defined foundational role in their system. For comparative purposes, our list includes annual production values for non-marine foundation species as well as some kelp, fucoid, and seagrass taxa that are common, but have not been demonstrated to provide critical habitat and therefore do not meet our definition of foundation species.

Table 1.

Taxon	Location	Annual Production (g C m ⁻² yr ⁻¹)
Kelps		
<i>Macrocystis laevis</i> ¹	Marion Is., Prince Edward Is.	3500
<i>Laminaria hyperborea</i> ²	Norway	3000
<i>Saccharina latissima</i> ³	Nova Scotia, Canada	2000
<i>Ecklonia radiata</i> ⁴	Western Australia	1600
<i>Laminaria pallida</i> ⁵	South Africa	1330
<i>Ecklonia radiata</i> ⁶	New South Wales, Eastern Australia	1100
<i>Macrocystis pyrifera</i> ⁷	California, USA	800–1000
<i>Ecklonia cava</i> ⁸	Japan	950
<i>Macrocystis pyrifera</i> ^{9,10}	southern California, USA	120–680
<i>Laminaria digitata</i> ¹¹	Scotland, U.K.	405
<i>Saccharina latissima</i> ¹¹	Scotland, U.K.	135
<i>Macrocystis integrifolia</i> ¹²	Barkley Sound, British Columbia, Canada	31
<i>Saccharina latissima</i> ¹³	Young Sound, Greenland	0.1–2
Fucoids		
<i>Sargassum platycarpum</i> ¹⁴	Curacao, Netherlands Antilles	2550
<i>Cystoseira mediterranea</i> ¹⁵	Northwestern Mediterranean	900
<i>Ascophyllum nodosum</i> ¹⁶	Cobscook Bay, Maine, USA	489–699
<i>Ascophyllum nodosum</i> ¹⁷	Massachusetts, USA	353.7
<i>Fucus vesiculosus</i> ¹⁸	Massachusetts, USA	127.8
<i>Cystoseira</i> spp. ¹⁹	Eastern Canary Islands	1.5–10.5
Other macroalgae		
<i>Cladophora gracilis</i> ¹⁸	Nauset Marsh, Massachusetts, USA	59–637
<i>Himantothallus grandifolius</i> ²⁰	Singy Island, Antarctica	16–56
Seagrasses		
<i>Posidonia oceanica</i> ²¹	Gulf of Naples, Italy	1170
<i>Cymodocea nodosa</i> ²²	Urbinu Lagoon, Corsica, France	844
<i>Zostera marina</i> ²³	Netarts Bay, Oregon, USA	838
<i>Zostera marina</i> ⁷	Denmark	800
<i>Thalassia testudinum</i> ⁷	Caribbean	800
<i>Zostera marina</i> ²⁴	Puget Sound, Washington, USA	707

Table 1. contd....

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Taxon	Location	Annual Production (g C m ⁻² yr ⁻¹)
<i>Halodule wrightii</i> ²⁵	Mississippi Sound, Gulf of Mexico, USA	256
<i>Thalassia testudinum</i> ²⁶	Corpus Christi Bay, Texas, USA	253
<i>Posidonia</i> spp. ²⁷	Australia	140
<i>Posidonia oceanica</i> ²⁸	Gulf of Naples, Italy	60–184
<i>Cymodocea nodosa</i> ²²	Mar Menor Lagoon, Spain	47.8–48.9
Non-macrophytes		
<i>Sequoia sempervirens</i> ²⁹	northern California, USA	700–1000
Zooxanthellate corals ³⁰	various locations	744.6
Mangroves ³¹	North Queensland, Australia	350–500

¹Attwood et al. (1991); ²Abdullah and Fredriksen (2004); ³Mann (1972); ⁴Kirkman (1984), as reported in Mann (2000); ⁵Field et al. (1977), as reported in Mann (2000); ⁶Larkum (1986), as reported in Mann (2000); ⁷Mann (2000); ⁸Reed et al. (2008); ⁹Yokohama et al. (1987); ¹⁰Jackson (1987); ¹¹Drew (1983); ¹²Wheeler and Druehl (1986); ¹³Borum et al. (2002); ¹⁴Wanders (1976), as reported in Mann (1982); ¹⁵Ballesteros (1989); ¹⁶Vadas et al. (2004); ¹⁷Roman et al. (1990); ¹⁸Roman et al. (1991); ¹⁹Johnston (1969), as reported in Mann (2000); ²⁰Drew and Hastings (1993); ²¹Ott (1980); ²²Agostini et al. (2003); ²³Kentula and McIntire (1986); ²⁴Nelson and Waaland (1997); ²⁵Moncreiff et al. (1992); ²⁶Lee and Dunton (1996); ²⁷Pergent et al. (1994); ²⁸Busing and Fujimori (2005); ²⁹Muscatine (1990); ³⁰Mann (1982); ³¹Miller (1972), as reported in Mann (1982).

The annual production of kelps (brown algae of the order Laminariales) is conspicuously higher than most marine foundation species, whether they be fucoids, seagrasses, or even mangroves and hermatypic corals (Table 1). Although annual production is highly variable among kelp taxa, species from at least four kelp genera (*Macrocystis*, *Laminaria*, *Saccharina*, and *Ecklonia*) have been reported to fix greater than 1000 g C per m² per year, with *Macrocystis* populations in the Prince Edward Islands having production rates as great as 3500 g C per m² per year (Attwood et al. 1991). These values should be interpreted with caution, however, as no studies have been conducted with the temporal sampling required to appropriately estimate annual rates of production. Therefore some values are likely to be overestimates of the actual annual productivity rates of these kelps. In each case, short-term production values were integrated over the year, obviating any seasonal or sub-annual trends in productivity, which is particularly important at higher latitudes because of the marked seasonal variation in solar irradiation (Deysher and Dean 1984, Jackson 1987, van Tussenbroek 1989). Although the methodologies for estimating primary production also varied among researchers, and thus among the taxa they studied, the among-taxa variability in estimated annual primary production is striking and suggests that marine macrophyte foundation species are “not created equally”.

Macrocystis, *Laminaria*, and *Ecklonia* are globally distributed, and present in the Indian Ocean and both the northern and southern hemispheres of the Pacific

and Atlantic Oceans. When production values of these taxa are integrated over the broad spatial scales across which the species are distributed, the contribution to local food webs is tremendous (Newell et al. 1982, Duggins et al. 1989, Graham 2004). With the exception of the prostrate kelp *Saccharina latissima* in Norway, the highest producing kelp taxa are also large in stature, extending either to the surface (e.g., canopy-forming *Macrocystis*) or well into the water column (e.g., the stipitate *Ecklonia radiata* or *Laminaria hyperborea*). Past research has shown that stature is important in determining the outcome of competitive interactions among kelp taxa and the structure of kelp assemblages (Dayton 1975, Dayton 1985, Foster and Schiel 1985), as well as the provisioning of habitat for associated species (Holbrook et al. 1990, Anderson 1994, Carr 1994). Kelps that reach further into the water column have superior access to light and can translocate internal resources and photosynthates to lower structures (juvenile fronds, sporophylls or holdfasts) via trumpet hyphae and/or sieve elements, thus maintaining a competitive advantage over low-lying taxa and increasing their overall productivity rates (Parker and Huber 1965, Schmitz and Lobban 1976, Lobban 1978, Schmitz and Srivastava 1979). Resource translocation also facilitates the higher productivity rates required to maintain biomass in such large kelp species, and the high per thallus productivity rates needed to support the production of their diverse associated foodwebs (Graham 2004).

The most productive kelp taxa tend to be found along mid-latitude temperate coastlines (Table 1, Fig. 2A), likely due to the combination of relatively low water temperatures and high nutrient concentrations driven by coastal upwelling, and greater integrated annual irradiance doses than higher latitude systems (Jackson 1987, Lüning 1990). Indeed, populations of *Macrocystis* in British Columbia and *Saccharina* in Greenland have production values 2-3 orders of magnitude less than their lower latitude counterparts (Table 1). Yet, although these values are low, they likely represent the consequences of light limitation associated with the effects of increasing latitude on primary production (Jackson 1987), rather than an inability of these taxa to function as foundation species within these systems (Graham et al. 2007). Critical experiments to test the role of kelps in the structure of nearshore communities in high latitude systems are rarely conducted, and when they are, the kelp taxa have been shown to play a critical role in enhancing biodiversity. This is exemplified by the high latitude kelp system in the Aleutian Islands, in which the annual canopy-forming kelp *Eularia fistulosa* clearly plays a foundational role (Estes and Palmisano 1974, Estes et al. 1978, Estes and Duggins 1995); unfortunately, the lack of primary production data and general ecological data for *Eularia* precludes comparisons to other foundation species. In the absence of additional field experimentation, it is not possible to determine whether the high variability in annual production among kelp taxa reflects subsequent variability in their role in the functioning of their associated communities.

Fucoids (rockweeds; brown algae of the order Fucales) lack trumpet hyphae or translocation mechanisms similar to those possessed by kelps (Moe and Silva 1981). Consequently, fucoids generally do not grow to the great lengths that many kelp taxa do, although they can form thick canopies in shallow temperate regions, especially in the absence of their kelp counterparts (Cousens 1984, Cousens 1985, Schiel and Foster 2006, Foster and Schiel 2010). Fucoid production values are also far less than those of the most productive kelps (Table 1), with the exception of the annual primary

production values reported by Wanders (1976) for *Sargassum platycarpum* and Haxen and Grindley (1985) for *Durvillaea antarctica*. Interestingly, *Durvillaea antarctica*, which does possess hyphae similar to those in kelps (Nizamuddin 1968), has similar daily primary production values (~ 7.1 g C per m^2 per day; Haxen and Grindley (1985)) in the Prince Edward Islands as its kelp counterpart *Macrocystis* (~ 7 – 11.5 g C per m^2 per day; Attwood et al. 1991) in the same region. *Durvillaea* is the most massive of the fucoids (Fig. 1E), and when daily production values are integrated annually, they are comparable to the most productive kelp systems (~ 2500 g C per m^2 per year; Table 1). Despite the exceptional biomass and extensive distribution of *Durvillaea* in the Southern Hemisphere, very little is known about its ecological role as most studies to date have estimated productivity for economic means. The massive, complex morphology of *Durvillaea* suggests that its role as a foundation species is context-dependent, much like that seen with *E. menziesii* in California (Hughes 2010). As one of the most productive algal species, future studies should examine the foundational role of *Durvillaea* through the examination of the habitat it provides and the influence of its high rates of primary productivity on the trophic structure of the systems in which it occurs.

The literature is rampant with productivity values for macroalgae and phycologists have made comparisons among macroalgal taxa for decades. For example, Littler and Arnold (1982) compared primary productivity across 70 taxa from central California to Baja California, Mexico and found that hourly productivities (g C per g dry weight per hr) varied among taxa by 2-3 orders of magnitude. These data were interpreted to represent inherent differences in primary productivity driven by differences in thallus functional form (e.g., thin blades vs. crusts) and were useful for understanding the effect of environmental change on algal assemblages Littler and Littler (1980). The most productive taxa in the (Littler and Arnold 1982) dataset were thin *Ulva* species (9.5–11 g C per g dwt per hr) that had far greater productivity rates than the estimated values for fucoid and kelp species (0.2–1.1 g C per g dwt per hr). Species within the top 80% of hourly productivity values in Littler and Arnold (1982) study, however, have never been identified as foundation species, and in most field situations, they likely never will. Again, the reason is that such macroalgae are small and lack the conductive mechanisms to move photosynthate and support large thalli, and thus they do not provide habitat architecture, although they can provision energy to the associated community. Consequently, although kelps have relatively low dry weight-specific hourly productivities, when integrated across their large thalli they support extremely high production and play a more distinct foundational role within their respective systems because of their ability to maintain large stature and provide critical habitat for their associated communities.

Much of the annual productivity of kelps is ultimately consumed by herbivores and detritivores, fueling food webs from the bottom up. Kelp contributions as a source of energy for consumers can be detected observationally and by using natural isotopic tracers. For example, Duggins et al. (1989) used stable isotope analysis to show that secondary production (i.e., growth) of suspension feeding and detritivorous invertebrates, all the way up to predatory fishes, was enhanced on islands with kelp compared to islands lacking kelp. Similarly, Salomon et al. (2008) demonstrated that the flow of carbon to filter feeding oysters and mussels was strongly influenced

by kelp contributions inside marine reserves characterized by high abundance of the kelp *Ecklonia radiata* and sea urchins, in contrast to fished areas outside of reserves where kelp densities were reduced by sea urchin grazing. Trophic subsidies from kelp-derived organic matter has also been shown to connect marine systems with terrestrial (Dugan et al. 2003), intertidal (Bustamante and Branch 1996), and submarine canyon ecosystems (Harrold et al. 1998, Vetter 1995) providing critical energetic subsidies that support higher than expected consumer biomass (Vanderklift and Wernberg 2008). Disturbances such as large storms can defoliate kelp beds and aid delivery to food-limited habitats outside the beds (Filbee-Dexter and Scheibling 2012), while the transport of kelp detritus over long distances can be aided by kelp morphology, such pneumatocysts and other float-like structures (Hobday 2000, Macaya et al. 2005, Hernandez-Carmona et al. 2006). Conversely, large-scale removal of kelp from a system can reduce food subsidies to local consumers and generate negative feed-back loops that can drive the system into an alternative stable state, such as the urchin barrens driven by El Niños in southern California (Ebeling et al. 1985, Tegner and Dayton 1991).

Seagrasses consistently exhibit high annual production values across a wide range of taxa (Table 1), likely due to the similar environmental conditions within which seagrasses grow. Seagrasses tend to flourish in more oligotrophic waters than kelps (Fig. 2C), preferring warm-temperate to tropical regions with high light (i.e., low turbidity), lacking a requirement for high ambient nutrient levels (Duarte 1995). Like kelps, however, high seagrass productivity rates are supported by internal structures (steles) that allow movement of photosynthates and gases through conducting cells (McRoy and McMillan 1997). Although few seagrasses attain large statures (Fig. 1G), especially relative to canopy-forming kelps, the seagrass translocation mechanisms allow for effective integration between the physiology of subsurface rhizomes (often growing in anoxic sediments) and photosynthetically active leaves (Marbà et al. 2006, Dean and Durako 2007). Thus, seagrasses are able to occupy relatively featureless, low productivity sediment-based systems and provide highly important resources and habitat structure to the organisms within these systems (Hemminga and Duarte 2000). The few studies that have directly addressed the functional role of seagrasses in their associated communities have clearly and consistently identified them as critical foundation species (Heck et al. 1995, Heck et al. 2003). Seagrasses provide energy for herbivorous fishes and invertebrates (Perkins-Visser et al. 1996, Beck et al. 2001, Heck Jr. et al. 2008), helping to fuel complex food webs, and they provide critical nursery habitat and shelter from predators for juvenile life history stages of many fishes and invertebrates (Heck et al. 1997).

In kelp forests, seagrass meadows, and rhodolith (maerl) beds, the foundational macrophytes also provide one of the dominant substrates for encrusting invertebrates and epiphytic algae. This coverage, particularly by epiphytic algae in seagrass meadows, constitutes a significant portion of the diets of associated grazers which in turn facilitates higher rates of primary production of the seagrasses (Moncreiff and Sullivan 2001, Duffy et al. 2003). As such, the indirect provisioning of resources should be considered when evaluating the foundational role of macrophytes. While secondary production is not the focus of this chapter, the influence of foundational macrophytes on this additional source of energy should not be overlooked. Given the

relative importance of some of these epiphytic communities, a fundamental question to ask is how does this trophic subsidy change following the removal of a foundation species?

Clearly, additional macrophyte taxa likely support their associated communities in a foundational way, yet we lack the quantitative data necessary to classify them as true foundation species. *Himantothallus grandifolius* is a massive brown alga of the order Desmarestiales that can dominate nearshore regions of Antarctica (Moe and Silva 1977, Amsler et al. 1995). An estimated annual production of 16–56 g C per m² per year (Drew and Hastings 1993) for *H. grandifolius* exceeds that of high latitude kelps in the north Pacific and Atlantic (Table 1), yet the availability of this fixed carbon relative to background primary productivity in the region is unknown. Similarly, *Cladophora gracilis* can be locally abundant along northwest Atlantic shores with annual production values of 10–114 g C per m² per year (Roman et al. 1990), but *C. gracilis* would only be considered a foundation species if this production was disproportionate relative to other sources of fixed carbon available to this system, which remains unknown. Therefore, although some oligotrophic systems have such low background production potential that it is safe to classify abundant macrophytes as foundation species in the absence of direct studies (e.g., floating *Sargassum* mats in the mid-Atlantic (Carpenter and Cox 1974) or rhodoliths in the sub-tropics; Fig. 1D,F), researchers should be wary of making such classifications in more productive systems.

Habitat Provision

All marine macrophytes are inherently edible and at some non-trivial spatial scale provide habitat to organisms, whether they be microfauna, meiofaunal, or charismatic megafauna. Two criteria, however, are required to distinguish macrophyte foundation species from simple habitat-forming macrophytes. First, as previously discussed, macrophyte foundation species should *simultaneously* provide energy and habitat to their associated community. Second, energy and habitat provisioning by macrophyte foundation species should be *disproportionate* relative to other taxa in the system (Dayton 1972). Yet, unlike studies of energy flow through a system, it is not possible to use chemical tracers (i.e., stable isotopes) to study direct connections between fauna and the marine macrophytes with which they associate. Most researchers have focused on targeted removal of conspicuous macrophyte taxa to study the role of these putative foundation species in structuring nearshore systems (Dayton 1975, Konar 2000, Schiel 2006, Hughes 2010, Shelton 2010, Byrnes et al. 2011). It is difficult if not impossible, however, to disentangle the provision of energy from that of habitat using such simple experiments (Graham et al. 2008), especially for those faunal taxa that eat the macrophyte habitat within or upon which they live (e.g., limpets, amphipods, kelp crabs).

The role of habitat provisioning by marine macrophyte foundation species has not been well studied beyond simple removal experiments at relatively large spatial scales. It is clear in the ecological literature that species diversity can reflect the availability of complex habitats (MacArthur 1965, Heck et al. 1997, Friedlander and Parrish 1998, Tews et al. 2004). In addition to determining whether a particular foundation species

does in fact disproportionately provide habitat to its associated system, it is important to study the distribution of biomass within and among the individual macrophyte thalli as this helps define the extent of habitat complexity. Marine macrophytes vary strikingly in their morphologies, even within species, and such morphological (and structural) variability is often linked to variability in physiological performance and productivity (Littler and Arnold 1982). Kelps with many fronds can be more productive than those with few fronds (Jackson 1977, Chapman and Lindley 1980, Zimmerman and Kremer 1986), and variability in frond shape can affect shading and mass transfer of nutrients (Gerard 1982, Carpenter 1990, Graham et al. 2007), both of which regulate physiology and subsequently ecosystem structure and function (Villegas et al. 2008). The two dominant canopy forming kelp species along the California coast, for example, provide fundamentally different habitat to their associated communities due to their morphological differences. *Nereocystis luetkeana* (bull kelp) is comprised of a single stipe that terminates in a large pneumatocyst and profusion of large blades at the surface (Fig. 1C); the surface canopy is the most structurally complex aspect of a *Nereocystis* bed, as the subsurface region simply consists of singular stalks. The subsurface region of a *Nereocystis* bed, therefore, provides a more featureless habitat than *Macrocystis* beds that have numerous bladed fronds extending throughout the water column (Fig. 1A). These structural differences in morphology can affect that role of kelps as a source of habitat for organisms in the community. Previous studies have suggested that fish abundance and diversity differ between adjacent *Nereocystis* and *Macrocystis* beds in central California (Bodkin 1986), although these results need to be supported by more rigorous studies.

Although relatively unstudied, morphological variability within and among marine macrophyte foundation species is likely to be a critical determinant of which taxa inhabit the macrophyte and how they utilize the habitat. Most kelps have holdfasts for attachment to substrate and many kelp holdfasts are formed from intertwined haptera that may or may not create interstitial spaces for organisms to recruit to and inhabit. Some kelps have large holdfasts with tightly bound haptera (e.g., *Egregia menziesii*), likely an adaptation for staying attached in wave exposed environments, that provide minimal habitat for associated taxa, whereas others have massive holdfasts with loosely bound haptera that can support 100s of taxa (e.g., *Macrocystis*; Andrews 1945, Ojeda and Santelices 1984). Furthermore, in the case of *Macrocystis*, the growth and biomass of the fronds on the thallus directly relates to the growth of haptera and the subsequent size of the holdfasts (Barilotti et al. 1985, McCleneghan and Houk 1985). It has also been shown that the density of fronds within a *Macrocystis* population is directly proportional to the abundance of fish that inhabit the fronds (Holbrook et al. 1990, Anderson 1994, Carr 1994), especially when the fronds reach the canopy. Again, the growth and biomass of the fronds on the thallus directly relates to the initiation and growth of new fronds (Lobban 1978, Fox 2013). Although furoid holdfasts are generally discoid and featureless, the morphological variability among the finely dissected fronds common in most fucoids can provide substantial structural habitat. In general, natural systems founded by different marine macrophytes will likely be characterized by striking changes in the complexity of habitats provided by the macrophyte thalli.

The link between morphological variability in marine macrophyte foundation species and their associated fauna may be one of the most useful and interesting, though understudied, aspects of nearshore marine ecology. The population dynamics of kelps and fucoids is complex (Foster and Schiel 2010) and driven largely by interactions between the macroalgal life histories and variability in local climatic and physical process (i.e., waves, light, nutrients, sedimentation, etc.). For any given marine macrophyte foundation species, such interactions determine the distribution of individuals within a system, as well as recruitment, which regulates the time at which individuals of different ages and sizes appear, and thus the resulting complexity of the habitat. The only clonal kelp taxon that has been described as a foundation species is the vegetative form of *Macrocystis pyrifera* (previously known as *M. integrifolia*; Demes et al. 2009, Macaya and Zuccarello 2010) that inhabits shallow waters along the Pacific coasts of North and South America (Graham et al. 2007). Although frond physiology is likely similar between the clonal and aclonal *Macrocystis* morphs, the distribution of fronds within the thallus is strikingly different and thus has great implications for the structure of the system. In the aclonal form, fronds arise from the apex of single conical holdfasts and can range from a few to 100s of fronds per holdfast, often forming a tangled bundle that rises to the surface to form a canopy in waters as deep as 60 m (Graham et al. 2007). The clonal form, on the other hand, creeps along the substrate, in shallow nearshore waters, with a vegetatively elongating rhizome that sends fronds to the surface individually, rather than an entwined bundle. Therefore, taxa inhabiting shallow waters dominated by the clonal form of *Macrocystis* will encounter a much more uniform distribution of fronds, and thus habitat, than in a system dominated by the aclonal form. Such striking differences in the spatial distribution of fronds between these two *Macrocystis* morphs will likely have consequences to determining which taxa inhabit the system, and how they utilize the habitat.

Population cycling will create variability in the density, size, age structure, and distribution of individual thalli of aclonal marine macrophytes. Following a disturbance that creates open space, most macrophytes recruit in mass during episodes that can be either random or synchronized to environmental parameters (e.g., daylength). Regardless of how or why they do so, such recruitment episodes inherently result in the system being populated simultaneously by numerous small thalli (Dayton et al. 1992, Graham et al. 1997, Reed et al. 2009). Over time, these populations thin in density as individual thalli become larger and outcompete neighbors; this self-thinning process is characteristic of most large marine macrophyte populations (Cousens and Hutchings 1983, Dean et al. 1989, Dayton et al. 1992) and is likely due to a carrying capacity in overall biomass density (g/m^2) that can be supported by available resources (Jackson 1977, Jackson 1987, Tegner et al. 1997). As a consequence of self-thinning, the population shifts from being densely populated by small individuals to sparsely populated by very large ones. Using empirical data, North (1994) showed that regardless of thallus size (i.e., number of fronds per thallus), *Macrocystis* populations never exceeded frond densities of greater than 10 fronds/ m^2 . Therefore, plant density decreases with increasing thallus size, as individuals become larger. This same pattern can be observed in terrestrial forests and grasslands following the trajectory of a system post-disturbance towards its climax state (White and Harper 1970, Connell and Slatyer 1977, Hamilton et al. 1995).

Spatiotemporal shifts in the distribution and complexity of available habitat will likely occur for all marine macrophyte populations that experience self-thinning. As with most studies on productivity and habitat provisioning, the best data for studying size vs. density tradeoffs exist for the giant kelp, *Macrocystis pyrifera*. North (1994) originally studied southern California *Macrocystis* populations with plants up to 80 fronds each and densities from 0.01 to 1.6 plants per m², from which he derived his 10 fronds/m² carrying-capacity estimate. Later, van Tussenbroek (1989) used a similar approach to distinguish among various populations of *Macrocystis* in the Southern Hemisphere and, although she found the same self-thinning pattern that North (1994) did, she observed that different populations (e.g., Argentina vs. Chile vs. Falkland Islands) were in strikingly different locations on a size vs. density plot. Tegner et al. (1997) also showed that temporal variability in environmental conditions within a site (e.g., nutrient concentrations regulated by ENSO cycles) resulted in variability in carrying-capacity of *Macrocystis* populations (i.e., North's (1994) estimate of 10 fronds/m²). We therefore compiled data from North (1994), van Tussenbroek (1989), and other globally distributed studies of *Macrocystis* size and density along with contemporary long-term monitoring studies in southern and central California to show the extreme variation that can exist in the distribution and complexity of available habitat within a single marine macrophyte foundation species (Fig. 3). Kelp forest taxa inhabiting a *Macrocystis* population can therefore move amongst 1-frond plants spaced every 0.25 m at the high density end of the spectrum, but experience shifts in space or time in which they may encounter 100-frond plants spaced every 10 m at the sparse end of the continuum. The consequences of such striking shifts in habitat-provisioning (driven by interactions between environmental parameters and kelp ecophysiology) on the diversity and productivity of nearshore kelp and fucoid systems have not been studied but are likely to be significant (Graham et al. 2008). The knowledge of such high variability in spatial habitat provisioning by certain species is fundamental to understanding how respective systems function and should be used to guide future research into the role of macrophytes as critical foundation species.

The variability of *Macrocystis* size vs. density on a global scale is exceptional (Fig. 3). It is important to note the geographic differences first observed by van Tussenbroek (1993) in the Southern Hemisphere appear to be consistent throughout the global range of this species. Of particular interest is the relative consistency with which particular regions occur on the plot. For example, many of the *Macrocystis* populations in Chile are dominated by the clonal 'integrifolia-form' or by small statured annual populations of the aclonal 'pyrifera-form' and therefore tend to structure unique high density, small sporophyte populations ranging from 1–9 sporophytes m⁻² and averaging approximately 5.1 fronds per individual. Conversely, the *Macrocystis* populations along the California coast rarely exceed 0.5 sporophytes m⁻² and average approximately 18.7 fronds per individual. The stark difference between these populations is most likely driven by changes in environmental parameters across regions. For example, the environmental conditions in Chile and Baja California are frequently unfavorable to high productivity rates and biomass production in *Macrocystis* due to varying combinations of temperature, nutrient, and salinity stress (Hernandez-Carmona et al. 2001, Buschmann et al. 2004, Edwards and Hernández-Carmona 2005, Buschmann

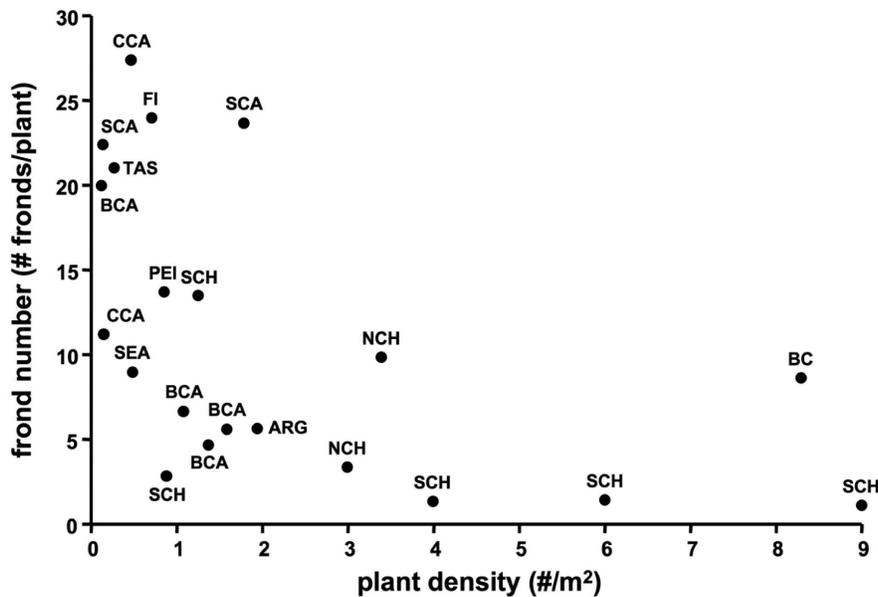


Figure 3. Maximum reported *Macrocystitis* density vs. mean plant size globally. *Macrocystitis* is the most globally distributed kelp species due to its large size, ability to float, and high degree of morphological and physiological plasticity. Throughout its distribution along the west coast of North America and the southern hemisphere, *Macrocystitis* forests exhibit a wide range of size structure and density which can influence the resources it provides as a foundation species. The data shown in this figure were generated from an extensive literature and only represents studies that reported both plant density and size data from the same location. To illustrate the large scale application of this trend, the maximum reported densities (individuals \cdot m⁻²) were used for each site, and sites were chosen to be representative of the large geographic area they occur within. All size data were determined by counting the number of fronds > 1 m in height per sporophyte. Site abbreviations: ARG-Argentina; BC-British Columbia; BCA-Baja California, Mexico; CCA-Central California; FI-Falkland Islands; NCH-Northern Chile; PEI-Prince Edward Island; SCH-Southern Chile; SEA-Southeast Alaska; TAS-Tasmania.

et al. 2014). Similarly, in the higher latitude island populations and along California the *Macrocystitis* populations inhabit stable, nutrient rich waters and the populations are primarily structured by wave disturbance, which favors the establishment of larger, less dense *Macrocystitis* beds (Graham et al. 2007, Reed et al. 2008, Reed et al. 2011). This global perspective helps to illustrate the differential role of the same macrophyte species in structuring communities in regions defined by different environmental parameters. Thus, it is imperative that the high variability in the morphology and ecophysiology of marine macrophytes across regions and within species be considered when conducting studies on the role of macrophytes as foundation species.

The *Macrocystitis* populations off California are arguably some of the well-studied populations of any marine macrophyte. As such, we compiled an extensive data set of plant size and density data from surveys ranging from Baja California to central California to investigate how regional variability in environmental conditions drives changes in habitat provisioning on a scale of 100s instead of 1000s of kilometers (Fig. 4). Perhaps, not surprisingly, we found that the carrying capacity first identified by North (1994) and Van Tussenbroek (1993) was confirmed by this new dataset.

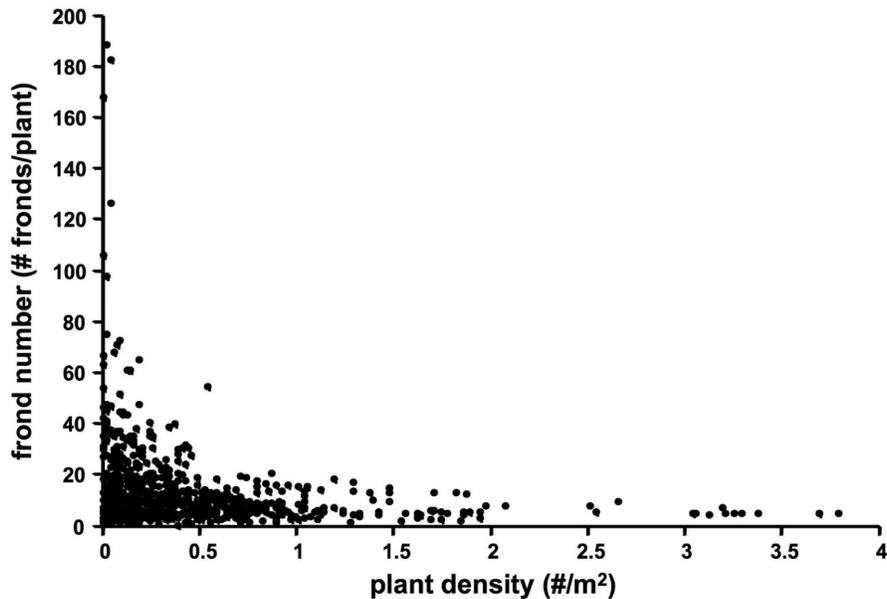


Figure 4. *Macrocystis* density vs. mean plant size for California. The density of *Macrocystis* sporophytes inversely influences the mean size of individuals within populations. High density *Macrocystis* forests are comprised of smaller individuals that turn over frequently, while low density populations are comprised mainly of larger, older sporophytes. Both biotic and abiotic forces such as competition for space, self-shading, and disturbance from wave action define the carrying capacity of *Macrocystis* forests in terms of plant density and size structure, which in turn alters the provisioning of resources by this species in different locations. Importantly, high regional variability in oceanographic conditions drives substantial changes in *Macrocystis* forest structure along the West Coast of North America and represents the range of forest structures shown globally in Fig. 3. The consideration of population-scale drivers on individual-scale processes is critically important for understanding how macrophyte foundation species provide resources and provision habitat differently in different systems and locations. The data for this figure were collected between 2006 and 2008 at 118 sites that range from central Baja California to Santa Cruz, California. The data were generously provided by Matt Edwards (Edwards 2004), the Partnership for the Interdisciplinary Studies of the Coastal Ocean (PISCO—UC Santa Barbara and UC Santa Cruz), the 2008 California Bight Survey (CRANE; Pondella et al. 2011). All data were collected using 60 m² swath surveys and compiled and reported here as individuals · m⁻² and number of fronds > 1 m long per sporophyte.

Interestingly, the entire global range of densities and size structure can be found within one region, highlighting the extreme variability in plant size vs. density that occurs for this foundation species over small spatial scales. Examined regionally, Baja California *Macrocystis* populations typically occur at higher densities and smaller plant sizes relative to the populations of *Macrocystis* north of Point Conception, which have the largest plant sizes and lowest densities of all populations along the west coast of North America (Fig. 3). Again, these differences can be attributed to distinct differences in the oceanographic regimes that have been well defined in this region (Graham et al. 2008). The large variability in plant size and density, even just within California, has the potential to greatly influence the role that *Macrocystis* plays as a foundation species in this system. Surprisingly, the context-dependent role of *Macrocystis* has not been studied to date.

To our knowledge, processes regulating habitat provisioning in other macroalgal foundation species have rarely been studied. The Sargasso Sea ecosystem presents unique logistical challenges to studying the relationships between habitat provided by the *Sargassum* and the diversity and abundance of their associated fauna. Conceptually, however, this pelagic oceanic environment, the intricate morphology of the *Sargassum* mats, and the apparent adaptation of many fauna to this isolated environment, may make this system the most conceptually interesting to explore. In this system, temporal variability in the productivity and morphology of the *Sargassum* mats will likely regulate the quantity and quality, respectively, of the available habitat; whether or not the associated taxa will respond to such changes is unknown. In the more tractable benthic *Sargassum* beds in Bahia Concepcion, Mexico, *Sargassum* thalli are important to promoting local diversity, but the annual nature to *Sargassum* population dynamics in the region limits the magnitude of the impact (Hinojosa-Arango et al. 2014). Similarly, little work has been done to study variability in the quantity and quality of the available habitat provided by rhodoliths, although again, it is clear that the complexity of rhodolith habitats enhances faunal diversity relative to the surrounding benthos (Steller et al. 2003), and that rhodolith beds can be important to the population dynamics of commercially-important fauna (Hinojosa-Arango et al. 2014).

All seagrasses are rhizomatous, and thus inherently clonal. As such, it is difficult to study the relationship between plant density and size to determine whether self-thinning occurs within seagrass populations, as with large macroalgae. It is relatively straightforward, however, to estimate shoot densities (number of shoots per m²) in the field to be compared to leaf biomass densities (g dry weight per m²). Such studies are standard in the seagrass literature and yield similar magnitudes of variability as seen in the size vs. density data for kelps (Fig. 5C; Duarte and Sand-Jensen 1990, Horinouchi and Sano 1999, Cabaço et al. 2013). Again, spatiotemporal variability in seagrass habitat provisioning can be conspicuous. Olesen and Sand-Jensen (1994) observed striking differences in biomass vs. density cycles between Chesapeake Bay and Nova Scotia populations (Fig. 5A,B). Leaf biomass and shoot density in the warm temperate Chesapeake Bay varied seasonally by almost two orders-of-magnitude, whereas the cold temperate Nova Scotia population varied seasonally by more than order-of-magnitude in biomass but showed much less variability in shoot density. Such cycling will likely drive similar cycles in the availability of fixed carbon to direct consumers and detritivores, as well as habitat available for algal epiphytes that are known to be important to the functioning of these system. Yet, as with most systems structured by marine macrophytes, the effects on associated fauna remain unknown.

The future of ecosystems founded by marine macrophytes?

It is clear that large and abundant marine macrophytes have a foundational role in regulating the structure, diversity and productivity of nearshore ecosystems. It is also clear that the most important marine macrophyte foundation species are those that provide tremendous energy and habitat to their associated communities, relative to the background environment. If we remove these foundation species over non-trivial spatial scales, the systems will change dramatically (Graham 2004). It is unclear, however,

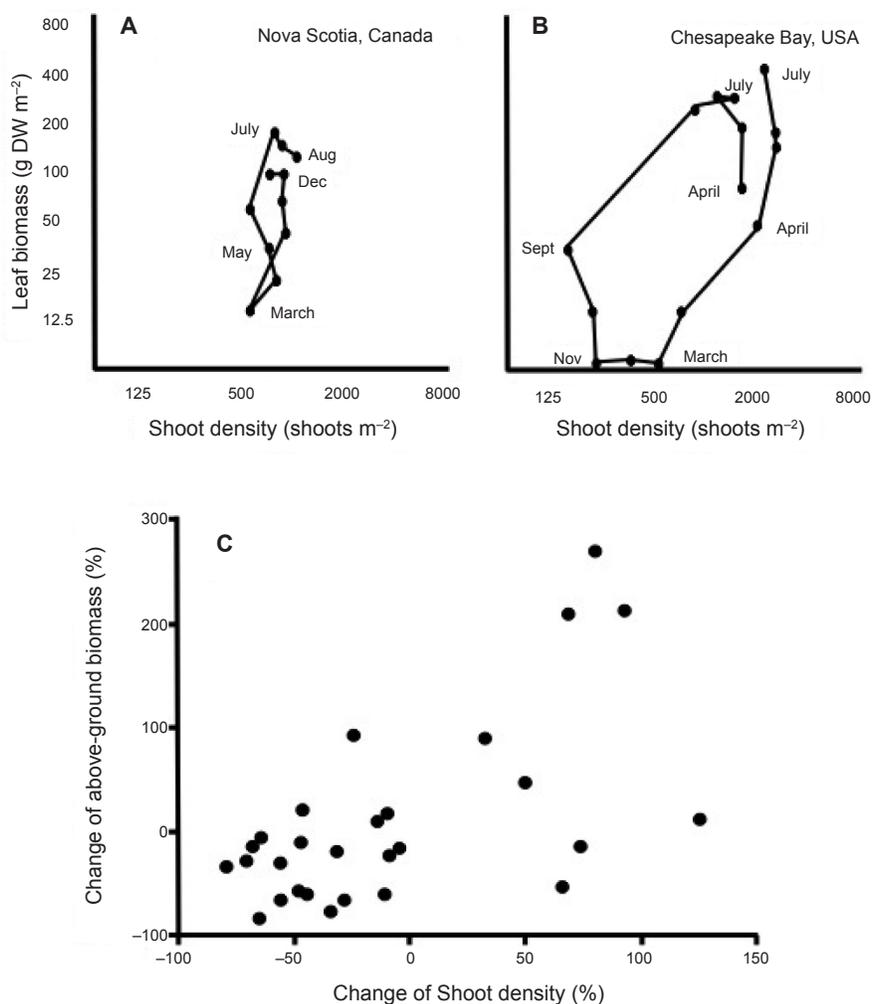


Figure 5. Changes in seagrass biomass vs. shoot density. For *Zostera marina*, populations in (A) Nova Scotia, Canada and (B) Chesapeake Bay, USA seasonally cycled through periods of high and low shoot density, with correlated changes in leaf biomass (Modified from Olesen and Sand-Jensen 1994). In a global survey, (C) above-ground biomass increases with shoot density for 14 seagrass species (Modified from Cabaco et al. 2013); original data were from experimental and descriptive studies of effects of nutrient addition of above-ground biomass and shoot density.

over what spatial and temporal scales such impacts will last, and whether sublethal perturbations to macrophyte ecophysiology will have similar impacts.

The tight linkage between environmental parameters and macrophyte ecophysiology suggests that changing climate will strongly impact systems founded by marine macrophytes (Harley et al. 2012). By definition, foundation species are disproportionate in their provisioning of energy to their associated system and changes

in light, temperature, sedimentation or nutrients that increase or decrease macrophyte productivity will impact energy flow and habitat provisioning in the system. In some scenarios, it is straightforward to predict outcomes: seagrasses will decline with increasing turbidity (Moore et al. 1997, Orth et al. 2006); kelps will decline with decreasing nutrients (Jackson 1977, Zimmerman and Kremer 1986, Dayton et al. 1999); rhodoliths will decline with increasing ocean acidification (Jokiel et al. 2008); macroalgae and seagrasses may flourish due to increased availability of dissolved CO₂ (Johnson et al. 2012, Connell et al. 2013, Koch et al. 2013). These effects, however, will not be consistent across species (Porzio et al. 2011, Campbell and Fourqurean 2014). Still, it is less straightforward to predict outcomes when climate change or other human impacts result in multiple environmental parameters changing simultaneously (Harley et al. 2012). Changes in runoff to nearshore systems can result in enhanced nutrient concentrations that fuel growth of phytoplankton and/or microalgal epiphytes, both of which can decrease light levels and negatively impact seagrass populations. Similarly, population explosions of filamentous microalgae in areas with both increased temperature and nutrients can inhibit the recovery of kelp populations following disturbance (Connell and Russell 2010). So, although it is clear that systems founded by marine macrophytes will fluctuate to reflect changes in the distribution, abundance and productivity of these foundation species, predicting the direction of such changes as a function of climate is far less certain. This uncertainty is a fundamental hurdle in the development of management strategies and predictive models aimed at determining the effects of climate change and other anthropogenic stressors on ecosystems around the world. Using the concepts defined in this paper, we propose that the links between environmental conditions and macrophyte ecophysiology that drive changes in energy and habitat provisioning within and among foundational macrophyte taxa be used to guide future research into the role of marine macrophytes in regulating ecosystem structure and function.

Acknowledgements

We thank the Vantuna Research Group at Occidental College for collecting and providing the Bight '08 data; Dr. Matthew Edwards provided the raw data from his dissertation; PISCO data was provided by the Partnership for Interdisciplinary Studies of Coastal Oceans, a long-term ecological consortium funded primarily by the Gordon and Betty Moore Foundation and David and Lucile Packard Foundation.

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