

Global seagrass distribution and diversity: A bioregional model

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Received 1 February 2007; received in revised form 31 May 2007; accepted 4 June 2007

Abstract

Seagrasses, marine flowering plants, are widely distributed along temperate and tropical coastlines of the world. Seagrasses have key ecological roles in coastal ecosystems and can form extensive meadows supporting high biodiversity. The global species diversity of seagrasses is low (<60 species), but species can have ranges that extend for thousands of kilometers of coastline. Seagrass bioregions are defined here, based on species assemblages, species distributional ranges, and tropical and temperate influences. Six global bioregions are presented: four temperate and two tropical. The temperate bioregions include the Temperate North Atlantic, the Temperate North Pacific, the Mediterranean, and the Temperate Southern Oceans. The Temperate North Atlantic has low seagrass diversity, the major species being *Zostera marina*, typically occurring in estuaries and lagoons. The Temperate North Pacific has high seagrass diversity with *Zostera* spp. in estuaries and lagoons as well as *Phyllospadix* spp. in the surf zone. The Mediterranean region has clear water with vast meadows of moderate diversity of both temperate and tropical seagrasses, dominated by deep-growing *Posidonia oceanica*. The Temperate Southern Oceans bioregion includes the temperate southern coastlines of Australia, Africa and South America. Extensive meadows of low-to-high diversity temperate seagrasses are found in this bioregion, dominated by various species of *Posidonia* and *Zostera*. The tropical bioregions are the Tropical Atlantic and the Tropical Indo-Pacific, both supporting mega-herbivore grazers, including sea turtles and sirenians. The Tropical Atlantic bioregion has clear water with a high diversity of seagrasses on reefs and shallow banks, dominated by *Thalassia testudinum*. The vast Tropical Indo-Pacific has the highest seagrass diversity in the world, with as many as 14 species growing together on reef flats although seagrasses also occur in very deep waters. The global distribution of seagrass genera is remarkably consistent north and south of the equator; the northern and southern hemispheres share ten seagrass genera and only have one unique genus each. Some genera are much more speciose than others, with the genus *Halophila* having the most seagrass species. There are roughly the same number of temperate and tropical seagrass genera as well as species. The most widely distributed seagrass is *Ruppia maritima*, which occurs in tropical and temperate zones in a wide variety of habitats. Seagrass bioregions at the scale of ocean basins are identified based on species distributions which are supported by genetic patterns of diversity. Seagrass bioregions provide a useful framework for interpreting ecological, physiological and genetic results collected in specific locations or from particular species. © 2007 Elsevier B.V. All rights reserved.

Keywords: Bioregional models; Diversity; Global distribution; Seagrass; Species; Temperate; Tropical

1. Introduction

The investigation of seagrass distribution globally is a complex and confounding task due to the wide range of species diversity patterns and areas where seagrasses are

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as yet undocumented as well as the fact that seagrass habitat is ever-changing. To facilitate a global assessment of seagrass distribution and diversity, we have developed bioregional models defined by the major oceans, climate, and seagrass species assemblages. Seagrass species distribution is, first, a baseline for understanding these complex habitats and their distinct bioregional characteristics. Additionally, knowledge of distribution allows comparisons of geography and evolution and provides a foundation for evaluating past and present human impacts to the global seagrass ecosystem.

Seagrasses form a critical marine ecosystem: their role in fisheries production, and in sediment accumulation and stabilization, is well documented (Green and Short, 2003; Larkum et al., 2006), but they contribute to the function of ocean ecosystems and have direct value to humanity (Duarte et al., in press). Seagrasses have relatively low biomass compared with terrestrial ecosystems, but have very high biomass compared to plankton-based oceanic communities. Highly productive seagrass ecosystems have a relatively complex physical structure, providing a combination of food and shelter that enables high biomass and productivity of commercially important fish species (Hemminga and Duarte, 2000; Beck et al., 2001). Seagrasses also provide an important nursery area for many species that support offshore fisheries and for adjacent habitats such as salt marshes, shellfish beds, coral reefs and mangrove forests. Worldwide, coastal peoples collect much of their protein from seagrass habitats (Green and Short, 2003). The association between commercially important species and seagrasses is not obligatory, as the same species are often found in other shallow marine habitats. However, the high animal biomass associated with seagrasses is greater than that of adjacent unvegetated areas (Hemminga and Duarte, 2000).

Seagrasses are the only submerged marine plants with an underground root and rhizome system. Seagrass below-ground biomass can equal that of above-ground biomass, and is often much higher (Duarte and Chiscano, 1999). The role of roots and rhizomes in binding sediments is highly important, as illustrated in a number of studies that have compared erosion on vegetated versus non-vegetated areas during storm events (Koch et al., 2006). The role of seagrass shoots in this process is also important, as this provides a stable surface layer above the benthos, baffling currents and thereby encouraging the settlement of sediments and inhibiting their resuspension (Short and Short, 1984; Ward et al., 1984). By enhancing processes of sedimentation, and through the relatively rapid uptake of nutrients both by seagrasses and their epiphytes, seagrass ecosystems remove nutrients and other contaminants from the water column. Once re-

moved, these nutrients can be released only slowly through a process of decomposition and consumption, thereby reducing problems of eutrophication and binding organic pollutants (Hemminga and Duarte, 2000).

Seagrass habitat is critical for a number of threatened species, including sirenians (dugong and manatee), sea turtles and sea horses, all widely perceived to have high cultural, aesthetic or intrinsic values. Other seagrass functions include the maintenance of genetic variability, with potential biochemical utility, and a possible, though poorly understood, role in supporting resilience of the coastal environment. Beyond this, seagrasses clearly have a minor but important role to play in carbon sequestration, removing carbon dioxide from the atmosphere and binding it as organic matter. Their high areal productivity gives them a disproportionate influence on oceanwide primary productivity, typically producing considerably more organic carbon than the seagrass ecosystem requires (Duarte and Cebrian, 1996; Short and Neckles, 1999). Any removal of carbon, either through binding of organic material into the sediments or export into the deep waters off the continental shelf, represents effective removal of carbon dioxide from the ocean–atmosphere system which plays some role in the amelioration of climate change impacts.

For all species of seagrass, distribution is a product of combined plant sexual reproduction and clonal growth, influenced by dispersal and environmental limitations (Spalding et al., 2003). Many seagrass populations are highly clonal, largely relying on asexual reproduction for population maintenance (Rasheed, 1999; Waycott et al., 2006). Other seagrasses produce large numbers of sexual propagules (Kuo et al., 1991) or vary their reproductive strategies depending on environmental conditions (Phillips et al., 1983a; Robertson and Mann, 1984). The relatively limited phylogenetic diversity of seagrasses results in a limited range of life history strategies. All seagrass species are capable of asexual reproduction, producing modular units (ramets) through horizontal rhizome growth that may be physiologically independent but are genetically identical to the parent plant (genet). Seagrasses are also capable of sexual reproduction by producing fruits and seeds or viviparous seedlings (Kuo and Kirkman, 1987). Some species of seagrass have long-lived seeds which may form a “seed bank” (McMillan, 1983), but there is evidence that many populations lack seed banks (den Hartog, 1971; Inglis and Waycott, 2001). Seeds for most seagrass species are poorly adapted for dispersal and many are released below the sediment surface at the plant stem (den Hartog, 1970; Orth et al., 1994). A reproductive strategy involving clonal growth and production of long-lived, locally

dispersed seeds may provide an evolutionary advantage to plants growing in environments subject to temporally unpredictable major disturbances (Rasheed, 2004).

Temperate seagrasses play a major role in providing habitat for commercially, recreationally and ecologically important fish and shellfish as well as food for many waterfowl species (Green and Short, 2003). Seagrass species in temperate areas are also important in reducing wave and current energy and trapping and binding of fine grained sediments. The close habitat linkage between seagrasses and bivalve species is evident in many temperate parts of the world.

Tropical seagrasses are important in their interactions with mangroves and coral reefs (Green and Short, 2003). All these systems exert a stabilizing effect on the environment, resulting in important physical and biological support for other communities (Gillander, 2006; Koch et al., 2006). Tropical barrier reefs protect coastlines, and the lagoon formed between the reef and the mainland is protected from waves, providing habitat for seagrass communities. In this context, seagrasses filter sediments from upland runoff while at the same time acting as nursery grounds and feeding areas for reef animal species. Sea turtles, dugong and manatee all directly depend on seagrasses for food in the world's tropical oceans.

Human impacts to seagrass distribution, diversity and health are profound and occur at several scales, most notably manifesting in the near absence of seagrasses in industrialized ports and other areas of intense human coastal development (Short and Wyllie-Echeverria, 1996; Orth et al., 2006). Seagrasses are being lost rapidly in developed and developing parts of the world (Short et al., 2006b), with only occasional efforts at mitigation and restoration. Direct impacts include dredging, filling, land reclamation, dock and jetty construction, and some fisheries and aquaculture practices. Indirect impacts such as nutrient and sediment loading from the watershed, removal of coastal vegetation and hardening of the shoreline, result in reduced water clarity which initiates the process of seagrass decline, as seagrasses are particularly sensitive to light limitation. The effects of global climate change on seagrasses are difficult to document, but whether they manifest as sea level change, heat stress, radiation exposure, or increased storm activity, all largely diminish seagrass habitat, distribution and diversity (Short and Neckles, 1999; Duarte et al., in press).

In many parts of the world, recent changes in species distributions have occurred as the result of human alteration of the physical environment or transport of species from their endemic locations. The invasion of *Halophila stipulacea* from the Red Sea into the Mediterranean after the opening of the Suez Canal has led to a widespread

distribution of *H. stipulacea* in the eastern Mediterranean, extending as far west as Sicily and now, probably due to boat traffic, to the Caribbean (Ruiz and Ballantine, 2004). Similarly, *Zostera japonica* was introduced to the west coast of North America since World War II and has successfully spread in both Canada and the U.S.A., occupying the intertidal and overlapping with *Ruppia maritima* and the shallower distributions of *Zostera marina* (Harrison, 1982). The expansion of *Cymodocea nodosa* beds in the western Mediterranean is often linked to competition with *Posidonia oceanica*; when the latter species is absent (as the result of abiotic factors), *C. nodosa* development is more extensive, particularly in lagoons and estuaries or harsh hydrodynamic conditions. The occurrence of invasive species in seagrass areas can lead to the regression or disappearance of seagrass. The expansion of the alga *Caulerpa taxifolia*, which was accidentally introduced to the Mediterranean during the 1980s, has led to localized regressions of both *C. nodosa* and *P. oceanica* beds (Meinesz et al., 1993; Ceccherelli and Cinelli, 1997).

Several seagrass species are currently undergoing reappraisal employing the genetic methodologies now available to supplement morphological and anatomical studies (Waycott and Les, 2000). In many cases, the research and/or publications are not finished and therefore the new level of certainty about species designations afforded by genetic testing is not yet complete. The genus *Halodule* has been a source of disagreement and confusion due to its overlapping morphological descriptors; the contribution of genetic analysis of phylogenetic relationships of species and biogeography should aid in resolving this debate. Also, species and even genus distinctions within what we refer to as the genus *Zostera* are confounded in the literature with potentially many new species of *Heterozostera* (*tasmanica*, *nigraulis*, *polychlamys*, *chilensis*; Kuo, 2005) and reclassified species of *Nanozostera* (eight species; Tomlinson and Posluzny, 2001), none of which is supported by genetic evidence to date. On the other hand, *Zostera muelleri* in southern Australia (Jacobs et al., 2006), formerly named *Zostera capricorni* (Les et al., 2002; Green and Short, 2003), has been shown through genetic and morphological analysis to be conspecific with several other species (*Z. capricorni*, *Zostera mucronata*, *Zostera novazelandica*). Similarly, the *Posidonia ostenfeldii* species complex has been suggested to include with *Posidonia robertsoniae*, *Posidonia denhartogii*, *Posidonia coriacea*, and *Posidonia kirkmanii* (Campey et al., 2000). The genus *Halophila* is one with some widely distributed species and many species of limited range, the latter needing further genetic and morphological analysis. As is standard in other

botanical disciplines, to appropriately change a seagrass species designation, published studies are needed which demonstrate both genetic and morphological/anatomical differentiation on the same plants. The approach we take here to species delineations is to use those most widely accepted by the seagrass science community, as laid out in the *World Atlas of Seagrasses* (Green and Short, 2003), originally from *The Sea-grasses of the World* (den Hartog, 1970), and updated where adequate published genetic and morphometric support is available.

To facilitate the discussion of seagrass distribution and diversity, we created six bioregions using what is known about the temperate vs. tropical distribution of most seagrass species, together with the logic imposed by the physical restrictions of the oceans, their tectonic origins, and climate. A previous delineation of seagrass regions and their species assemblages (Short and Coles, 2001) showed 10 regions, many of which were disjunct, particularly in the southern hemisphere. The new regional framework presented here is pan-oceanic and truly global in logic. The bioregion model provides a geographical focus for understanding seagrasses around the world and allows comparison of similar species that fulfill certain niches in the environment within their area of distribution. The temperate–tropical distinction is important, as is the limit of a certain species assemblage to a given sea or ocean basin. Using the bioregion model, it is possible to know what seagrasses and what combinations of species to expect in a particular area and to gain insight into seagrass ecology via the implications of their distribution on the globe.

2. Methods

The distribution of seagrasses worldwide (adapted from Green and Short, 2003), was developed at UNEP-WCMC, based on literature review and outreach to expert knowledge (<http://www.unep-wcmc.org/marine/seagrass-satlas/references>). Initial efforts focused on the acquisition of point source information which was compiled into a spreadsheet with details on species as well as information on location in both descriptive terms and, wherever possible, including geographic coordinates. The work continued throughout a second data-gathering phase, during which maps on the distribution of seagrasses were developed on a geographical information system (GIS). The two datasets were closely linked: the point locations from the first phase were linked to the GIS, and the GIS layer also allowed for the incorporation of boundary information delimiting seagrass areas (polygons). A third phase involved the presentation of the initial maps prepared by UNEP-WCMC to a Global Seagrass Workshop in Florida, 2001, where they were thoroughly checked by regional and national seagrass experts. As a result, new data points were added, new datasets and references were provided, and incorrectly located or spurious data points were removed. Bioregions were formulated to describe seagrass distribution and species assemblages (Short et al., 2001); a new formulation of seagrass bioregions and seagrass diversity (Fig. 1, Table 1) has been developed for this paper.

To create a global map of seagrass biodiversity, biogeography data from the same seagrass distribution

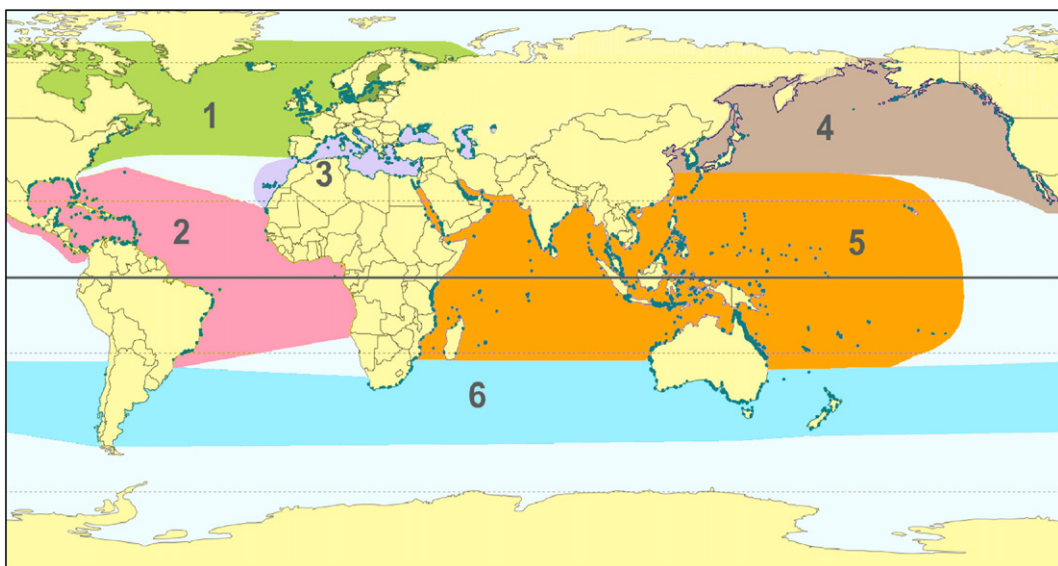


Fig. 1. Global seagrass distribution shown as blue points and polygons (data from 2005 UNEP-WCMC) and geographic bioregions: 1. Temperate North Atlantic, 2. Tropical Atlantic, 3. Mediterranean, 4. Temperate North Pacific, 5. Tropical Indo-Pacific, 6. Temperate Southern Oceans.

datasets were used to generate species range maps (Green and Short, 2003) for all seagrass species except *Ruppia*. By amalgamating the species range maps, a global map of seagrass biodiversity was created (Green and Short, 2003). The biodiversity map indicates the number of seagrass species in various parts of the globe.

3. Results and discussion

3.1. Assessing seagrass species distribution across bioregions

In a broad sense, seagrass species are limited in their geographic range to either temperate or tropical regions

Table 1

The global distribution of seagrass species within 6 geographic bioregions (Fig. 1) based on assemblages of taxonomic groups in temperate and tropical areas and the physical separation of the world's oceans (revised from Short et al. (2001)).

Bioregion	Description	Species
1. <i>Temperate North Atlantic</i> (North Carolina, USA to Portugal)	Low diversity temperate seagrasses (5 species) primarily in estuaries and lagoons.	<i>Ruppia maritima</i> , <i>Zostera marina</i> , <i>Zostera noltii</i> , <i>Cymodocea nodosa</i> ⁺ , <i>Halodule wrightii</i> ⁺
2. <i>Tropical Atlantic</i> (including the Caribbean Sea, Gulf of Mexico, Bermuda, the Bahamas, and both tropical coasts of the Atlantic)	High diversity tropical seagrasses (10 species) growing on back reefs and shallow banks in clear water.	<i>Halodule beaudettei</i> , <i>H. wrightii</i> (<i>H. bermudensis</i> , <i>H. emarginata</i>), <i>Halophila baillonii</i> , <i>Halophila decipiens</i> , <i>Halophila engelmanni</i> , <i>Halophila johnsonii</i> , <i>R. maritima</i> , <i>Syringodium filiforme</i> , <i>Thalassia testudinum</i> , <i>Halophila stipulacea</i> ⁺
3. <i>Mediterranean</i> (including the Mediterranean Sea, the Black, Caspian and Aral Seas and northwest Africa)	Vast deep meadows of moderate diversity and a temperate/tropical mix of seagrasses (9 species) growing in clear water.	<i>C. nodosa</i> , <i>Posidonia oceanica</i> , <i>Ruppia cirrhosa</i> , <i>R. maritima</i> , <i>Z. marina</i> , <i>Z. noltii</i> , <i>H. wrightii</i> ⁺ , <i>H. decipiens</i> ⁺ , <i>H. stipulacea</i> ⁺
4. <i>Temperate North Pacific</i> (Korea to Baja, Mexico)	High diversity of temperate seagrasses (15 species) in estuaries, lagoons and coastal surf zones.	<i>Phyllospadix iwatensis</i> , <i>Phyllospadix japonicus</i> , <i>Phyllospadix scouleri</i> , <i>Phyllospadix serrulatus</i> , <i>Phyllospadix torreyi</i> , <i>R. maritima</i> , <i>Zostera asiatica</i> , <i>Zostera caespitosa</i> , <i>Zostera caulescens</i> , <i>Zostera japonica</i> , <i>Z. marina</i> , <i>H. wrightii</i> ⁺ , <i>H. decipiens</i> ⁺ , <i>Halophila euphlebica</i> ⁺ , <i>Halophila ovalis</i> ⁺
5. <i>Tropical Indo-Pacific</i> (East Africa, south Asia and tropical Australia to the eastern Pacific)	Largest and highest diversity bioregion; tropical seagrasses (24 species) predominantly on reef flats but also in deep waters, many commonly grazed by mega-herbivores.	<i>Cymodocea angustata</i> , <i>Cymodocea rotundata</i> , <i>Cymodocea serrulata</i> , <i>Enhalus acoroides</i> , <i>Halodule pinifolia</i> , <i>Halodule uninervis</i> , <i>H. wrightii</i> , <i>Halophila beccarii</i> , <i>Halophila capricorni</i> , <i>H. decipiens</i> , <i>Halophila hawaiiiana</i> , <i>Halophila minor</i> , <i>H. ovalis</i> , <i>Halophila ovata</i> , <i>Halophila spinulosa</i> , <i>H. stipulacea</i> , <i>Halophila tricostata</i> , <i>R. maritima</i> , <i>Syringodium isoetifolium</i> , <i>Thalassia hemprichii</i> , <i>Thalassodendron ciliatum</i> , <i>Zostera capensis</i> ⁺ , <i>Z. japonica</i> ⁺ , <i>Zostera muelleri</i> ⁺ [<i>Zostera capricorni</i>]
6. <i>Temperate Southern Oceans</i> (New Zealand and temperate Australia, South America, and South Africa)	Extensive meadows of low-to-high diversity temperate seagrasses (18 species) often growing under extreme conditions.	<i>Amphibolis antarctica</i> , <i>Amphibolis griffithii</i> , <i>Halophila australis</i> , <i>Posidonia angustifolia</i> , <i>Posidonia australis</i> , <i>Posidonia ostenfeldii</i> complex, <i>Posidonia sinuosa</i> , <i>R. maritima</i> , <i>Ruppia megacarpa</i> , <i>Ruppia tuberosa</i> , <i>Thalassodendron pachyrhizum</i> , <i>Z. capensis</i> , <i>Z. muelleri</i> [<i>Z. capricorni</i>], <i>Zostera tasmanica</i> [<i>Heterozostera tasmanica</i>], <i>H. decipiens</i> ⁺ , <i>H. ovalis</i> ⁺ , <i>S. isoetifolium</i> ⁺ , <i>T. ciliatum</i> ⁺

The boundaries of each bioregion are described and the seagrass species of each bioregion are presented alphabetically, followed by species of seagrass that have their center of distribution in an adjacent bioregion or are invasive to a bioregion, designated with a “+”. Species listed in brackets are conspecific with the preceding species. Species listed in parentheses require further genetic and morphometric investigation and may be conspecific with the preceding species.

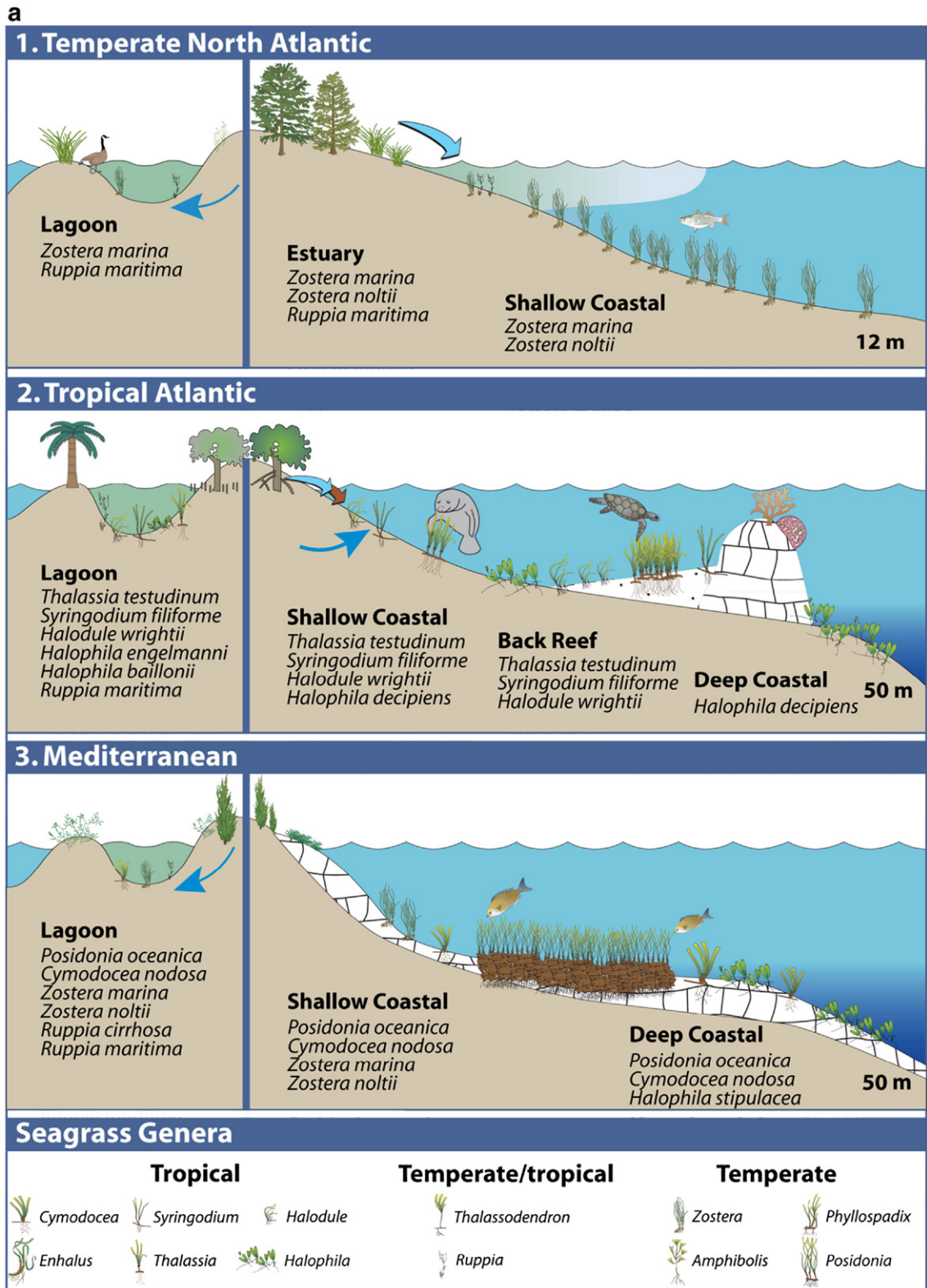


Fig. 2. Seagrass habitat diagrams for (a) Bioregions 1–3 and (b) Bioregions 4–6. Major species for each bioregion listed according to dominance within habitats. Maximum reported depths.

b

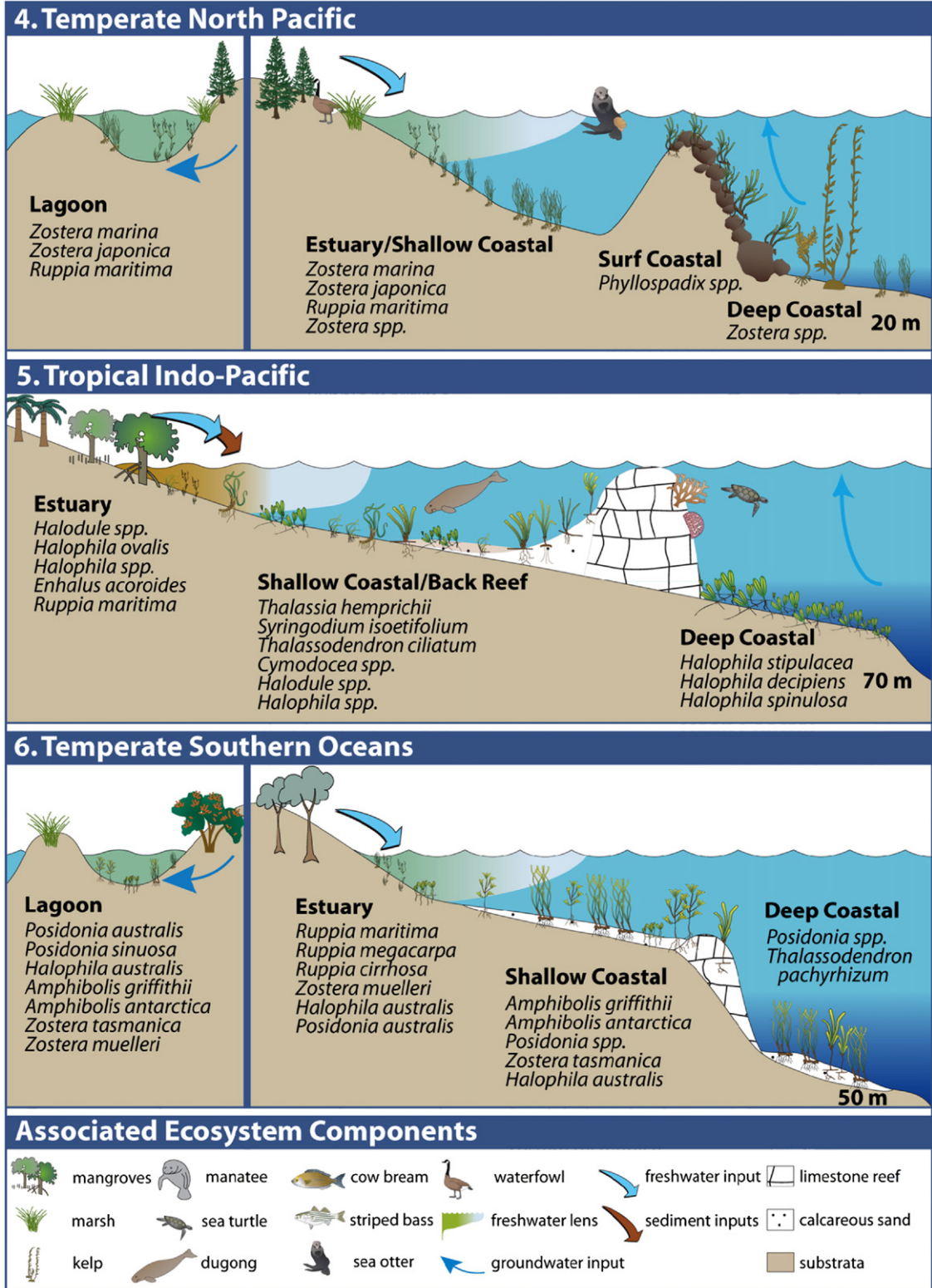


Fig. 2 (continued).

(Fig. 1, Table 1). The temperate–tropical distinction is useful in considering seagrass species distribution, and the exceptions of species emigrating into neighboring regions are likely driven by thermal anomalies or propagule dispersal resulting from ocean circulation patterns. Temperate seagrasses, including those of arctic regions, have roughly the same numbers of species as those of the tropics, with a few species overlapping. North and south temperate regions split the temperate species list roughly in half. Two north temperate regions (Bioregions 1 and 4) are dominated by species in the genus *Zostera*, while the Mediterranean and the south temperate regions (Bioregions 3 and 6) are dominated by species of *Posidonia*; however, both genera are represented north and south. In temperate areas, the stresses and limitations to seagrasses are varied, including cold temperatures toward the poles, warm temperatures toward the tropics, freshwater discharge and anthropogenic impacts, as many temperate coastlines tend to be heavily populated and industrialized. Additionally, areas of great tidal range may have light limitation at high tide and, at low tide, intertidal high or low temperature stress and radiation exposure (high irradiance and UV) as well as air exposure. Temperate seagrasses exist in conjunction with other important habitats. In the North Atlantic, proximal occurrence of *Z. marina* meadows and salt marshes as well as kelp beds, and oyster and mussel reefs, enhances the functions and values of the combined habitats and their contributions to estuaries and coastal embayments.

Tropical bioregions (Bioregions 2 and 5) have high species diversity with the genus *Halophila* representing the greatest number of species. SeagrassNet monitoring has shown that even near the Equator, seagrasses show seasonal growth variation (Short et al., 2006b). The platform shoreward of emergent coral reefs (the back reef) is a unique feature in the tropics that provides extensive shallow water seagrass habitat. Stresses and limitations to seagrasses in the tropics include high temperature and radiation exposure, particularly at low tide. Thermal impacts result from high water temperatures or overexposure to warm air; osmotic impacts result from hypersalinity due to evaporation; radiation impacts result from high irradiance and UV exposure. Ultraviolet radiation exposure in the tropics can turn seagrass leaves a deep purple, may reduce their productivity, and may also have led to increased speciation via mutation. Tropical seagrass ecosystems are prone to nutrient limitation due to the oligotrophic nature of much of the world's tropical oceans. Human impacts in the tropics, except for some extreme localized cases, are more often sedimentation and suspended sediments resulting from watershed deforestation and mangrove clearing rather

than nutrient pollution. Direct human use of the seagrass habitat for collection of food species is much higher in tropical than in temperate seagrasses.

3.1.1. Temperate North Atlantic, Bioregion 1

In the Atlantic from North Carolina (USA) to Greenland and Norway and along European coastlines south to Portugal, *Z. marina* is found in vast intertidal areas to depths of 12 m MSL in clear ocean water. *Z. marina* occurs in most marine soft bottom environments (lagoons, estuaries and shallow coastal areas) with good water clarity (Fig. 2a). Plant size generally increases with latitude, with plants in North Carolina (USA) averaging approximately 0.2 m and in northern Maine (USA) vegetative plants reaching 3 m and reproductive shoots, 4 m (Moore and Short, 2006). The division between temperate and tropical regions is not always clearly distinguished by seagrass species assemblage in this region of 5 species, since two of the 5 species are only found near the region's southern boundaries (Table 1). On the east coast of the USA in North Carolina, *Z. marina*, at the southern end of its temperate range, grows intermixed with *Halodule wrightii*, a tropical species (Thayer et al., 1984); similarly, in Portugal, *C. nodosa* occurs intermixed with temperate seagrasses. In the north temperate oceans, *Z. marina* tends to form broad mono-specific stands. In Europe, *Zostera noltii* is found in the shallow intertidal, generally inshore of *Z. marina*. Eelgrass was severely impacted by the wasting disease in the 1930s in this region, but now repopulates much of its former habitat except in areas of poor water clarity; sporadic, localized recurrences of the disease have been observed since the 1980s (Short et al., 1987; Burdick et al., 1993). Low salinity stress to eelgrass occurs in the Baltic Sea as well as Hudson Bay. On the temperate coasts of North America and Europe, *R. maritima* occurs in both brackish estuarine areas and hypersaline salt marsh pools.

3.1.2. Tropical Atlantic, Bioregion 2

The Tropical Atlantic, with 10 seagrass species (Table 1; including one recent invasive), is dominated by three species, *Thalassia testudinum*, *Syringodium filiforme*, and *H. wrightii*, which predominate in the western tropical Atlantic (including the Gulf of Mexico and the Caribbean Sea) and which can occur in single species stands but often occur intermixed or sequentially in ecological succession (Creed et al., 2003). Other species of *Halodule* are also reported for the region (e.g., *Halodule bermudensis*), but the taxonomy is still unclear. The region is predominantly a carbonate environment, occupying areas from shallow back reefs to

broad deep sand banks (Fig. 2a). *T. testudinum* and *S. filiforme* have been reported to 20 m, while *Halophila decipiens* grows to 50 m. Manatee and sea turtles directly consume many seagrass species in this region. High temperatures, primarily in bays and lagoons, can restrict seagrass growth and distribution, as in Laguna Madre, Texas (USA) where *H. wrightii* and *R. maritima* tolerate high temperatures and hypersaline conditions (Onuf et al., 2003). Brazil and the southeastern tropical Atlantic are dominated by *H. wrightii*, with the possibly conspecific *Halodule emarginata* (De Oliveria et al., 1983; Creed, 1999) and some species of *Halophila* present. The west coast of Africa has only *H. wrightii* and, extending from the Mediterranean Bioregion, *C. nodosa* and *Z. noltii*. *Halophila johnsonii*, a species on the U.S. Federal Threatened Species List, is limited in distribution to the east coast of Florida, ranging from very shallow flats to channel bottoms in relatively turbid water (Virmstein et al., 1997), but may actually be a form of *Halophila ovalis* (Waycott et al., 2006). *Halophila engelmanni* is found throughout the northern Caribbean and the Gulf of Mexico (Green and Short, 2003), while *Halophila baillonii*, a similar-looking species, is reported in Brazil (De Oliveria et al., 1983), in the southern Caribbean, and in Belize (Short et al., 2006a). The invasive seagrass *H. stipulacea* was recently discovered off the island of Grenada, where it is believed to be an introduction from the Mediterranean (Ruiz and Ballantine, 2004).

3.1.3. Mediterranean, Bioregion 3

P. oceanica, *Z. marina*, *Z. noltii*, and *C. nodosa* as well as *H. stipulacea* (an invasive species) all form single species meadows in the Mediterranean Bioregion, which has a total of 9 seagrass species with two species that occur only at the region boundary (Table 1). Deep *P. oceanica* beds (to 45 m) and, to a lesser extent, *C. nodosa* (30–40 m) in clear water, are characteristic of this region (Procaccini et al., 2003). *H. stipulacea*, although scarce below 50 m, was collected by dredge off Cyprus from 145 m (Lipkin et al., 2003) and is the deepest seagrass reported worldwide. *P. oceanica* is long-lived and forms a deep “matte” of root and rhizome material which may be several meters deep and thousands of years old. In the western Mediterranean, there is a typical complex occupying fairly predictable zones from the intertidal *Z. noltii* to deeper *C. nodosa* and, at depth, meadows of *P. oceanica* (Fig. 2a). In the Mediterranean, *Z. marina* is present on the open coast (France, Italy, Spain) and also in the Adriatic Sea. *Z. marina* occurs regularly in coastal lagoons of the western Mediterranean (Laugier et al., 1999), where it is often

found with *Z. noltii*. The temperate–tropical mix of species in the Mediterranean makes it a unique region with the two endemic species (*P. oceanica*, which is predominantly temperate, and *C. nodosa*, which has tropical congeners in the Tropical Indo-Pacific Bioregion) occurring throughout the entire Mediterranean. *H. stipulacea* appeared in the eastern Mediterranean after the opening of the Suez Canal in 1869; this species was recorded in Malta in 1970, and then in Italy in the 1990s (Cancemi et al., 1994). The Black, Azov, Caspian, and Aral Seas are rather isolated and are dominated by *Z. marina* (in the Black and Azov Seas) and *Z. noltii* (in the Caspian and Aral Seas). *Ruppia cirrhosa* and *R. maritima* are both found within the Mediterranean and Black Seas (Milchakova, 1999; Phillips et al., 2006). Northwest Africa, both inside and outside the Mediterranean Sea, has *C. nodosa* and *Z. noltii*. *H. wrightii* and *H. decipiens* occur outside the Mediterranean on the northwest coast of Africa. The Canary Islands have *C. nodosa* and *H. decipiens*.

3.1.4. Temperate North Pacific, Bioregion 4

The Temperate North Pacific Bioregion has 15 species of seagrass, of which 4 occur only at the region boundary, and is dominated by three temperate genera: *Zostera*, *Ruppia*, and *Phyllospadix* (Table 1). Eelgrass, *Z. marina*, dominates the north temperate Pacific, occurring around the Pacific Rim from Japan, Korea and China to the northern Bering Sea and down to the Gulf of California, with other *Zostera* species centered in east Asia. A related species, *Zostera caulescens*, was found to have reproductive shoots reaching 7.8 m in length in Japan (Aioi and Nakaoka, 2003) and 8 m in Korea (Lee and Lee, 2003). *Z. marina* grows to about 10 m depth in this region (Fig. 2b), with other *Zostera* species having more limited or deeper ranges, including *Zostera caespitosa* and *Z. caulescens*, which reach 20 m and 17 m, respectively (Aioi and Nakaoka, 2003). *Z. marina* grows near the Arctic Circle in Alaska and is found growing under the ice (McRoy, 1969). On the west coast of North America, in Baja, Mexico, *Z. marina* grows much further south than anywhere else in the world and at some locations is a winter annual (Meling-Lopez and Ibarra-Obando, 2000). In Baja, the range of *Z. marina* overlaps with *H. decipiens* and *H. wrightii*. In Japan, the tropical species *H. ovalis* and *Halophila euphlebia* (Uchimura et al., 2006) are reported where only temperate species would be expected. *Z. marina*, *Z. japonica*, other *Zostera* species in Asia, several *Phyllospadix* species and *R. maritima* often form single species meadows in this region. *Z. japonica* is an introduced species on the west coast of

North America and has been relatively recently reported in British Columbia (Canada) and Washington, Oregon, and California (USA). *Phyllospadix* is found on both sides of the Pacific, with 2 species in Asia and 3 species in North America, all of which have a modified rhizome allowing them to inhabit exposed coasts, attached to rocks in the high-energy surf zone.

3.1.5. Tropical Indo-Pacific, Bioregion 5

The Tropical Indo-Pacific is a vast tropical region stretching from the east coast of Africa to the eastern Pacific Ocean with more seagrass species than any other region; we identify 24 species, of which 3 have their center of distribution in an adjacent region (Table 1). In the western Pacific, there is a trend of decreasing species numbers from west to east with (north of the Equator) 14 species in the Philippines, 10 in Micronesia, and 2 in the Marshall Islands and (south of the Equator) 12 species in Papua New Guinea and Vanuatu, 6 in Fiji, and 2 in Western Samoa and French Polynesia (Green and Short, 2003). In many parts of the region, seagrasses are found on coral reef flats, between the reef break and shore. Typically, the three species *Thalassia hemprichii*, *Syringodium isoetifolium*, and *Halodule uninervis* dominate reef platforms and are found throughout the western two-thirds of the region, with *Cymodocea rotundata* and *Cymodocea serrulata* also common in the same area. Most tropical species are found in water less than 10 m deep (Fig. 2b). Of the 13 species identified in northeastern Queensland by Lee Long et al. (1993), all occurred in water depths less than 6 m below MSL and only four occurred in water more than 20 m below MSL. Species of the genus *Halophila* are common throughout the Tropical Indo-Pacific and can be found in a range of habitat types from shallow estuarine environments to very deep clear water, with *H. decipiens* reaching to 58 m in the Great Barrier Reef (Lee Long et al., 1996) and *Halophila spinulosa*, *H. ovalis*, *Halophila tricosata* and *Halophila capricorni* common below 35 m (Coles et al., 2000). At the western edge of this bioregion, *H. stipulacea* has been observed to 70 m in the Red Sea. There are two *Halophila* species in Hawaii, *Halophila hawaiiiana* and *H. decipiens*, as well as *R. maritima*. *Enhalus acoroides*, a unique Indo-Pacific species, has flowers that are fertilized on the water surface by floating pollen, limiting its distribution to intertidal and shallow waters. *Thalassodendron ciliatum* is often found on reef edges exposed to wave action as well as back reef areas, protected from damage by its flexible, woody stem and strong root system. *H. wrightii*, which has its center of distribution in the Tropical Atlantic Bioregion, has been widely reported in the western Tropical Indo-Pacific; however, there is some question

about whether this is an issue of taxonomy or range extension. High seagrass diversity typifies the western side of the Tropical Indo-Pacific, with 12–14 species currently identified for the tropical areas of the Indian Ocean. Most of these species are found on the southeast coast of India (Jagtap, 1996; Jagtap et al., 2003), the Red Sea and eastern Africa, with fewer species in the Persian Gulf.

3.1.6. Temperate Southern Oceans, Bioregion 6

Species of *Ruppia* and *Zostera* occur on all the continents within this circumpolar region: South America, Africa, and Australia. A total of 18 seagrass species occur here (Table 1), of which 4 are found only at the region's boundaries; seagrasses are found in a wide range of habitats including surf zones (Fig. 2b). In the southeast temperate Indian Ocean and the Southern Ocean around Australia, single species meadows of *Posidonia australis* occur as well as complexes of temperate species meadows that include several other species of *Posidonia*, *Halophila australis*, *Thalassodendron pachyrhizum*, *Amphibolis antarctica*, *Amphibolis griffithii*, *Z. muelleri* and *Zostera tasmanica*. The south temperate coast of Australia has several species which overlap and blur temperate–tropical boundaries on both the east and west coasts, including *H. ovalis*, *H. uninervis*, and *S. isoetifolium*, with *H. decipiens* extending into the temperate zone only on the west coast. In New Zealand, *Z. muelleri* is found throughout the islands; wasting disease outbreaks caused by *Labyrinthula* occurred in the 1960s (Armiger, 1964). *P. australis*, *A. antarctica* and *Z. tasmanica* are reported from the southern Australian island state of Tasmania. In temperate South America, only *R. maritima* (in the Atlantic) and *Z. tasmanica* (on the Pacific coast of Chile) occur (Phillips et al., 1983b, Creed, 2003). The southernmost seagrass in the world is *R. maritima*, collected from the Straits of Magellan by Lucia Mazzella; herbarium specimens are on file at the Stazione Zoologica Anton Dohrn (Zupo pers. com.). In temperate southern Africa, *Zostera capensis* and *Ruppia* spp. dominate, with the tropical species *H. ovalis* and *T. ciliatum* also present along the Indian Ocean side of South Africa.

3.2. Identifying regional levels of seagrass species diversity

Seagrasses globally have five centers of high diversity (Fig. 3), all of which occur in the eastern hemisphere and four of which occur in the Tropical Indo-Pacific bioregion; the fifth, southwestern Australia, occurs in

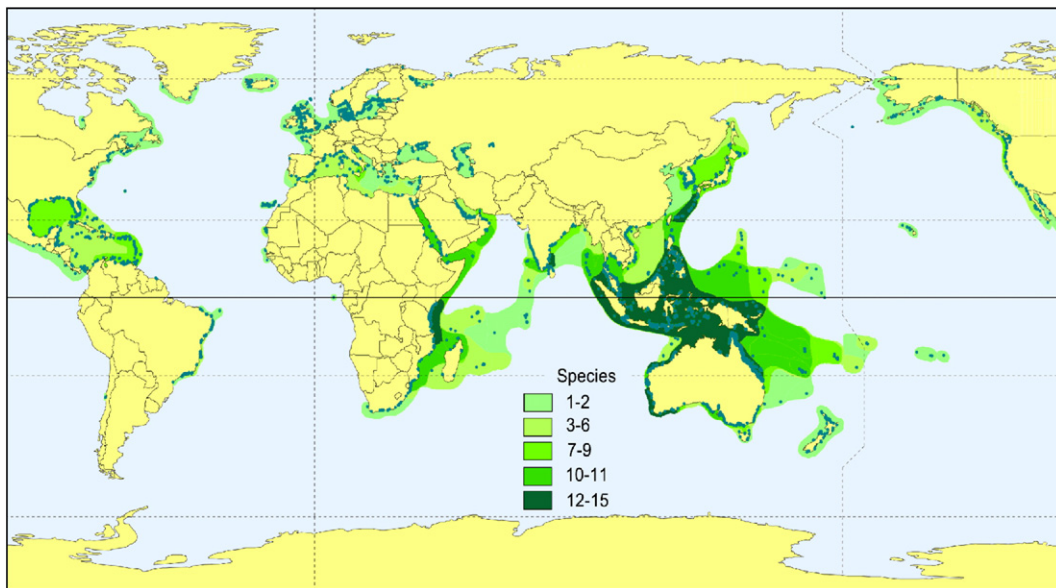


Fig. 3. Global seagrass diversity and distribution. Shades of green indicate numbers of species reported for an area; blue points and polygons indicate documented reports of seagrass occurrence (from 2005 UNEP-WCMC).

the adjacent Temperate Southern Oceans bioregion (Appendix A). The first and largest of these, with by far the greatest number of seagrass species (19), lies over insular Southeast Asia and extends across north tropical Australia, including the Great Barrier Reef; all but two of the species, *Z. muelleri* and *Z. japonica*, contributing to this region's high diversity are tropical seagrasses. A second, much smaller center of diversity is found in southeastern India, represented by 13 all tropical species. The three other centers high diversity globally, located in eastern Africa, southern Japan, and southwestern Australia, obtain this designation by being located at or near a bioregional interface, encompassing both tropical and temperate seagrass species. East Africa, with 12 species, has only one temperate species, *Z. capensis*, contributing to its mix of mostly tropical species. Southern Japan also has 12 species, with *Z. japonica* the one temperate species that contributes to the diversity of this tropical region. In the Temperate Southern Oceans bioregion, southwestern Australia with 13 species has 4 tropical species contributing to its high diversity. Looking at diversity patterns in more detail (Fig. 3), and also at the individual species ranges that underpin them (Green and Short, 2003), seagrass bioregions are discussed from greatest to least seagrass diversity.

The Tropical Indo-Pacific (Bioregion 5) is the region of highest species diversity globally with four of the five areas of high seagrass diversity worldwide located in this

bioregion. By far the largest center of high seagrass diversity is insular Southeast Asia and north tropical Australia (Fig. 3). Mirroring the biodiversity found in coral reefs and mangrove forests as well as in tropical fish assemblages, this is a region dominated by tropical seagrass species (Table 1). Other high diversity foci are found in India and the east coast of Africa as well as southern Japan, with relatively rapid attenuation of diversity eastward across the Pacific islands. The Indian, east African and southern Japan centers of diversity have similar seagrass genera and large overlaps of species with each other and with insular Southeast Asia. Theories for the development of the insular Southeast Asian center of biodiversity have been advanced not only for seagrasses but for a number of taxa. Three models have been suggested to explain this area being a center of species accumulation: 1) the intersection of favorable ocean currents, i.e., the vortex model of coral reef biogeography (Jokiel and Martinelli, 1992); 2) the location of benign climatic conditions during recent ice ages (McCoy and Heck, 1976); and 3) a combination of both benign conditions and changing sea levels contributing to species evolution known as the eustatic diversity pump model (Rosen, 1984).

The Temperate Southern Oceans (Bioregion 6), a highly diverse and circumglobal region, is dominated by temperate seagrass species. The fifth global high area of diversity occurs here, in southwestern Australia, with a mix of temperate and tropical species from the genera

Amphibolis, *Halophila*, *Posidonia* and *Zostera*. Other parts of the region are less diverse, including New Zealand which has only one species (Appendix A). Chile has two species, *Z. tasmanica* (formerly *Heterozostera*), found at two locations along its Pacific coast and *R. maritima* on its Atlantic coast as well as along the coast of Argentina. South Africa is another location where temperate and tropical species mix.

The Temperate North Pacific (Bioregion 4) is also a high diversity region which, although adjacent to insular Southeast Asia, is dominated by temperate species including *Z. marina* and *Z. japonica*, which are found on both coasts of the Pacific. The genus *Phyllospadix* is unique to the North Pacific, with different species east and west. The western North Pacific has higher diversity (Table 1), with three endemic *Zostera* species and two endemic *Phyllospadix* species, than the eastern North Pacific, which has three endemic *Phyllospadix* species.

The Tropical Atlantic (Bioregion 2), a tropical area with moderate seagrass diversity, includes species of *Halodule*, *Halophila*, *Syringodium* and *Thalassia* (and the recently introduced *H. stipulacea*, Table 1). The Caribbean Sea has the highest diversity in the region, while the adjacent Gulf of Mexico has fewer species. Although the tropical communities of South America are geographically isolated and have low species diversity (limited to species of *Halodule*, *Halophila* and *Ruppia*), they are not sufficiently distinct to merit consideration as a separate flora. In West Africa, only one species, *H. wrightii*, has been recorded.

The Mediterranean (Bioregion 3) is an area of moderate seagrass species diversity with both temperate and tropical seagrasses, including seagrass communities just outside the Mediterranean in northwest Africa as well as communities in the Black Sea Basin and the Caspian and Aral Seas. *C. nodosa*, *P. oceanica* and *Z. marina* and *noltii* are common (with one introduced species, *H. stipulacea*), the first two being endemic. *Ruppia* spp. also play an important role in the region, particularly in the Black, Caspian and Aral Seas (Table 1).

The Temperate North Atlantic (Bioregion 1) is the lowest diversity region with only 5 species total, two of which have their center of distribution in adjacent bioregions. The region is dominated by *Z. marina*, with *R. maritima* widespread; *H. wrightii* reaches its northern limit at 35°N in North Carolina, USA. Europe is distinguished by having a second species of the *Zostera* genus, *Z. noltii*. *C. nodosa* from the Mediterranean occurs in Spain and Portugal (Table 1). Seagrasses in the North Atlantic have been isolated from the areas of higher temperate diversity in the Pacific and southern Australia by both physical and hydrodynamic circumstances.

In the discussion of seagrass diversity it is important to consider the evolutionary origin of seagrasses (Orth et al., 2006). The relatively low number of seagrass species overall suggests a recent evolutionary history; however den Hartog (1970) reports evidence for the existence of marine angiosperms as long ago as 100 million years, and there are clear examples of seagrass fossils from the Cretaceous. There is no evidence of any massive seagrass diversification or major extinction events, and so it may be that seagrasses have simply followed a relatively conservative evolutionary pathway.

3.3. Investigating distribution of seagrass genera across bioregions

Seagrass distributions at the generic level are remarkably similar between the northern and southern hemispheres (Short et al., 2001). The number of genera in both hemispheres is the same, with 11 in each and the hemispheres have 10 genera in common. The only unique northern hemisphere seagrass genus is *Phyllospadix*, while in the southern hemisphere, *Amphibolis* is unique. Tropical genera are widely dispersed on both sides of the equator in the Indo-Pacific, but in the Atlantic only the tropical genera *Halodule* and *Halophila* are found south of the equator. *Zostera* and *Posidonia* are the only temperate genera found in both hemispheres.

The only truly global seagrass genus is *Ruppia*, found in both tropical and temperate zones on both sides of the Equator. *Ruppia* grows in quiet backwaters, from fresh water to hypersaline conditions; its ecological plasticity accounts for its presence in all six bioregions. For the most part, seagrass genera are either tropical or temperate, with the center of occurrence clearly delineated. The exceptions are *Ruppia*, *Thalassodendron* (both temperate and tropical in Western Australia), and *Cymodocea* which is found in the tropics and in the less easily characterized temperate–tropical Mediterranean.

Zostera is primarily a temperate genus, dominating the north temperate oceans (Bioregions 1 and 4) and occurring in all temperate bioregions, but also extending into both tropical bioregions: the Tropical Atlantic Bioregion (2) in west Africa and the Tropical Indo-Pacific Bioregion (5) in east Africa, east Australia and Vietnam. Nearly as widespread as *Ruppia*, *Zostera*'s near-global distribution is accounted for by its presence in arctic, temperate and some tropical oceans.

Halophila is the genus with the greatest number of species (ca. fifteen, depending on unresolved taxonomic ambiguities), primarily tropical and occupying both tropical regions, but extending into all four temperate regions, as well. Two species of the genus (*H. ovalis* and

H. decipiens) are globally widespread, while most other members of the genus are confined to a single bioregion. *Halophila* has one, and possibly two, species that are invasive. Several species of *Halophila* are endemic and have limited distribution, but there are unresolved issues of species designation among these. *Halodule*, another widespread tropical genus, is found throughout the Tropical Indo-Pacific (5) and the Tropical Atlantic (2) but only extends into temperate waters at a couple of locations. Other genera (including *Amphibolis*, *Enhalus*, *Thalassodendron*, and *Phyllospadix*) are generally confined to a single region or make a slight appearance at the fringe of a second.

Interestingly, the Mediterranean has both temperate (*Posidonia* and *Zostera*) and tropical (*Cymodocea* and *Halophila*) genera, all of which have congeners in other temperate or tropical regions. *Posidonia* dominates the Mediterranean Sea and the south coasts of Australia, but is found nowhere else in the world. Only one species of the genus is present in the Mediterranean Bioregion (3) while four species are present in the Temperate Southern Oceans Bioregion (6). One species of *Posidonia* extends into the Tropical Indo-Pacific (5) on the north coast of Australia. The Mediterranean also has a species of *Cymodocea* that ecologically parallels the three members of *Cymodocea* in the Tropical Indo-Pacific.

A number of genera have congeneric species in the Atlantic and Pacific Oceans; among these, the most notable are *Thalassia*, *Syringodium* and *Halodule*. All three have species occurring in the Tropical Atlantic Bioregion (2) and in the Tropical Indo-Pacific Bioregion (5). In general, these three genera occupy the same physical habitat and fulfill similar successional roles in both the Atlantic and the Indo-Pacific.

The occurrence of ecologically similar seagrass genera in both the north and south temperate oceans presents an interesting situation. Found on both sides of the North Pacific, one of the most divergent seagrass genera is *Phyllospadix*. Its five species have root and rhizome structures that attach to rocks in the surf zone of rocky coasts. These surf-grasses have thin, in some species rolled, leaves that reduce hydrodynamic drag and allow survival in even pounding surf. Ecologically, but not morphologically, similar seagrasses from south temperate Australia are found in the genus *Amphibolis*, which also has roots and rhizomes that can cling to rocks, but unlike the long-bladed *Phyllospadix*, has a strong erect stem with clusters of leafy bundles. *Phyllospadix* and *Amphibolis* have similar grappling anchors on their seeds and seedlings, respectively.

4. Conclusions

Seagrasses are a widely dispersed group of plants comprising relatively few species (less than 60 worldwide) and are often overlooked due to their submerged environment. They are widely distributed compared to most other marine and coastal plant types. *R. maritima*, until recently not considered to be a seagrass, is one of the most widely distributed of all flowering plants on Earth. Analysis of seagrasses within and between the six bioregions provides valuable perspectives for understanding seagrass distribution and diversity. The bioregion diagrams are a framework for understanding seagrass habitats, their dynamics in a geographic context, their trophic pathways, and a structure for comparisons and hypothesis-testing throughout the world. Given the relatively low number of seagrass species globally, it is interesting to see the near worldwide distribution of both genera and species representatives and the importance and ecological role of seagrasses in the Earth's coastal oceans.

Seagrass distribution change occurs on the micro-scale over very short time periods, as seagrasses are by their nature constantly responding to local environments. Places to watch for more macro-scale seagrass distributional changes include the edges of the bioregions, where tropical–temperate mixing of species may occur rapidly with global climate change, as well as the various centers of diversity, areas of high human impact, areas where seagrasses are already stressed by light and temperature, and areas susceptible to invasion, either from adjacent waterways or from import of plant material.

Genetic analysis holds both the promise of increased clarification of species identity when joined with morphological and anatomical studies, as well as increased understanding of species diversity and distribution worldwide. The biodiversity of seagrasses indicates areas of seagrass species richness that may reflect their evolutionary origins and ongoing patterns of colonization. Diversity of seagrasses parallels the biodiversity patterns of many other aspects of the biosphere.

We still have much to learn about seagrass distribution: virtually no seagrass species is fully investigated as to its global occurrence or widespread genetic diversity across the range. However, there are clear trends of seagrass loss in all areas of the world where development and human population pressure impact coastal watersheds and the coastal oceans themselves. Analysis of distribution per se is interesting and illuminates seagrass habitat biogeography. Changes in seagrass distribution patterns and extent, as well as species shifts both local and global, will in part determine the long-term well-being of the world's oceans.

Acknowledgements

Support was provided to the Global Seagrass Trajectories Working Group by the National Center for Ecological Analysis and Synthesis, a center funded by the National Science Foundation (grant DEB-0072909), the University of California at Santa Barbara, and the state of California. Support to SeagrassNet and F. Short was provided by the David and Lucile Packard Foundation, the Oak Foundation and the New Hampshire Charitable Foundation in conjunction with Tom Haas. Thanks to our colleagues in the Global Seagrass Trajectories Working Group; group discussions contributed to the manuscript. Thanks to Cathy Short for editing and to Gregg Moore for work on the figures. We gratefully acknowledge the Integration and Application Network, University of Maryland and Jane Thomas and Kate Boicourt for contributions to the figures. Seagrass data extracted from version 2.0 of the global polygon and point dataset compiled by UNEP World Conservation Monitoring Centre (UNEP-WCMC), 2005. Jackson Estuarine Laboratory contribution number 449. UMCES contribution number 4111. [SS]

Appendix A

Seagrass species identified by global bioregions (updated from Short and Coles (2001)) and by area or country. The list provides the names of species that can be expected within regions. Dominant species are listed first (when known) and marginal species last with distribution information given for seagrasses that are invasive to a bioregion or have their center of distribution in an adjacent bioregion. Information compiled from documentation of species distributions (Short and Coles, 2001; Green and Short, 2003). Where there have been recent species changes, we list the accepted species with congeneric species in parentheses. Where species differentiation is unclear or disputed, we list the base species with its possible congeners indented below. Co-occurring macrophytes that may be confused with seagrasses are marked with †.

Bioregion 1: Temperate North Atlantic [5 species]

North American Coast

Zostera marina (dominant)
Ruppia maritima
Halodule wrightii — North Carolina only

Europe

Zostera marina (dominant)
Zostera noltii
Ruppia maritima
Cymodocea nodosa

Bioregion 2: Tropical Atlantic [10 species]

Caribbean Sea and Gulf of Mexico

Thalassia testudinum (dominant)
Syringodium filiforme (dominant)
Halodule wrightii (dominant)
H. bermudensis — Bermuda only
Halodule beaudettei
Halophila baillonii
Halophila decipiens
Halophila engelmanni
Halophila johnsonii — east Florida only
Halophila stipulacea (Grenada, introduced)
Ruppia maritima

Brazil

Halodule wrightii (dominant)
H. emarginata
Halophila baillonii
Halophila decipiens
Ruppia maritima

Bioregion 3: Mediterranean [9 species]

Mediterranean Sea

Posidonia oceanica (dominant)
Cymodocea nodosa
Ruppia cirrhosa (*spiralis*)
Ruppia maritima
Zostera marina
Zostera noltii
Halophila stipulacea (introduced)

Atlantic Northwest Africa, Canary Is.

Cymodocea nodosa
Halodule wrightii
Halophila decipiens
Zostera noltii

Black Sea

Zostera marina
Zostera noltii
Potamogeton pectinatus†
Ruppia maritima
Ruppia cirrhosa (*spiralis*)

Caspian Sea and Aral Sea

Zostera noltii

Bioregion 4: Temperate North Pacific [15 species]

Asian Coast

Zostera marina (dominant)
Phyllospadix iwataensis
Phyllospadix japonicus

Ruppia maritima
Zostera asiatica
Zostera caespitosa
Zostera caulescens
Zostera japonica
Halophila ovalis — Japan only
Halophila euphlebia — Japan only

North American Coast

Zostera marina (dominant)
Phyllospadix scouleri
Phyllospadix serrulatus
Phyllospadix torreyi
Ruppia maritima
Zostera asiatica
Zostera japonica (introduced)
Halodule wrightii — Mexico only
Halophila decipiens — Mexico only

Bioregion 5: Tropical Indo-Pacific [24 species]

Red Sea and East Africa

Thalassodendron ciliatum (dominant East Africa)
Halophila stipulacea (dominant Red Sea)
Cymodocea rotundata
Cymodocea serrulata
Enhalus acoroides
Halodule uninervis
Halodule wrightii
Halophila decipiens
Halophila minor
Halophila ovalis
Syringodium isoetifolium
Thalassia hemprichii
Zostera capensis

Persian Gulf

Halodule uninervis
Halophila ovalis
Halophila stipulacea
Syringodium isoetifolium

India

Cymodocea serrulata (dominant)
Halodule uninervis (dominant)
Halodule pinifolia (dominant)
Thalassia hemprichii (dominant)
Cymodocea rotundata
Enhalus acoroides
Halophila beccarii
Halophila decipiens
Halophila minor
Halophila ovalis

Halophila stipulacea
Ruppia maritima
Syringodium isoetifolium

Vietnam

Halophila decipiens
Halophila ovalis
Syringodium isoetifolium
Thalassia hemprichii
Zostera japonica

Insular Southeast Asia

Cymodocea rotundata
Cymodocea serrulata
Enhalus acoroides
Halodule pinifolia
Halodule uninervis
Halophila beccarii
Halophila decipiens
Halophila minor
Halophila ovalis
Halophila ovata
Halophila spinulosa
Ruppia maritima
Syringodium isoetifolium
Thalassia hemprichii
Thalassodendron ciliatum

Philippines

Cymodocea rotundata
Cymodocea serrulata
Enhalus acoroides
Halodule pinifolia
Halodule uninervis
Halophila beccarii
Halophila decipiens
Halophila minor
Halophila ovalis
Halophila ovata
Halophila spinulosa
Ruppia maritima
Syringodium isoetifolium
Thalassia hemprichii
Thalassodendron ciliatum

Southern Japan

Cymodocea rotundata
Cymodocea serrulata
Enhalus acoroides
Halodule pinifolia
Halodule uninervis
Halophila decipiens

Halophila minor
Halophila ovalis
Ruppia maritima
Syringodium isoetifolium
Thalassia hemprichii
Zostera japonica

Hawaii

Halophila hawaiiiana
Halophila decipiens
Ruppia maritima

Northeast Australia

Cymodocea rotundata
Cymodocea serrulata
Enhalus acoroides
Halodule pinifolia
Halodule uninervis
Halophila capricorni
Halophila decipiens
Halophila minor
Halophila ovalis
Halophila spinulosa
Halophila tricostata
Ruppia maritima
Syringodium isoetifolium
Thalassia hemprichii
Thalassodendron ciliatum
Zostera muelleri (capricorni)

Northwest Australia

Cymodocea angustata
Cymodocea rotundata
Cymodocea serrulata
Enhalus acoroides
Halodule pinifolia
Halodule uninervis
Halophila decipiens
Halophila minor
Halophila ovalis
Syringodium isoetifolium
Thalassia hemprichii
Thalassodendron ciliatum

Bioregion 6: Temperate Southern Oceans [18 species]

Southeast Australia and Tasmania

Amphibolis antarctica
Halophila australis
Halophila decipiens
Halophila ovalis
Zostera tasmanica (Heterozostera tasmanica)
Lepilaena cylindrocarpa†

Posidonia australis
Ruppia megacarpa
Zostera muelleri (capricorni; mucronata)

New Zealand

Zostera muelleri (capricorni; novazelandica)

Southwest Australia

Posidonia australis (dominant)
Amphibolis antarctica (dominant)
Amphibolis griffithii (dominant)
Halophila australis
Halophila decipiens
Halophila ovalis
Lepilaena marina†
Posidonia angustifolia
Posidonia sinuosa
Posidonia ostenfeldii complex
P. coriacea
P. denhartogii
P. kirkmanii
P. robertsoniae
Ruppia megacarpa
Ruppia tuberosa
Syringodium isoetifolium
Thalassodendron pachyrhizum
Zostera tasmanica (Heterozostera tasmanica)

Chile

Zostera tasmanica (Heterozostera tasmanica)
Ruppia maritima

Argentina

Ruppia maritima

South Africa

Zostera capensis (dominant)
Halophila ovalis
Ruppia maritima
Thalassodendron ciliatum

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