Accelerating Tropicalization and the Transformation of Temperate Seagrass Meadows

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Climate-driven changes are altering production and functioning of biotic assemblages in terrestrial and aquatic environments. In temperate coastal waters, rising sea temperatures, warm water anomalies and poleward shifts in the distribution of tropical herbivores have had a detrimental effect on algal forests. We develop generalized scenarios of this form of tropicalization and its potential effects on the structure and functioning of globally significant and threatened seagrass ecosystems, through poleward shifts in tropical seagrasses and herbivores. Initially, we expect tropical herbivorous fishes to establish in temperate seagrass meadows, followed later by megafauna. Tropical seagrasses are likely to establish later, delayed by more limited dispersal abilities. Ultimately, food webs are likely to shift from primarily seagrass-detritus to more direct-consumption-based systems, thereby affecting a range of important ecosystem services that seagrasses provide, including their nursery habitat role for fishery species, carbon sequestration, and the provision of organic matter to other ecosystems in temperate regions.

Keywords: Tropicalization, ecosystem function, megagrazers, herbivores, fish, invertebrates

Climate-driven changes in species composition and the novel ecological interactions that follow can alter the production and functioning of biotic assemblages in terrestrial and aquatic environments. A growing body of literature has documented range shifts in plants and animals, changes in body size, and altered behavioral and ecological interactions such as competition and predation (Poloczanska et al. 2013, Vergés et al. 2014).

Dramatic changes have occurred where the poleward expansion of herbivore populations has led to the consumption of major habitat-forming plants, resulting in rapid shifts in ecosystem states. Clear examples are transitions from complex, highly productive algal forests to simple turf or barren substrates as tropical and warm-temperate herbivores have immigrated to higher latitudes (Vergés et al. 2014 and references therein). This has been documented in the Mediterranean, Japan and Australia (Vergés et al. 2014), with widespread loss of extremely productive macroalgal forests through either direct overgrazing by tropical fishes or heat stress followed by intense grazing by tropical herbivores. Collectively, such changes have been termed *tropicalization*, which has been defined as an increase in the ratio of tropical to temperate taxa in a given region (cf. Wernberg et al. 2013) or the entire suite of changes in species composition, abundances, and interactions (Vergés et al. 2014).

Shallow coastal waters contain numerous and exceptionally rich and productive habitats, including mangrove forests, salt marshes, coral, rocky, oyster and mussel reefs, and seagrass meadows. Of special concern here—but comparatively less well known and appreciated by the public (Duarte et al. 2013)—are the extraordinarily productive, biologically diverse and economically valuable seagrass meadows that are abundant in coastal areas of all continents except Antarctica. These habitats provide valuable ecosystem services, including serving as important habitats for a range of iconic species (figure 1) and nursery grounds for numerous economically important finfish and shellfish, sequestering carbon, improving water quality by intercepting the nutrients and organic matter carried by land runoff, stabilizing sediments and preventing erosion (Barbier et al. 2011), and exporting seagrass detritus that supports productivity in other ecosystems (Hyndes et al. 2014). Despite providing these important services, seagrass meadows are among the planet's most threatened habitats, with their known global areal extent declining by 29% since the late 1800s and losses
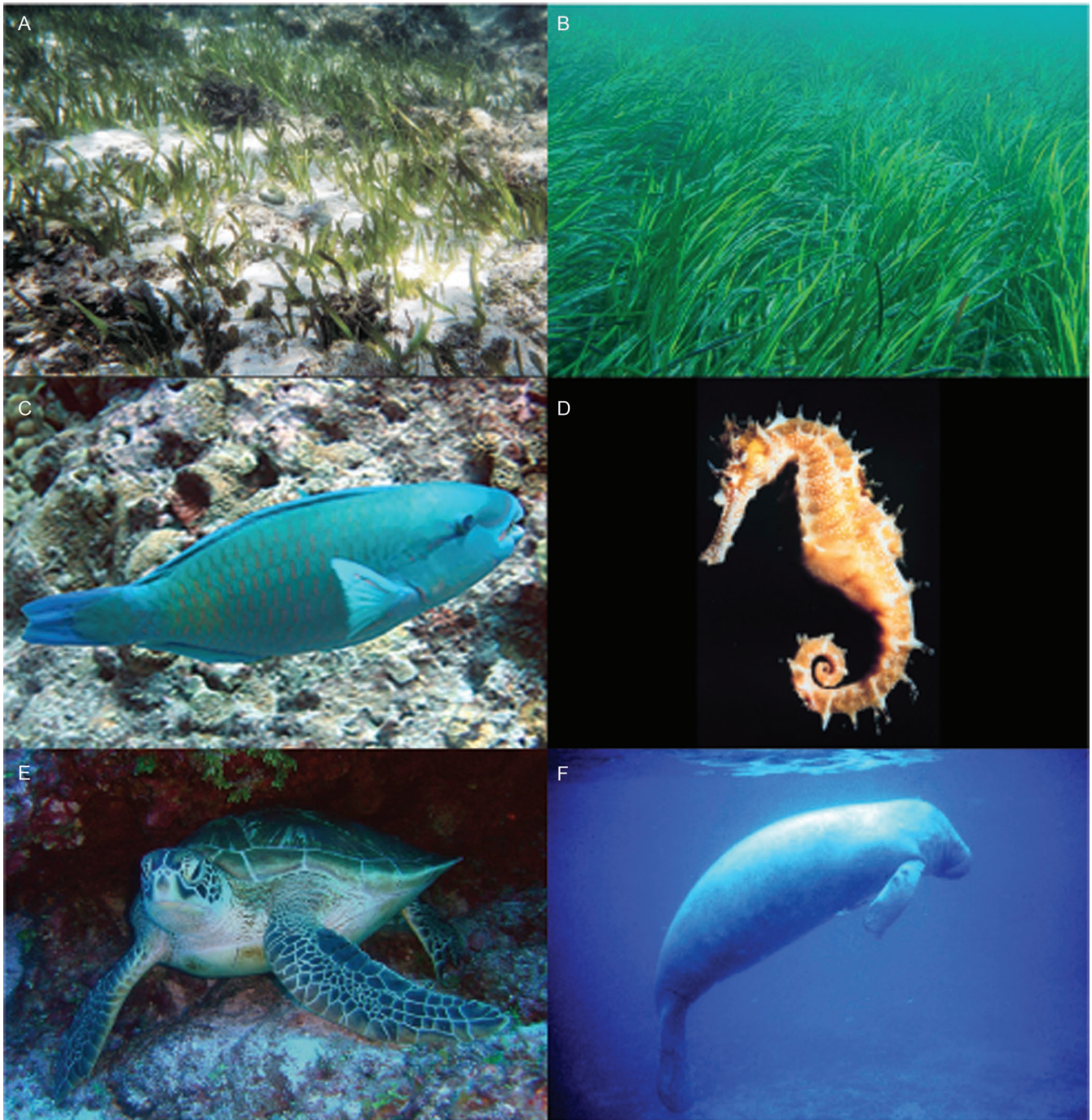
Figure 1. Examples of seagrass species (a, b; photos by K. McMahon) and iconic fauna (c, d, e, f; photos from NOAA) found in seagrass meadows.

rapidly accelerating in the last two decades (Waycott et al. 2009). This has significant economic ramifications, because on a global scale, seagrass meadows (combined with algal beds) have been estimated to provide ecosystem services for nutrient cycling alone valued at approximately US$29,000 per ha per year (Costanza et al. 2014). Although substantial, this value is far lower than the valuation of AU$230,000 per ha per for enhanced fishery production in southern Australia (Blandon and zu Ermgassen 2014). Regardless of the precise

monetary value, the potential economic impact of seagrass loss is significant.

These globally significant undersea meadows are highly susceptible to human-induced perturbations that reduce the quantity and quality of light (Orth et al. 2006). Temperature changes also affect seagrasses profoundly (Fraser et al. 2014). Recent worldwide increases in sea temperature, along with the predicted rises during the coming decades (IPCC 2013), raise concern for the long-term persistence of seagrasses in

many areas. If temperate seagrass meadows of the world, most of which are already stressed and in decline (Waycott et al. 2009), are further reduced by warming, major reductions in the quality and quantity of ecosystem services they provide may be expected to take place. There is therefore a clear and compelling need to evaluate and predict the consequences of these changes.

Declining populations of seagrasses are expected as temperatures rise beyond their thermal tolerances. This is already happening to some extent in Chesapeake Bay in the United States, where the temperate eelgrass *Zostera marina* is experiencing losses caused by summer temperatures exceeding its thermal limits (Moore et al. 2012). But many other indirect effects are likely to influence temperate seagrass meadows if poleward migration by tropical seagrasses, algae, herbivores and other taxa takes place. For example, tropical herbivores can shift food-web structure from one based on detritivory to one based on direct plant consumption (Kelkar et al. 2013). Indeed, Heck and colleagues (2015) suggested that the continuing influx of tropically associated herbivores into the northern, warm temperate Gulf of Mexico would likely result in seagrass meadows that are cropped down to the height of closely mowed lawns, greatly reducing their value as nursery grounds for many economically important finfish and shellfish species (Heck et al. 2015).

In this article, we begin by synthesizing existing knowledge to develop generalized scenarios of the most likely effects of tropicalization on the structure and functioning of seagrass-dominated ecosystems. We then apply the lessons learned from this synthesis and, when possible, make specific predictions about the expected changes that are likely to occur to the expansive and globally significant temperate seagrass meadows along the west coast of Australia. We focus on this region because it is (a) a biodiversity hotspot (Hopper 2009) with high numbers of endemic species and (b) an ocean warming hotspot that is likely to be a sentinel of subsequent change elsewhere (Hobday and Pecl 2014). Furthermore, seagrass meadows in southwestern Australia form one of the most extensive, productive and species rich temperate seagrass assemblages in the world (Carruthers et al. 2007), and they have recently experienced temperature increases previously unrecorded, leading to defoliation and loss of meadows (Fraser et al. 2014). Therefore, there is a compelling reason to develop predictions of the most likely future effects of tropicalization on these significant Australian seagrass meadows and their many inhabitants (figures 2a and 2b). These predictions will be particularly important to coastal zone managers worldwide, because seagrasses underpin the support system of many coastal systems in the world.

Mechanisms facilitating seagrass range expansion and contraction

Seagrasses have two principal mechanisms for colonizing new habitats: the dispersal of propagules (seeds, fruits, and reproductive shoots) and clonal growth (Kendrick et al. 2012, McMahon et al. 2014). However, the usually slow rate of meadow expansion by clonal growth dictates that rapid expansion of tropical species into temperate waters will occur mainly through the recruitment and establishment of sexually derived propagules. Scales and rates of expansion will depend primarily on the buoyancy of those propagules, with floating fruit or reproductive shoots dispersing tens to hundreds of kilometers over days to weeks and negatively buoyant seeds dispersing locally (McMahon et al. 2014). Long-distance dispersal can also occur via biological vectors such as mammals, turtles, and waterbirds (McMahon et al. 2014), but range expansions are likely to be more often influenced by coastal oceanography, prevailing winds, the availability of habitat for colonization, temperature tolerances, and light and nutrient requirements (Kendrick et al. 2012).

Range expansion of tropical or subtropical *Halophila* species into temperate regions has already been observed along the east coast of Florida in the United States (*Halophila johnsonii* and *H. decipiens*; Virnstein and Hall 2009) and Korea (*H. nipponica*; Kim et al. 2009), with warmer winters and increased water clarity suggested as potential environmental drivers. In comparison, range contractions are more difficult to demonstrate and require greater sampling effort (Bates et al. 2014). However, it is likely that range contractions will occur and be associated with temperature stress. For example, increased shoot mortality in *Posidonia oceanica* in the Mediterranean Sea has been associated with increased temperature (Diaz-Almela et al. 2007). Temperature increases of 1–2 degrees Celsius (°C) have, on several occasions, coincided with increased flowering intensity by *P. oceanica* across a large portion of the Mediterranean, although this was combined with high levels of seed abortion (Diaz-Almela et al. 2007). Similarly, 100% seed abortion was reported from *Posidonia australis* meadows in Shark Bay during and after a heatwave in 2011 (Sinclair et al. 2016).

Temperatures for optimal growth of temperate seagrasses (11.5–26°C; Lee et al. 2007) are lower than those of tropical species (e.g., 32–35°C; Pedersen et al. 2016). Furthermore, temperate seagrasses are typically exposed to greater annual temperature ranges, and they commonly show large seasonality in growth and photosynthetic parameters that are controlled in large part by water temperature (Bulthuis 1987). Extreme changes in temperature can result in dramatic declines in photosynthesis, productivity and survival of seagrasses (Marba and Duarte 2010). Temperature can affect a host of other plant functions, such as nutrient uptake, nutrient partitioning, and respiration, with the result that the optima for growth are often lower than those for photosynthesis (Lee et al. 2007) and can interact with other factors such as light intensity (Lee et al. 2007). We therefore predict reduced photosynthesis, growth, and survival for at least some temperate seagrass species with warming water temperatures. However, when predicting future distribution shifts of seagrass species, it is important to recognize that range expansions will not only be determined by the ability
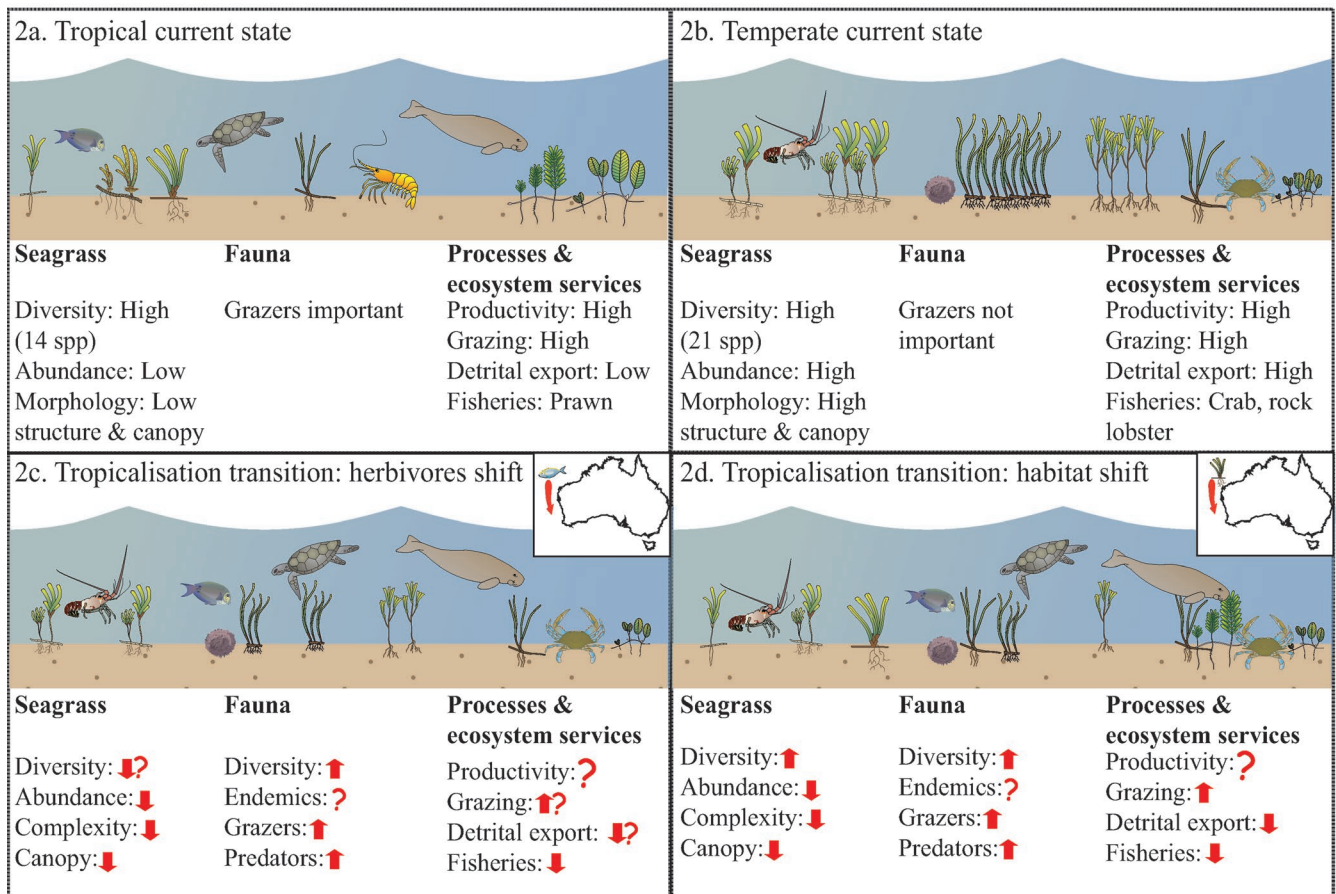
Figure 2. A conceptual diagram representing the current features and processes in tropical (a) and temperate (b) seagrass systems, as well as predicted features and processes in two scenarios (c and d) of tropicalization along the west coast of Australia.

of species to successfully recruit and survive in new locations but also by interspecific interactions such as competition (Bando 2006) and herbivory (Fourqurean et al. 2010).

Herbivory on seagrasses

A diverse array of herbivores, ranging from larger manatees and dugongs to small fish and invertebrates, can occur in seagrass meadows and remove large amounts of seagrass biomass (Heck and Valentine 2006). Although manatees and dugongs target seagrass, herbivorous fishes and green turtles can feed on macroalgae as well as seagrass (Heck and Valentine 2006), and omnivorous fishes may supplement their diet with small amounts of seagrass or may remove seagrass incidentally when targeting epiphytic flora and fauna (cf. Heck et al. 2015). Invertebrates such as urchins may target seagrass leaves (Heck and Valentine 2006), whereas others, including crabs and amphipods, can target seagrass reproductive tissue, compromising sexual reproductive potential.

Species and functional diversity of many herbivores are typically higher in the tropics (Floeter et al. 2005). Megagrazers—including manatees (figure 1f; *Trichechus*

manatus and *Trichechus senegalensis*), dugongs (*Dugong dugon*), and green turtles (figure 1e; *Chelonia mydas*)—are often abundant in the tropics, where they have not been overharvested, and can consume very large quantities of seagrass (Fourqurean et al. 2010). Dugongs (and sometimes manatees) can feed in large herds comprising 100s of animals, removing 30%–67% of above- and belowground biomass of seagrass (Marsh et al. 2011). In comparison, green turtles (*Chelonia mydas*) aggregate in tropical, subtropical and temperate seagrass meadows (Marquez-Guzman 1990). Although they are omnivorous, their diet is dominated by either algae or the aboveground portion of seagrass (Bjorndal 1997). Green turtles have a primary functional role in seagrass ecosystems (Bjorndal 1997), similar to manatees and dugongs, by modifying the species composition, structure, and nutritional value and by short-circuiting the detritus cycle (Lal et al. 2010). Bjorndal and Jackson (2003) estimated that green turtles would have consumed half the total annual Caribbean seagrass biomass of 1.2×10^{10} kilograms prior to European settlement.

The diversity and abundance of herbivorous fishes in the tropics is also high (figure 1c; Floeter et al. 2005). On the

basis of Cheung and colleagues (2012), the centers of distribution of tropical species are expected to shift poleward by up to 245 kilometers (km) over 100 years, suggesting that they will affect temperate seagrass meadows over that timeframe. Unvegetated "haloes" surrounding coral reefs and experiments demonstrate intense grazing on tropical seagrass by reef-associated parrotfish and other fish (Ogden 1977, Unsworth et al. 2007). Feeding and consumption rates of seagrass may, however, vary among herbivorous species, seasons, locations, as well as the seagrass species and condition. For example, seagrass only becomes a major part of the diet of some tropical fish species once they are mature adults (Nakamura et al. 2003). Therefore, tropical grazers recruiting to temperate seagrass meadows may need to survive several winters before they significantly affect local seagrass communities. In addition, because increased grazing rates on seagrass leaves can result from previous grazing (Holzer et al. 2013) or high nitrogen content (Goecker et al. 2005), those meadows under stress from other types of grazers or eutrophication may be more susceptible to grazing by herbivorous fishes.

Sea urchins form another important herbivorous group in the tropics, where they can consume large amounts of both living and detrital seagrass (Alcoverro and Mariani 2002). In some instances, urchin-grazing rates can exceed local rates of production and lead to overgrazing (Eklof et al. 2008). Because the abundance of urchins can fluctuate dramatically, the relative importance of urchin grazing on seagrass biomass and productivity can vary greatly from year to year and range from trivial to massive (Heck and Valentine 2006).

Temperate seagrass herbivores include only a handful of waterfowl, turtles, fish and invertebrates (Heck and Valentine 2006). Marine waterfowl—including ducks (e.g., the red-head duck, *Aythya americana*), coots (*Fulica atra*), geese (e.g., the brant goose, *Branta bernicla*), and swans (e.g., the black swan, *Cygnus atratus*)—are all known to graze significantly on seagrass (Heck and Valentine 2006). Waterfowl feed by removing both above- and belowground material; for example, black swans can remove over 90% of shoots and rhizomes (Dos Santos et al. 2012). Although the diversity of herbivorous fish in temperate systems is relatively low (Floeter et al. 2005), their abundances can be high (Vergés et al. 2009). However, few species target seagrass as a primary food source (Heck and Valentine 2006). Large invertebrates, including sea urchins, can also be major herbivores in temperate systems (Ling et al. 2009), but similar to fish, few species appear to solely feed on seagrasses.

From the above, there appears to be a strong tropical to temperate gradient in herbivore diversity and, in some instances, in grazing rates. The net impact of herbivores on seagrass biomass, however, does not currently vary consistently across latitude (Poore et al. 2012), probably because higher levels of production in warmer latitudes compensate for greater losses to herbivores. The overall interpretation of these patterns is complicated by the historical overharvesting of turtles and manatees in the tropics, which suggests

natural levels of herbivory in warmer latitudes were much higher 100–200 years ago (Jackson et al. 2001). Indeed, large impacts on species composition and standing stock of seagrass meadows have been recorded in regions where green turtle numbers have increased through conservation efforts (Fourqurean et al. 2010, Lal et al. 2010). If these megagrazers continue to increase their numbers and expand their ranges, both diversity and grazing rates are likely to increase in temperate waters, and this will have a significant impact on seagrass meadows if plant growth is not enhanced at a compensatory rate. This should be of particular concern in the winter months, when temperate seagrass growth is strongly limited by light availability (Fourqurean et al. 2010) and herbivory levels are generally low (close to nil; Prado et al. 2007).

Trends and predictions along the west coast of Australia

The west coast of Australia, in the southeastern Indian Ocean, is strongly influenced by the Leeuwin Current (LC), a warm poleward flowing current forming in northwest Australia from water flowing through the Indonesian Archipelago. The LC is unusual for Eastern Boundary Currents, which normally flow toward the equator, and is thought to have influenced the west coast of Australia for over 16 million years (Wyrwoll et al. 2009) and to be responsible for the presence of corals and other tropical fauna in the southern, temperate region of this coast. The strength of the LC is related to the Southern Oscillation Index, making its influence on more southern waters highly variable (Pearce and Feng 2007).

Rising water temperatures. Underlying the variability in the Leeuwin Current, there has been a gradual rise in sea surface temperature (SST) over the last 100 years. For example, SST on the midwest coast of Australia rose by over 1°C at a mean rate of approximately 0.1°C per decade between 1900 and 2013, although the rate of warming has been variable (figure 3). Similar rates of change along the northwest coast between 1950 and 2007 are considered equivalent to a southward isotherm shift of more than 100 km (Lough 2008). The southeastern Indian Ocean has, in fact, been identified as one of a number of global "hot spots" experiencing enhanced warming rates (Pearce and Feng 2007, Hobday and Pecl 2014).

These larger-scale SST patterns may not be representative of the nearshore waters, especially during winter months when heat loss to the atmosphere leads to a sharp cooling of the shallow coastal zone (Pearce et al. 2006), and there can be a temperature differences of approximately 4°C between the coast and the shelf break. However, water temperatures near Perth (approximately 31.5°S) rose approximately 0.13°C per decade between 1951 and 2002 (Pearce and Feng 2007) and approximately 0.3°C per decade from 1985 to 2004. On this basis, Lough (2008) predicted a rise of up to 2°C in southwestern Australian waters by 2100. Superimposed on these
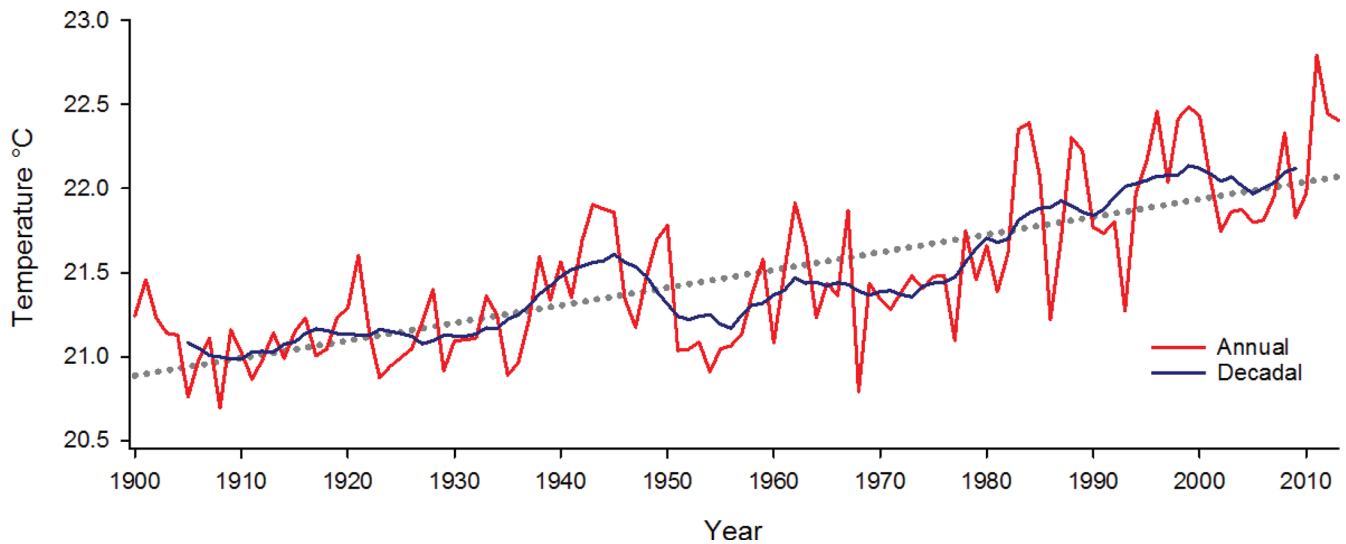
Figure 3. The annual mean surface temperatures (red line) at the Houtman Abrolhos Islands (28°–29°S) off the midwest coast of Western Australia between 1900 and 2013, from the HadISST data set (http://apdrc.soest.hawaii.edu/datadoc/ hadisst1.php), and the 11-year moving average to approximate decadal variability (blue line). The straight dotted line is the linear trend for the individual annual mean temperatures. The mean temperature rise was about 0.1°C per decade.

trends are intermittent warming events such as the 2011 heat wave (Pearce and Feng 2013), which produced record high sea temperatures off southwestern Australia (figure 3), with devastating consequences for marine life (Wernberg et al. 2013). Daily water temperatures along the midwest coast reached as much as 5°C above the normal February–March mean as a result of strong (and seasonally early) southward transport of warm tropical water by the LC, supplemented by anomalously high air–sea heat flux into the ocean surface (Pearce and Feng 2013). Such extreme events are forecast to increase in frequency (and possibly in intensity) into the future, continuing to drive poleward shifts in marine communities (Wernberg et al. 2013).

Predicted seagrass response to rising temperatures. The west coast of Australia supports both tropical Indowest Pacific (IWP) and Australasian temperate species of seagrasses. We predict that IWP species will likely extend their ranges under elevated temperatures, whereas temperate species will likely contract southward by 2100. We have taken a long-term multigenerational view of range extension for tropical species because colonization rates may vary with the individual species characteristics of the propagule (e.g., seeds, floating fruits, floating reproductive fragments with viable seeds) dispersal (Kendrick et al. 2012) and movement ecology (McMahon et al. 2014). Range extensions have already been observed for mobile fish and molluscs, corals, kelp, and seaweed communities along Australia's west coast (Wernberg et al. 2016). To predict range expansions and contractions by the end of the twenty-first century, we have estimated the annual mean temperature at the southern limit of species' current distribution and where that annual mean

temperature is expected to be in 2100 (see supplemental material for details). These potential southern distributional limits of IWP species are based on temperature as the sole determinant of their southern distributional limit, although we recognize that other factors such as connectivity and life-history traits, substrate limitation, competition, or herbivory can and will also influence distributions (as we discussed above). Furthermore, because our focus is on tropicalization of temperate seagrass meadows, we have not considered the contraction of distributions in the tropics.

We expect that several IWP species—including *Cymodocea rotundata*, *Enhalus acoroides*, and *Thalassodendron ciliatum*—will extend their southern limit by over 500 km by 2100 and therefore occur in a much larger area than at present (figure 4). Species known to be important forage habitats for a range of herbivores (e.g., *Halophila spinulosa* and *Halodule uninervis*) will likely extend approximately 200 km southward. In comparison, the range of *Syringodium isoetifolium*, which already occurs in temperate waters in Western Australia, is predicted to expand slightly and be similar to that of *H. ovalis*, which ranges across the spectrum of latitudes in Australia (figure 4). Because the temperature shift could allow *S. isoetifolium* to round the southwest corner of the continent, the large east–west expanse of the south coast potentially becomes available for colonization. Therefore, for these species, the range expansion is potentially very large.

For the major habitat-forming temperate species *Amphibolis antarctica*, *Posidonia australis*, and *P. sinuosa*, photosynthesis generally increases with increasing temperature across a 13–23°C temperature range (Masini and Manning 1997). The optimum temperatures for these species are south of their northern limit, suggesting that increasing
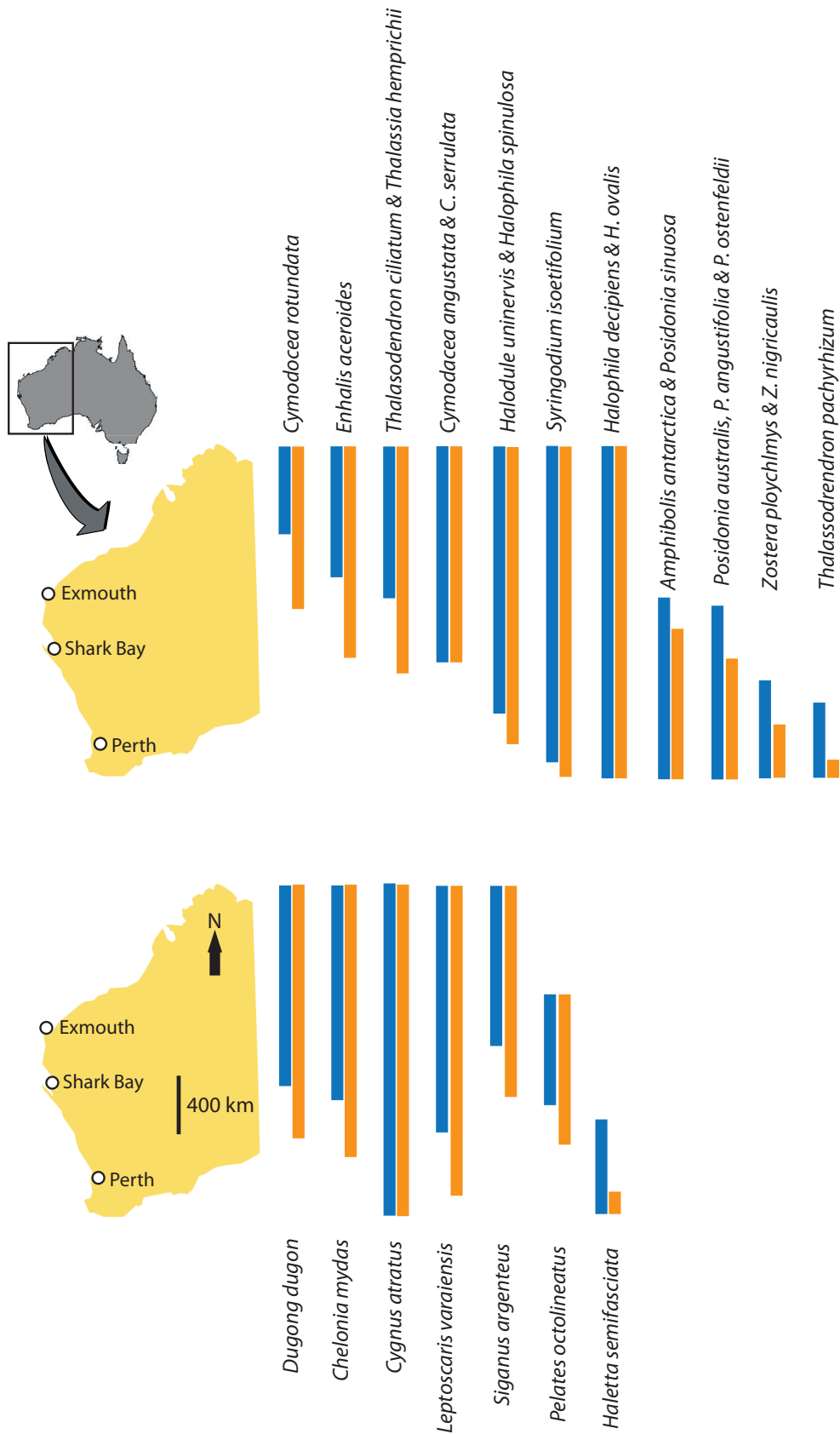
Figure 4. The current (blue) and predicted end-of-century (orange) distributions of seagrasses (top) and herbivores (bottom) along the west coast of Western Australia. See the supplemental material for methods to determine distributions and their shifts.

water temperatures should result in a southward contraction of their distributions. We predict that the northern limit of *A. antarctica* and *Posidonia* species will contract approximately 200–400 km by 2100 (figure 4). Supporting this prediction are studies showing that *A. antarctica* shoot density was dramatically reduced following extreme temperatures in 2011, as was the reproductive effort of *P. australis* (Fraser et al. 2014, Thomson et al. 2015). We therefore predict that although the species will continue to be present along the lower west coast, shoot density and production will likely be reduced near their new northern distribution limits, potentially compromising their abilities to compete with tropical species expanding southward and reducing their tolerance to multiple disturbances. Over decades to centuries, they most likely will contract southward, which could result in their disappearance from the Shark Bay Marine Park and World Heritage Area.

Zostera nigricaulis and *Z. polyclamys* are already limited in distribution to the lower southwest coast of Australia, with a further contraction of half their latitudinal range likely by 2100 (figure 4). If correct, this would restrict these species to the south coast (figure 4). Similarly, the temperate species *Thalassodendron pachyrhizum*, which is endemic to the southwest of Australia, is likely to be restricted to deeper waters and the south coast.

Herbivore responses to rising temperature. Dugongs currently graze on a variety of seagrass species across northern Australia, where herds can remove 60%–99% of the aboveground biomass and 31%–75% of belowground biomass in a single grazing trail (Marsh et al. 2011). In Shark Bay, their southern limit along the west coast of Australia (Preen et al. 1997), dugongs forage preferentially on tropical species (Burkholder et al. 2012) and can remove 50% of production in *Halodule uninervis* meadows (Masini et al. 2001). On the basis of the assumption that there will be no geographic barrier preventing a southward migration, we predict that dugongs will extend over 300 km southward into the warming water (water temp above 16°C) by 2100 (figure 4; see supplemental material for methods), perhaps initially making southward forays during warmer months. Because dugongs can feed extensively on *Amphibolis antarctica* during winter in Shark Bay, they have the ability to consume this and possibly other temperate seagrass species.

Similar to dugongs, green turtles (*Chelonia mydas*) currently form aggregations in waters north of Shark Bay (Preen et al. 1997), although resident green turtles can occur in waters as far south as Perth (32°S). Although no grazing data exist for the west coast of Australia, green turtles can consume up to approximately 200 grams dry weight per square meter per day of *Thalassia testudinum*, resulting in significant impacts on the seagrass canopy in the Caribbean Sea (Bjorndal and Jackson 2003). Although green turtles occur across a wide temperature and latitudinal range (Marquez-Guzman 1990), cooler temperate waters support lower numbers of turtles, often with nonreproductive individuals

(Marquez-Guzman 1990). We predict that warmer temperate waters will likely lead to increased turtle abundances extending nearly 400 km into southwestern Australia over the next century (figure 4), most likely leading to significant grazing on seagrasses in the region (figures 2c and 2d).

The black swan (*Cygnus atratus*) has a broad distribution throughout Australia but is common and the main macrograzer on seagrasses in estuaries of temperate Western Australia. It is a significant grazer in the Swan River Estuary near Perth, where it can remove 23% of production of *Halophila ovalis* (Choney et al. 2014). A range shift in black swans seems unlikely (figure 4) because of their current broad distribution. However, a habitat shift from wetlands to estuaries is possible, because the black swan occurs in greater abundances in estuaries in summer and autumn, when freshwater wetlands often dry out (Choney et al. 2014) and declining rainfall due to climate change is likely to further reduce the habitat value of wetlands. In this scenario, we suggest that estuaries will provide permanent water and habitat for swans, possibly leading to increased grazing pressure on estuarine seagrasses. *Halophila ovalis* is able to cope with high levels of swan grazing via compensatory growth, but only in the summer (Choney et al. 2014); therefore, any increases in grazing through the winter are likely to have a deleterious effect.

Of the suite of herbivorous fish species in northwest Australia, the marbled parrotfish *Leptoscarus vaigiensis* is among the most likely species to have an impact on seagrasses. It is common in the region (Lim et al. 2016) and is capable of consuming up to 10 times the rate of local seagrass growth in the Indo-Pacific (Unsworth et al. 2007). We predict its distribution to expand poleward approximately 500 km over the next century (figure 4; see supplemental material for methods), leading to a likely impact on seagrasses in southwest Australia. Similarly, the forktail rabbitfish *Siganus argenteus* is predicted to expand to at least Shark Bay over the next century (figure 4). However, these predictions already underestimate the expansion rates of some species, because viable breeding populations of *Siganus* spp. are now established in the temperate coastal waters near Perth, possibly because of the 2011 heatwave described above (Nic Caputi, Department of Fisheries, Western Australia, personal communication, 2014), and anecdotal evidence shows they have already started targeting temperate seagrasses such as *Posidonia australis* as food (Michael Tropiano, School of Plant Biology, University of Western Australia, personal communication, 12 October, 2015). Similarly, the tropical range-shifting *Siganus luridus* has been seen decimating temperate *Posidonia oceanica* meadows in the eastern Mediterranean (Ozvarol et al. 2011).

Fishes grazing predominantly on seagrass in temperate and subtropical seagrass meadows are rare, whereas the species diversity and abundances of omnivores, which feed predominantly on epiphytes, not seagrasses, are high (Edgar and Shaw 1995). However, we predict that the distribution of some temperate omnivore species, such as the blue weed

whiting *Haletta semifasciata,* will become restricted to the southwest corner of Australia (figure 4). Furthermore, with the possibility of more extreme range shifts for seagrass-associated fishes than those predicted by Cheung and colleagues (2012), some species endemic to temperate regions may become extinct, especially if they have specific habitat requirements or are co-dependent on other species. Increasing temperatures are therefore likely to decrease the diversity of temperate species, as well as promote the poleward expansion of tropical herbivorous fish (as we described above), which is likely to alter the number and identity of herbivorous species in temperate systems and increase consumption rates and lower the standing biomass of temperate seagrasses (figures 2c and 2d).

Although sea urchins consume significant proportions of seagrass production in some temperate ecosystems such as the Mediterranean (Alcoverro and Mariani 2002), they are not abundant in temperate Western Australian seagrass meadows (less than 1 individual per square meter), although there have been occasional reports of elevated abundances in small localized areas. *Tripneustes gratilla*, which has caused several overgrazing events in tropical Indo-Pacific (reviewed by Eklof et al. 2008), is present but in low abundances in tropical Western Australian seagrass meadows. However, "boom and bust" population cycles demonstrated by sea urchins (Eklof et al. 2008) might promote rapid expansion of populations of warm-adapted species in temperate regions, similar to the successful poleward range extension of the sea urchin *Centrostephanus rodgersii* on the east coast of Australia (Ling et al. 2009). This may lead to increased grazing rates on temperate seagrasses (figure 2c), but this is likely to occur sporadically because of those cycles.

Conclusions

Tropicalization implies a shift in species distributions and/or relative species abundances. There are likely to be winners and losers, with the likelihood of some, but certainly not all, existing species being replaced with new ones. This reconfiguration of ecosystem structure implies a potential for shifts in species interactions and/or the likely appearance of novel ecosystem configurations. For tropicalized seagrass meadows, we predict there will be changes both among the seagrasses themselves and among their associated communities, including herbivores. Although changes in climate have disrupted ecosystems and trophic interactions in the past over time scales ranging from years to millennia, the changes we are observing now are much more rapid than in previous eras (Marcott et al. 2013). These changes are particularly fast in southwestern Australia (Hobday and Pecl 2014), creating a natural experiment and an opportunity to test our predictions for seagrass systems more generally. We hypothesize that in temperate regions, the new configuration of species will not initially resemble the original temperate or tropical assemblages, and the biodiversity of seagrass meadows may increase substantially until a new equilibrium in the number of species of plants and animals

is reached. We also predict that tropicalization will lead to an increase in herbivory because of the range expansion of plant-eating fishes and megafauna (figure 2c), something already observed as a result of a recent marine heatwave on the west coast of Australia and elsewhere around the world (Vergés et al. 2014). Green turtles already occur in small numbers in the temperate west coast of Australia, but their numbers will likely increase as water temperature increases. With their narrower thermal tolerance, dugongs should take longer to make their initial seasonal forays over the 200 km of coast that lacks seagrasses between Shark Bay and the next meadows to the south, creating uncertainty regarding their rate of expansion southward.

We predict that the establishment of tropical seagrasses will likely form the next, later phase of expansion from tropicalization (figure 2d) because of the more limited dispersal abilities of seagrass seeds and fruits. Once established, clonal growth should allow meadows to gradually expand within temperate regions. The direct physiological effects of increasing temperatures may be more positive for tropical than temperate seagrass species, but temperature-related increases in plant productivity may be counteracted by increased grazing rates on seagrasses. This effect is likely to be greatest in winter months, when reduced solar radiation in temperate regions limits seagrass growth.

Currently, the food web of seagrass meadows in southwest Australia is largely based on detritus and epiphytic algae (Smit et al. 2005), with large biomass of seagrass exported to adjacent ecosystems (Hyndes et al. 2014). Ultimately, we expect this detrital-based food web to shift to one that is based more on direct consumption of seagrass. This has been shown in tropical seagrass meadows of the Indo-Pacific, where turtle populations have greatly increased, overgrazing and reducing the stature of seagrasses (Kelkar et al. 2013), which is likely to have flow-on impacts for seagrass-associated fish and invertebrates and, importantly, the juveniles of economically important fish and invertebrate species that rely on seagrasses as habitat (Lal et al. 2010). For example, reduced food availability for subadult western rock lobster *Panulirus cygnus*, which forage in temperate seagrass meadows in southwest Australia (MacArthur et al. 2011), could reduce harvests in a commercial fishery valued at approximately AU$200 million. Also, increased consumption of seagrasses will likely result in less detrital material flowing into other coastal ecosystems (e.g., beaches) that rely on that material as a habitat and/or food and nutrient source (Hyndes et al. 2014). This predicted reduced detrital outflow would, have flow on effects on coastal systems well beyond the boundaries of seagrass meadows.

If our predictions for the west coast of Australia are accurate, there are likely to be far-reaching consequences of the tropicalization of temperate seagrasses there and elsewhere that will affect the many valuable ecosystem services they provide. There is clearly a need to evaluate the accuracy of these predictions as the symptoms of tropicalization become more visible and to experimentally test a range of scenarios

to inform management of how to adapt to the impacts of tropicalization on the functioning of temperate seagrass meadows, not only in Australia but also in seagrass meadows around the world.

Acknowledgments

Supplemental material

The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biw111/-/DC1.*

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