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Report

Seaweed Communities in Retreat from Ocean Warming

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Summary

In recent decades, global climate change [1] has caused profound biological changes across the planet [2–6]. However, there is a great disparity in the strength of evidence among different ecosystems and between hemispheres: changes on land have been well documented through long-term studies, but similar direct evidence for impacts of warming is virtually absent from the oceans [3, 7], where only a few studies on individual species of intertidal invertebrates, plankton, and commercially important fish in the North Atlantic and North Pacific exist. This disparity of evidence is precarious for biological conservation because of the critical role of the marine realm in regulating the Earth's environmental and ecological functions, and the associated socioeconomic well-being of humans [8]. We interrogated a database of >20,000 herbarium records of macroalgae collected in Australia since the 1940s and documented changes in communities and geographical distribution limits in both the Indian and Pacific Oceans, consistent with rapid warming over the past five decades [9, 10]. We show that continued warming might drive potentially hundreds of species toward and beyond the edge of the Australian continent where sustained retreat is impossible. The potential for global extinctions is profound considering the many endemic seaweeds and seaweed-dependent marine organisms in temperate Australia.

Results and Discussion

The sparse evidence for climate-driven shifts in marine species arises mainly from the scarcity of data sets with which to measure change [3, 6]. Herbarium records collected and kept for up to 3 centuries have recently been discovered as an important source of historical information on the presence and phenology of terrestrial plants (e.g., flowering land plants, [11]) where no other empirical data existed [12]. Macroalgae (seaweeds) are the ecological foundations of most near-shore temperate marine ecosystems. Their diversity supports a multitude of other taxa and provides essential ecosystem services in the coastal zone [13]. Like botanists working in terrestrial habitats, phycologists have also preserved marine macroalgae in herbaria for decades (see Figure S1 available online). Yet, with few exceptions (e.g., [14, 15]), these collections have only been used as taxonomical references and not as historical archives. We use past herbarium records of temperate marine macroalgae to assess recent changes in the distribution of communities and species in the richest algal flora in the world [16].

We found that, on both the Indian and Pacific Oceans sides of the Australian continent, macroalgal communities in the southern (poleward) part of the tropical-temperate transition (east coast: 33°–36° S; west coast: 30°–33° S) progressively came to resemble past macroalgal communities farther north (toward the equator; east: 30°–33°S; west: 27°–30°S) (Figure 1B). The change was of similar magnitude on both coasts, despite these being separated by ~3,500 km and belonging to different biogeographic provinces [17], albeit greatest on the east coast where the dissimilarity between assemblages was reduced 42% by 1990–2009. This is compelling evidence for rearrangement of entire local communities rather than mere shifts of a few individual species. In addition to a poleward shift of temperate species (see below), it is possible that the increasing similarity to communities from warmer waters is also a consequence of poleward range extensions of more tropical species [18, 19]. Although a shift in the distribution of single species, or a set of closely related species, is in itself serious, changes to whole communities can have negative impacts on ecosystem function [20, 21] that might cascade up through the trophic web [22, 23].

We also found poleward shifts in the distribution of several temperate species on both coasts (Figure 1C): 85% (6 of 7) of the species passing our selection criteria on the east coast and 56% (25 of 45) on the west coast were only recorded farther poleward in 1990–2009 compared to 1940–1960. Thus, the median shift across all 52 species was poleward (two-tailed Wilcoxon's matched-pairs signed-ranks test: $W_+/W_- = 356/1{,}129$, n = 52, p < 0.001), and the median poleward shift in range limits of 1.92° latitude on the east coast was greater than the 0.46° shift on the west coast (Mann-Whitney U-test, $U_{45,7} = 249$, p = 0.028). It is important to take species identity into account when considering the realized community-wide impacts of such shifts. For example, several large and common species retreated south (Table S1). These seaweeds provide food and shelter for thousands of associated animal and plant species, and their loss or replacement could have substantial negative implications for ecological function and biodiversity [13, 24].

Some species (15% and 44% on the east and west coasts, respectively) shifted north toward the equator, although

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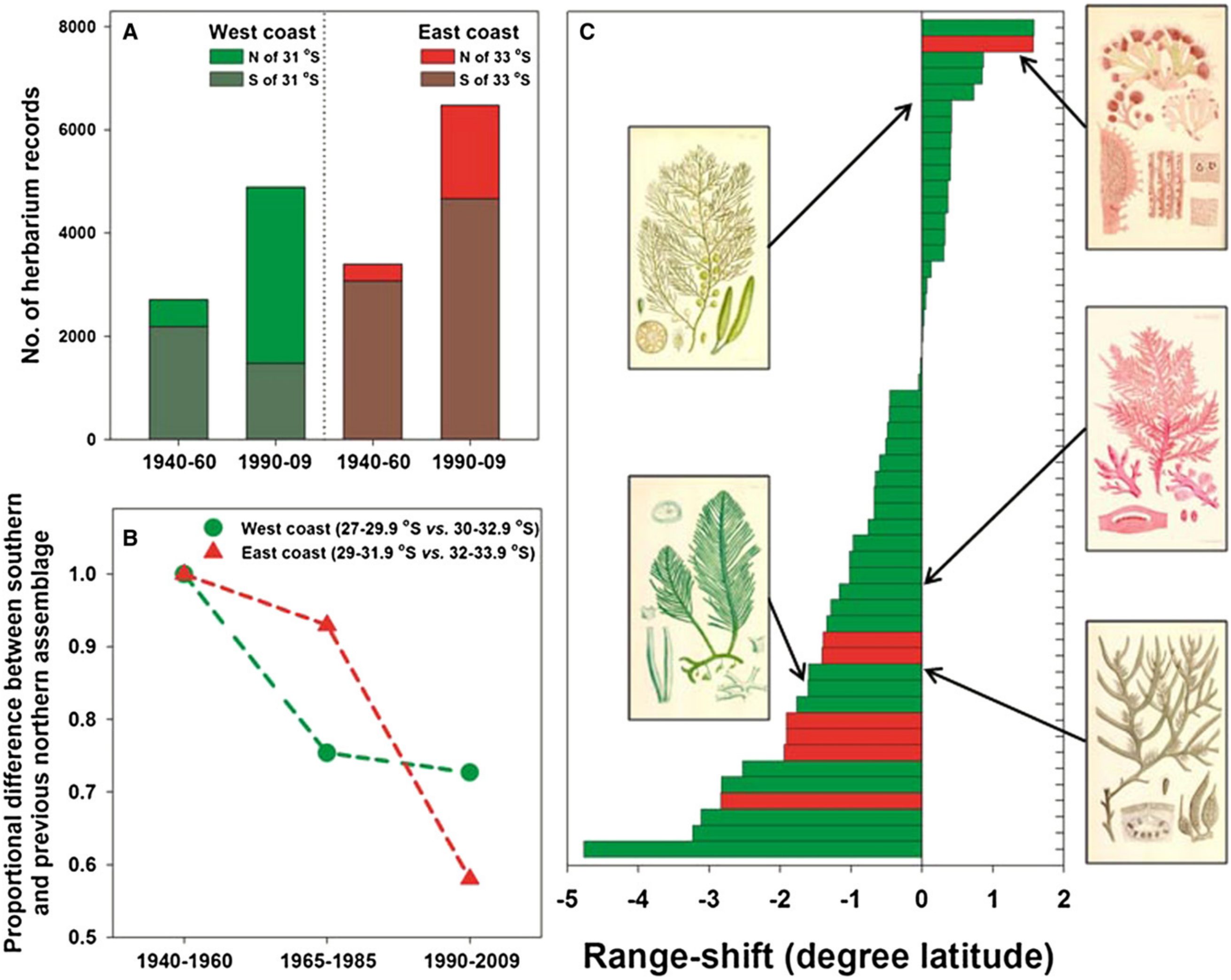

Figure 1. Poleward Shifts in Temperate Macroalgae in Australia Assessed from Herbarium Records

(A) Sampling intensity (records from Australia's Virtual Herbarium) on the west and east coasts of Australia during 1940–1960 and 1990–2009.

(B) Multivariate dissimilarity in assemblage structure (proportional Sorensen dissimilarity) between past northern and subsequent southern floras.

(C) Shift in northern range limits of temperate macroalgae in Australia from 1940–1960 and 1990–2009. Inserts: Color plates of selected algae from Henry Harvey's *Phycologia Australica* (1858–1863); from top left, *Caulocystis uvifera* and *Caulerpa flexilis* and top right, *Martensia fragilis*, *Pterocladia lucida*, and *Scytothalia doryocarpa* (source: http://users.ugent.be/phycology/harvey). A complete list of species can be found in Table S1 (see G and H).

northward shifts were not as pronounced in magnitude as the southward shifts (Figure 1C). Similar, seemingly counterintuitive shifts have also been observed elsewhere [18, 19]. Several mechanisms can account for this pattern, including competitive release with the range contraction of competitors [21] or human-assisted dispersal against prevailing currents [25]. The data set available here cannot distinguish between these alternate hypotheses, but they suggest that not all species' distributions are primarily a function of temperature or climate, adding to the complexity of community-wide responses.

The median rate of poleward retreat in seaweed distribution was more than twice as fast on the east (1.67° latitude $^{\circ}C^{-1}$) than on the west coast (0.71° latitude $^{\circ}C^{-1}$), perhaps suggesting that rates of biological change might increase at higher rates of physical change. Considering the current northern limits of macroalgal species on the east and west coasts (Figure 2A), and assuming simple linear relationships, this implies that 77 species on the east coast, and 28 species on the west coast, could be displaced beyond the margins of the continent per 1°C of temperature increase (Figure 2B). Given projected sea surface temperature increases of between 1°C by 2030 and 3°C by 2070 [26], these rates imply an additional poleward shift of 0.7° to 2.1° (~64–192 km) and 1.7° to 5.0° latitude (~150–450 km) by 2030 and 2070 and the potential loss of 100–350 species over the next 60 years (Figure 2B). This corresponds to as much as ~25% of the current southern seaweed flora (Figure 2B), of which as much as a quarter or more is endemic to Australia [27]; even if our simple back-of-the-envelope calculation is an overestimate, it implies a considerable risk of substantial loss of global species diversity. In contrast, only one macroalgal species to date has been reported globally extinct [28]. Still, our estimated potential species loss could be conservative because it does not consider hundreds of species currently restricted to the south coast or species that might have been buffered thus far from increasing temperatures via physiological acclimatization. Acclimatization is,

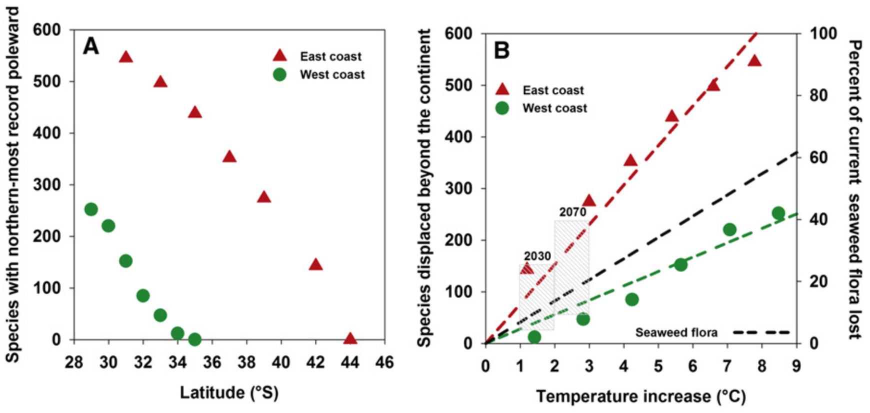

Figure 2. Current Distribution Limits and the Frequency of Species Potentially Displaced Beyond the Continental Margin Given Different Warming Scenarios

(A) Number of species with their current (1980–2009) distribution limit (northern-most record) poleward (south) of different latitudes. The species richness of the east coast is particularly high because it captures two biogeographic provinces: Peronia toward the north and Maugea toward the south around Tasmania. The west coast is centered in the Flindersian province [17].

(B) Species displaced beyond the continent (~44°S and ~35°S on the east and west coasts—red and green symbols, respectively) given different temperature increases and assuming the median range shifts on each coast (cf. Table S1G and S1H) are representative for all populations. The red and green lines indicate linear regressions through the origin, which yielded species displacement rates of 77 ($R^2 = 0.96$) and 28 ($R^2 = 0.94$) species °C^{-1} temperature increase for the east and west coasts, respectively. The black line indicates the projected relative total species loss (out of 1,454 species). The shaded boxes indicate the range of current temperature projections for 2030 and 2070 [26].

however, energetically costly [29] and is often achieved at the expense of processes that maintain reproduction and growth [29, 30]. Projected increases in temperature will therefore continue to reduce population resilience [30] and increase the likelihood of sudden range shifts in synergy with other stressors such as nutrient input and coastal development [6, 31]. Indeed, change does not tend to occur gradually but abruptly as physiological and ecological thresholds are exceeded [32–34].

Reconstructing past distributions from historical records is often challenging [12, 35], and herbarium records can provide biased information if particular taxa have been insufficiently or unequally recorded [11]. However, if carefully considering assumptions and limitations, this should not preclude their use because alternative historical records often do not exist [35]. We are assuming here that the collections reflect real species distributions and that rates of change in a flora can be estimated from a small, yet unbiased subset of its species. To increase the robustness of these assumptions, we selected species entirely based on their recorded frequencies. Still, our estimates of poleward range contractions are probably conservative because any potential sampling biases should have reduced the magnitude of observed southern shifts; substantially more specimens were recorded to the north during the latter period of comparison (Figure 1A), thus potentially biasing the data to detecting range shifts toward the equator. Importantly, the consistency of the response on two biogeographically distinct [17] but similar coasts where the magnitude of change corresponds to the pattern of documented warming (southwest and southeast temperatures increasing of 0.013°C and 0.023°C year^{-1}, respectively, [9, 10]) is compelling evidence that the overall results reflect a real and ecosystem-wide rearrangement of macroalgal communities and poleward contraction in the distribution of temperate species in Australia.

Ocean warming is rearranging ecologically important species in subtidal communities and driving temperate species toward the edge of the Australian continent, beyond which there is no refuge. Although natural decadal cooling and warming cycles, or physiological adjustments, might enable species to maintain or reexpand their ranges temporarily [21, 30], the predicted rate and strength of warming in the coming decades is likely to force many retreating species beyond the limits of available habitat at the southern margins of the continent. This is analogous to, but because of the geographic extent more serious than, high-altitude species contracting to extinction as suitable microclimates disappear from mountaintops [36]. The implied increase in global extinctions is profound because 25% or more of all macroalgal species in the world are found only in southern Australia [27], and these marine habitats maintain equally unique fish and invertebrate communities [6].

Experimental Procedures

From a marine perspective, Australia is a unique continent because both the west and east coasts run north-south and are bounded by distinct, major warm-water currents that both flow poleward [9, 10]. We assessed changes in macroalgal assemblages for the west and east coasts separately (here defined as west and east of 126°E and 146°E, respectively) because they belong to separate biogeographic provinces and have distinct algal floras [17]. We focused on the tropical-temperate transition on both coasts because we anticipated greatest changes in the distribution of temperate species near their warm range limits and because the east-west orientation of the south coast would obscure latitudinal patterns of shifts farther south. This transition is located slightly farther south (~2° latitude, ~180 km) on the east than on the west coast (Figure S1).

We obtained distribution data from records in Australia's Virtual Herbarium (AVH, http://www.chah.gov.au/avh/). AVH is a publically available database containing the location and year of collection for a substantial part of all plant specimens lodged in Australia's nine major state herbaria. At the time of query (May 2009), AVH included ~22,000 records of macroalgae representing a total of 897 species from the east and west coast, and the number of specimens recorded (a proxy for sampling effort) was similar on both coasts (Figure S1). Importantly, more records were collected between 1990–2009 (the latter period of comparison) than between 1940–1959 (the earlier period of comparison), emphasizing that patterns of southward (poleward) shifts were not biased by low recollection effort in recent times. Moreover, although inconsistent identification can be a potential source of error associated with natural history collections [12], this would be minimal for herbarium records from temperate Australia as a result of the monumental efforts of algal taxonomist Professor Bryan Womersley (1922–2011) over his >60 year career at the State Herbarium of South Australia.

We pooled species records from the east and west coasts into 20 year periods for analyses, where the earliest period encompassed the onset of increasing collection effort (1940 onward; Figure S1) and accelerated ocean warming in southwestern [9] and southeastern [10] Australia. Our choice of time-period size was a pragmatic trade-off between time required to accumulate enough observations for robust comparisons between time periods and the need to keep the environmental changes within each period small [35]. The analyses of shifts were also restricted to species with at least five records in the later period to minimize the risk of shifts being driven by single collections that were not representative of the species' distribution limits. Only a small subset of species passed these selection criteria, particularly on the east coast; even if the subsample of species is unbiased, being based purely on collection characteristics, its representativeness of the flora should be interpreted with caution. Sensitivity analyses using 10, 20, and 30 year periods and species with at least five or ten records showed that either fewer or more species passed our selection criteria for inclusion in the analyses depending on the length of the period and the required minimum number of records. However, although the absolute number of observed shifts depended on the length of the period and records thresholds, responses of individual species, and the overall direction and magnitude of shifts, were predominantly consistent (Table S1). Shifts greater than 5° latitude north or south were likely due to insufficient recording or identification errors, and these species were excluded from the analyses. Such shifts were relatively few (<10% of all shifts recorded) and showed no pattern of direction.

We used Sorensen's similarity index for presence and absence of all species recorded to compare northern (east: 30°S–33°S; west: 27°S–30°S) and southern (east: 33°S–36° S; west: 30°S–33°S) communities in subsequent periods for 1940–1959, 1965–1984, and 1990–2009. From Sorensen's similarities we calculated the multivariate distance between the centroids of all six space-time communities on each coast and standardized values to the difference between northern and southern communities in 1940–1960 on each coast.

The resulting plot (Figure 1B) shows the multivariate distance between the northern communities in 1940–1960 and 1965–1985 and the southern communities in 1965–1985 and 1990–2009, respectively, relative to the difference between north and south in 1940–1960.

To test for range shifts in individual species, we listed all the temperate species that in 1940–1959 had their northern-most herbarium record north of 31°S on the west coast and 33°S on the east coast and that had at least five records again in 1990–2009. We calculated range shift as the difference in latitude between the northern-most records in each time period.

Supplemental Information

Supplemental Information includes one figure and one table and can be found with this article online at doi:10.1016/j.cub.2011.09.028.

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