








Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming

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Abstract

Aim: Understanding the relative importance of climatic and non-climatic distribution drivers for co-occurring, functionally similar species is required to assess potential consequences of climate change. This understanding is, however, lacking for most ecosystems. We address this knowledge gap and forecast changes in distribution for habitat-forming seaweeds in one of the world's most species-rich temperate reef ecosystems.

Location: The Great Southern Reef. The full extent of Australia's temperate coastline.

Methods: We assessed relationships between climatic and non-climatic environmental data known to influence seaweed, and the presence of 15 habitat-forming seaweeds. Distributional data (herbarium records) were analysed with MAXENT and generalized linear and additive models, to construct species distribution models at 0.2° spatial resolution, and project possible distribution shifts under the RCP 6.0 (medium) and 2.6 (conservative) emissions scenarios of ocean warming for 2100.

Results: Summer temperatures, and to a lesser extent winter temperatures, were the strongest distribution predictors for temperate habitat-forming seaweeds in Australia. Projections for 2100 predicted major poleward shifts for 13 of the 15 species, on average losing 78% (range: 36%–100%) of their current distributions under RCP 6.0 and 62% (range: 27%–100%) under RCP 2.6. The giant kelp (*Macrocystis pyrifera*) and three prominent fucoids (*Durvillaea potatorum*, *Xiphophora chondrophylla* and *Phyllospora comosa*) were predicted to become extinct from Australia under RCP 6.0. Many species currently distributed up the west and east coasts, including the dominant kelp *Ecklonia radiata* (71% and 49% estimated loss for RCP 6.0 and 2.6, respectively), were predicted to become restricted to the south coast.

Main conclusions: In close accordance with emerging observations in Australia and globally, our study predicted major range contractions of temperate seaweeds in coming decades. These changes will likely have significant impacts on marine biodiversity and ecosystem functioning because large seaweeds are foundation species for 100s of habitat-associated plants and animals, many of which are socio-economically important and endemic to southern Australia.

KEYWORDS

climate change, kelp forests, macroalgae, range contraction, species distribution models, temperate reefs

1 | INTRODUCTION

Shifts in the geographic distribution of species, in response to increasing temperature, have been reported from virtually all ecosystems on Earth (Parmesan & Yohe, 2003; Poloczanska et al., 2013; Thomas et al., 2004; Wernberg, Russell, Thomsen et al., 2011). This is not surprising as temperature has long been recognized as a major driver of broad-scale species distributions (Brown, Stevens, & Kaufman, 1996; Gaston, 2009; Hedgpeth, 1957; van den Hoek, 1982b; Sunday, Bates, & Dulvy, 2012). Shifts in the distribution of habitat-forming species are expected to compromise the biodiversity and functioning of ecosystems because these species provide food and shelter, and reduce environmental stress for other species, contributing disproportionately to the cycling of energy and matter (Halpern, Silliman, Olden, Bruno, & Bertness, 2007; Thomsen et al., 2010). Consequently, habitat-forming species are important conservation targets (Halpern et al., 2007; Hastings et al., 2007) and predicting their possible shifts in distribution under global climate change is of particular importance.

Advances in ecological theory, spatial modelling, remote sensing techniques, statistical methods and increases in computational power have led to great progress in the capacity to model and predict the distribution of organisms. Species distribution models (SDMs) link the occurrence of an organism to climatic and other spatially explicit environmental variables (Austin, 2002; Guisan & Zimmermann, 2000). SDMs are powerful tools to forecast the effects of global change on macro-ecological patterns. For example, SDMs have been used to track trends in biodiversity at continental scales, to select protected areas, to explain trends in invasions of alien species and in a wide range of biogeographic studies (e.g., Embling et al., 2010; Lobo, Lumaret, & Jay-Robert, 2002; Recio & Virgós, 2010; Rissler, Hijmans, Graham, Moritz, & Wake, 2006). However, in contrast to numerous studies from terrestrial ecosystems, examples of modelling and forecasting species distribution patterns for marine organisms are far fewer, in particular for seaweeds, even though they are key habitat-formers in many coastal ecosystems (Lüning, 1990) and under acute pressure from anthropogenic activities (Filbee-Dexter & Wernberg, 2018; Krumhansl et al., 2016; Wernberg, Russell, Moore et al., 2011). A few exceptions include modelling distribution of subtidal kelps (Assis, Lucas, Bárbara, & Serrão, 2016; Bekkby, Rinde, Erikstad, & Bakkestuen, 2009; Franco et al., 2017; Gorman, Bajjouk, Populus, Vasquez, & Ehrhold, 2013; Raybaud et al., 2013), invasive seaweeds (Báez et al., 2010; Tyberghein et al., 2012), threatened fucoids (Jueterbock et al., 2013; Martínez, Viejo, Carreño, & Aranda, 2012) and red seaweed assemblages (Gallon et al., 2014).

The marine flora of Australia's Great Southern Reef (Bennett et al., 2016) is one of the most species rich in the world, with many endemic species and genera (Bolton, 1994; Phillips, 2001). While there are several possible contributing factors, this mega-diversity is primarily attributed to Australia's long geological history, historical isolation, stable climate, lack of mass extinction events and extensive reef areas (Kerswell, 2006; Phillips, 2001). Both the east and west coasts are bound by poleward-flowing warm currents, the East

Australian Current (EAC) and the Leeuwin Current (LC), respectively (Wernberg, Thomsen et al., 2013). Consequently, from tropical (north) to temperate (south) Australia, there is a consistent latitudinal temperature gradient with associated shifts in biogeographic provinces (Waters et al., 2010; Wernberg, Thomsen et al., 2013). The Southern Ocean waters around Victoria and Tasmania experience regular upwelling and are significantly cooler than other temperate regions in Australia (Ridgway, 2007). The waters off both eastern and western Australia have experienced some of the highest rates of ocean warming in the world (Hobday & Pecl, 2014). Along these coasts, sea surface temperatures have increased between 0.5 and 1.5°C in the last 50 years (Pearce & Feng, 2007; Ridgway, 2007) and this increase has already caused poleward shifts of temperate species (Last et al., 2011; Poloczanska et al., 2013; Wernberg, Russell, Thomsen et al., 2011). Moreover, the warming trend is predicted to continue another 1–3°C in the coming 50–70 years (Poloczanska et al., 2007), and further poleward shifts are expected to follow in conjunction with an increase in occupancy of tropical and/or generalist flora and fauna (Cheung et al., 2012; Hyndes et al., 2016; Molinos et al., 2015; Vergés et al., 2014).

Evidence that Australian seaweeds are shifting poleward is increasing (Johnson et al., 2011; Smale & Wernberg, 2013; Wernberg, Russell, Thomsen et al., 2011; Wernberg, Bennett et al., 2016) in agreement with observations of ongoing contractions of macroalgae around the world (Díez, Muguerza, Santolaria, Ganzedo, & Gorostiaga, 2012; Filbee-Dexter, Feehan, & Scheibling, 2016; Nicastró et al., 2013; Tanaka, Taino, Haraguchi, Prendergast, & Hiraoka, 2012). For example, declines of the cool-temperate giant kelp *Macrocystis pyrifera* in Tasmania have been associated with increasing temperatures and nutrient limitation linked with incursion of warm, low-nutrient EAC water (Johnson et al., 2011). Similarly, several large fucoids and kelp (*Durvillaea potatorum*, *Phyllospora comosa*, *Scytothalia dorycarpa* and *Ecklonia radiata*) have been declining and shifting southwards on the east and west coasts (Smale & Wernberg, 2013; Valentine & Johnson, 2004; Wernberg, Russell, Moore et al., 2011; Wernberg, Bennett et al., 2016). High seawater temperatures have been shown to lower the resilience of *E. radiata* kelp forests in Western Australia, reducing their tolerance to additional perturbations such as storms (Wernberg et al., 2010), and an extreme marine heatwave led to substantial loss of canopy cover across several hundred kilometres (Smale & Wernberg, 2013; Wernberg, Smale et al., 2013; Wernberg, Bennett et al., 2016). Such substantial changes in canopy cover would have severe implications for the whole coastal ecosystem, as these species are habitat-formers which provide three-dimensional structure, food and environmental conditions supporting a broad array of associated organisms (Coleman, Vytopil, Goodsell, Gillanders, & Connell, 2007; Connell, 2003; Ling, 2008; Tuya, Wernberg, & Thomsen, 2008; Wernberg & Goldberg, 2008). These temperate canopy-forming seaweeds are therefore bioindicators of the integrity of Australian reef ecosystems which support a multitude of recreational, commercial and scientific interests (Bennett et al., 2016; Coleman & Wernberg, 2017; Poloczanska et al., 2007; Wernberg, Krumhansl, Filbee-Dexter, & Pedersen, 2018).

In this study, we developed SDMs for 15 ecologically important species of habitat-forming seaweeds in temperate Australia. Our aims were to (1) increase our understanding of the relative importance of climatic and non-climatic environmental conditions for the biogeography of ecologically relevant seaweeds and (2) to predict their future distribution, illustrating the magnitude of likely changes in response to ongoing warming of Australia's temperate waters.

2 | MATERIALS AND METHODS

2.1 | Environmental predictor variables

All predictor data were obtained from the Remote Sensing Division of the Commonwealth Scientific and Industrial Research Organisation (CSIRO, Australia) as part of the information managed for the National Marine Bioregionalisation project of the Australian Government (<http://www.environment.gov.au/coasts/mbp/imcra/nmb.html>). We extracted environmental data known to influence the distribution of seaweeds (reviewed in Lüning, 1990; Lobban & Harrison, 1994),

retaining only those for which pairwise Pearson correlations were less than 0.85, a threshold indicative of excessive autocorrelation between pairs of predictors (Elith, Kearney, & Phillips, 2010). Variables representing extreme conditions of ecophysiological relevance were preferred (e.g., maximum and minimum monthly means were used rather than intermediate values). Predictor variables included mean summer (January) and winter (July) sea surface temperatures (SSTs) from one decade of data (1993–2003), annual mean concentrations of major macronutrients (dissolved Nitrogen and Phosphorous) and salinity from 1990 to 2000 (Table 1, Figure 1, Appendix S1). We also extracted data for monthly mean pelagic primary productivity for July and October peaks (available for 2003), as it integrates biologically relevant responses to nutrient concentrations, available light and water transparency, identifying coastal regions of favourable conditions for seaweed growth. Finally, we considered averaged surface current strength from 2 months (April and October, means from 1990 to 2000) with contrasting current strengths reflecting variability in forces that could affect seaweed dispersal, settlement and recruitment (Coleman et al., 2011).

TABLE 1 Environmental predictors showing their units, corresponding period of time, data source, and main patterns around Australia

Environmental predictors	Units	Time period	Source	Main pattern around Australia
SST January (summer)	°C	1993–2003 monthly mean	NOAA ^a satellites	Latitudinal increase northwards. Warming in the east coast due to EAC
SST July (winter)	°C	1993–2003 monthly mean	NOAA ^a satellites	Latitudinal increase northwards. Warming in central Western Australia and South Australia due to LC
Dissolved Nitrogen	μM	1990–2000 annual mean	CARS ^b	Low in the tropics. High in Southern Ocean where primary production is light and iron limited
Dissolved Phosphorus	μM	1990–2000 annual mean	CARS ^b	Low in the tropics. High in Southern Ocean. Reflects localized terrestrial inputs
Primary Productivity July	mg C m ⁻² d ⁻¹	2003 monthly mean	Global observations of ocean colour data from MODIS ^c	Dominated by mesoscale processes (currents, land run-off, depth and tidal mixing)
Primary Productivity October	mg C m ⁻² d ⁻¹	2003 monthly mean	Global observations of ocean colour data from MODIS ^c	Dominated by mesoscale processes (currents, land run-off, depth and tidal mixing)
Salinity	‰	1990–2000 annual mean	CARS ^b	High in warm-temperate areas. Low in the tropics due to high precipitation and run-off. Increases in large embayments
Surface Currents October	m/s	1990–2000 monthly mean	Geostrophic currents derived from annual and semi-annual temperature and salinity cycles from CARS ^b	EAC main boundary current flowing South. Regional variations reflecting fronts, boundary currents and eddy fields
Surface Currents April	m/s	1990–2000 monthly mean	Geostrophic currents derived from annual and semi-annual temperature and salinity cycles from CARS ^b	EAC main boundary current flowing South. Western LC flowing south. Regional variations reflecting fronts, boundary currents and eddy fields

EAC, East Australian Current; LC, Leeuwin Current.

^aNOAA: US national oceanographic and atmospheric administration at 1° resolution.

^bCARS: CSIRO Atlas of Regional Seas, means in CARS are calculated from available oceanographic data: ship-based conductivity, temperature and depth sensors (CTD) and hydrology casts from the CSIRO marine archives and the NOAA World Ocean Database 98 (Ridgway, Dunn, & Wilkin, 2002) at 0.5° resolution.

^cPrimary Production Estimates (daily carbon fixation from the surface to the bottom of the euphotic zone) from the moderate resolution (0.2°) imaging spectroradiometer (MODIS) of the USA National Aeronautics and Space Administration (NASA) using the Behrenfeld–Falkowski Vertical Generalised Production Model (Behrenfeld & Falkowski, 1997), SOURCE: (Hayes, Sliwa, Migus, McEnulty, & Dunstan, 2005).

Ocean cells not contiguous with land areas and deeper than 50 m were excluded from the environmental training grid because they are outside the potential seabed habitat for large macroalgae. The Geospatial Data Abstraction Library (GDAL, <http://www.gdal.org/gdalwarp.html>) using the Bilinear Resampling (Metz, Rocchini, & Neteler, 2014; Tyberghein et al., 2012; Vazquez, Perry, & Kilpatrick, 1998) was the preferred method to downscale the environmental gradient (of a minimal resolution of 0.5° , e.g., CSIRO CARS, Table 1) to the resolution of the species distributional records of 0.2° (see below). Additionally, we also considered the Nearest Neighbour correction (Neteler, 2010), if software specific error issues were detected, that is, MODIS Reprojection Tool software (MRT) was used instead of GDAL.

2.2 | Target species and records

We targeted 15 species of habitat-forming furoid (13 species) and laminarian (2 species) seaweeds (Table 2), representing all major

taxa and historical and current distribution patterns around temperate Australia within these groups (Figures 2, 3 and 4). Species distributions were inferred from presence-only records lodged in the Australian Virtual Herbarium (www.sapac.edu.au/avh/), a public database which comprises >90,000 records—the most complete and up-to-date inventory of Australian seaweeds. As of 14 September 2009, there were 3,370 individually georeferenced records for the 15 target species, dated from 1844 onwards, but mostly collected after the 1950s. Each record corresponded to a specimen deposited in the state herbaria of Adelaide (South Australia), Brisbane (Queensland), Canberra (Australian Capital Territory), Darwin (Northern Territory), Hobart (Tasmania), Melbourne (Victoria), Perth (Western Australia) and Sydney (New South Wales). All records were downloaded and checked for taxonomic consistency, and names updated to follow current nomenclature according to AlgaeBase (Guiry & Guiry, 2016). We checked the position of every presence record in ArcGIS® 10.3.1. software

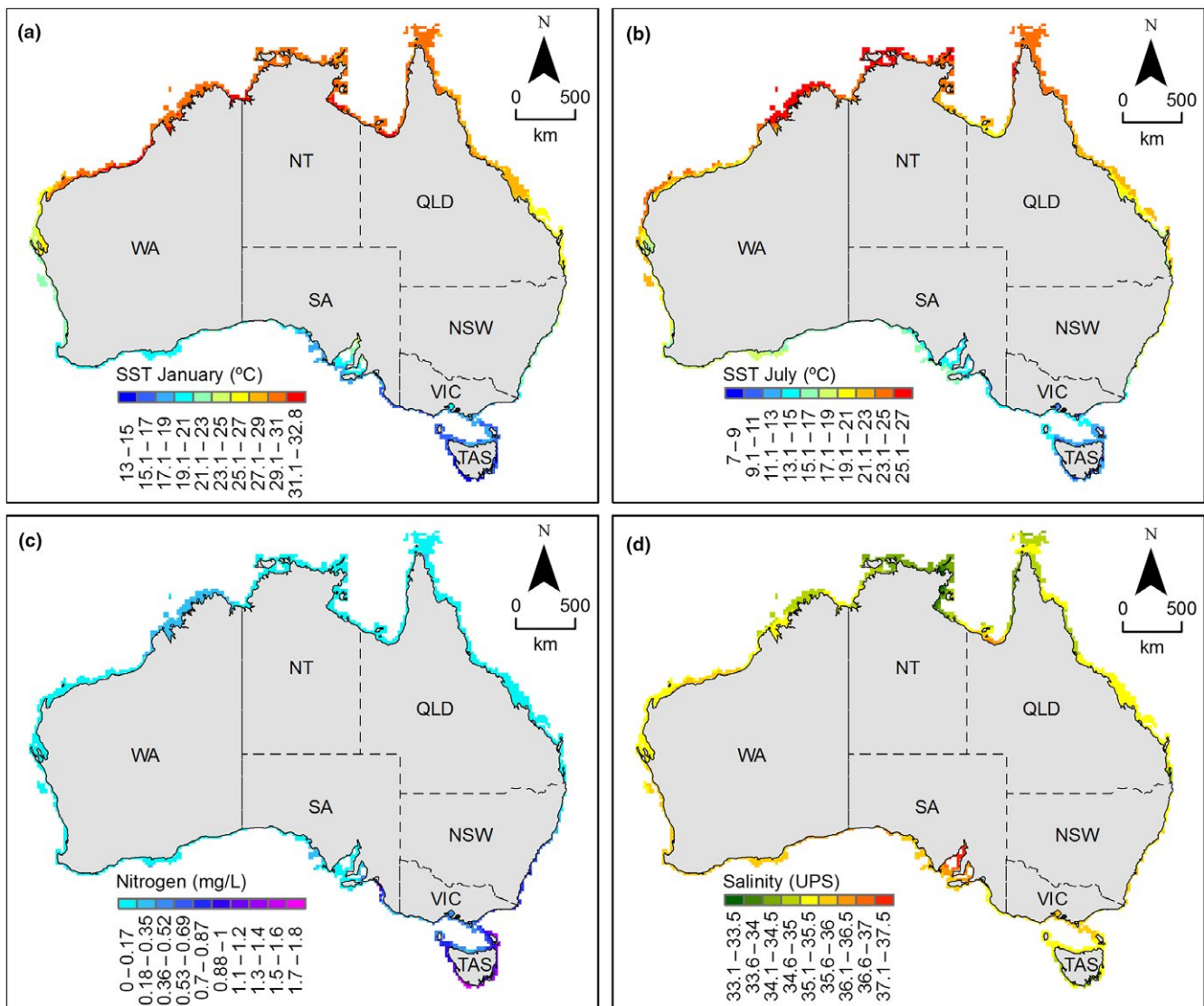


FIGURE 1 Mean Sea Surface Temperature of (a) January (SST January) and (b) July (SST July), (c) Mean Annual Dissolved Nitrogen, and (d) Mean Annual Salinity, in Australian waters. See Appendix S1 for distribution maps of additional environmental variables [Colour figure can be viewed at wileyonlinelibrary.com]

(ESRI, Redlands, CA, USA) and Google Earth (<https://earth.google.es/>) to delete or re-allocate those erroneously located on the littoral fringe. A final resolution of 0.2° reflects realistically that of the distributional records after this correction. A few cells contained repeated records, that is, more than one presence, that were omitted and converted to a single presence for data modelling (see below).

2.3 | Data modelling

We first modelled the present distribution of each species with Maximum Entropy Modelling using the software MAXENT v3.3.3, given that herbarium records do not include absences (Phillips, Anderson, & Schapire, 2006; Phillips, Dud, & Schapire, 2004). Maximum entropy modelling results in better model performance for presence-only data than alternative approaches by comparing the actual species distribution pattern with background points of maximum entropy distribution (Elith et al., 2010, 2011). Nevertheless, as the choice of statistical modelling method may affect the selection of the significant predictors, we supplemented the MAXENT analyses with generalized linear (GLM) and additive (GAM) models using the R package BIOMOD2 (Thuiller, 2003; Thuiller, Lafourcade, Engler, & Araújo, 2009). These are regression-like approaches that rely on randomly generated pseudo-absences for areas of absence of the species, when real zeros are not available (Senay, Worner, & Ikeda, 2013). To select the most parsimonious models, that is, models explaining most of the seaweed distribution data with the least possible environmental predictors, we used BIOMOD2 stepwise variable selection procedures based on the Bayesian information criterion (BIC). To allow comparison with MAXENT procedures, the full background points (1,560) along the temperate and tropical coastlines of the Australian continent and Tasmania were considered as pseudo-absences in GLMs and GAMs. To check for potential over-fitting in this procedure, that is, inflated absence points, five sets of 600 pseudo-absences were also generated along this area, and for cold-temperate species appearing around the south-eastern corner of Australia (*Macrocystis pyrifera*, *Durvillaea potatorum*, *Xiphophora chondrophylla* and *Phyllospora comosa*), the modelling was repeated excluding tropical areas and 300 pseudo-absences were generated for this smaller area. After running these models, we considered as significant predictors those suggested with high consensus among the different approaches and re-ran MAXENT with these significant predictors to construct the final predictive models.

Parsimonious models based on biological knowledge of the species are generally recommended for predictive purposes (Araújo & Guisan, 2006; Austin, 2002; Elith et al., 2010). Consequently, to further control for potential over-fitting, the statistical modelling above was guided by prior ecological knowledge (Araújo & Guisan, 2006; Austin, 2002). We investigated the shape of the response curves by plotting the frequency of presences of the target species at different intervals of the environmental predictors (Figure 2, others not shown). Settings were adjusted accordingly, using linear and

quadratic features in MAXENT (Appendix S2) and GLMs (setting as “simple”) (Elith et al., 2010), and restricting GAM knots to 3 ($k = 3$) when fitting GAMs (Hastie, 1991).

2.4 | Model performance

Model accuracy was tested using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot, as a measure that does not rely on any threshold of presence. We used the software included in the MAXENT package to calculate AUCs for the models including all predictors (full models) and the whole dataset, and for datasets obtained using internal (data-splitting) validation (Fielding & Bell, 1997; Guisan & Zimmermann, 2000). We performed 10 iterations using 70% of the herbarium data for model training and 30% for testing. AUCs for the final models, that is, reduced models including only the significant variables used in predictions, are also provided. Model accuracy of supplementary model algorithms used to confirm variable selection was additionally assessed by calculating AUC values for GLMs and GAMs with the R package BIOMOD2 (Thuiller et al. 2016).

Additionally, several threshold-dependent estimates of accuracy were calculated with BIOMOD2 for MAXENT, GLM and GAM full models. We checked the correct and incorrect classification of test data (30%) by calculating the ‘Sensitivity’ of the models, here defined as the ratio of corrected classified presences; the ‘Specificity’, that is, ratio of corrected classified absences; and the Kappa coefficients (k). We also checked that the final variables included in the model were the same before and after the data-splitting procedure irrespectively of the statistical model used.

2.5 | Projections

For species with distributions strongly related to temperature (all but two species), the final reduced models constructed by MAXENT were used to project future distributions from projected temperature increases. Of the four available Representative Concentration Pathways (RCPs) (IPCC 2014), 2.6 and 6.0 were chosen as they have minimal redundancy between them and represent, respectively, the most optimistic climate change scenario assuming low greenhouse gas concentration levels by the end of this century (RCP 2.6) and a stabilization at medium levels (RCP 6.0). The monthly maximum and minimum averaged Sea Surface Temperatures for 2100 under these two scenarios were obtained from the Bio-ORACLE repository (Assis et al., 2018). Layers, at a resolution of 5 arcmin (approximately 0.08°), were cut to temperate Australia and added as projection layers in MAXENT to construct the maps of projected habitat suitability in future warming scenarios (Phillips et al., 2006). GLMs and GAMs were not used for predictions, but as explained above, allowed a check of the selection of final predictors.

To illustrate the magnitude of potential distributional changes in response to ongoing warming, we compared the projected extent of coastline of future distributions with the historical distribution of the species represented by herbarium records. For this, we

TABLE 2 Summary of the per cent gain contribution coefficients explained by each environmental predictor for the 15 species distribution models (SDMs) suggested by MAXENT, results from generalized linear and additive models (GLMs and GAMs, respectively), and performance metrics of SDMs

Environmental predictors	MPYR	DPOT	XCHO	PCOM	CRER	ERAD	CSUB	PDEC
SST January (summer)	53.5*	70.8**	67.9**	57.8**	50.1**	78.7**	66.8**	38.9
SST July (winter)	34.9**	2.3	18.2	8.6	9.5	3	20.9*	43.1**
Dissolved Nitrogen	2.4	15.8*	5.0	14.4*	15.4	3	8.9	2.7
Dissolved Phosphorus	4.5	2.4	0.4	5.1	4.7	0.8	0.0	0.1
Primary Productivity July	1.2	4.6	0.1	4.1	2.4	0.6	0.0	1.3
Primary Productivity October	3.1	1.5	0.0	2.0	1.1	0.4	0.1	0.2
Salinity	0.3	0.8	0.2	0.0	0.0	3.8	0.3	8.9*
Surface Currents October	0.0	0.4	5.7	4.1	7.1	0.1	2.7	4.0
Surface Currents April	0.1	1.6	2.7	3.9	9.8	9.7	0.2	0.8
Number of grid cells with presences (N)	58	26	41	59	46	115	92	78
AUC MAXENT	0.938	0.957	0.928	0.937	0.923	0.847	0.898	0.890
MEAN AUC 70% ^a MAXENT	0.936	0.953	0.936	0.937	0.924	0.850	0.895	0.895
AUC FINAL MODEL MAXENT	0.923	0.936	0.892	0.913	0.893	0.812	0.858	0.864
Sensitivity MAXENT	96.5	100.0	95.1	96.6	91.3	97.4	100.0	96.1
Specificity MAXENT	87.3	91.9	86.6	88.3	83.7	72.0	73.2	78.1
Kappa MAXENT	0.456	0.322	0.312	0.435	0.403	0.451	0.430	0.310
AUC simple GLM	0.950	0.959	0.936	0.943	0.906	0.855	0.909	0.892
Kappa simple GLM	0.399	0.309	0.270	0.368	0.231	0.419	0.375	0.298
AUC GAM	0.950	0.959	0.937	0.943	0.907	0.855	0.910	0.892
Kappa GAM	0.399	0.309	0.268	0.367	0.235	0.419	0.380	0.295

(Continues)

binarized the projected maps into presence and absence categories of habitat suitability (Figures 3 and 4) using the 'Equal Training Sensitivity and Specificity' criterion calculated with MAXENT, a threshold indicative of the presence of the species. That is, values above this threshold indicating high likelihood of presence of the species in the corresponding cells. Then, the length of the stretches of coastline (historical vs. forecasted) was calculated on a vector layer in ArcGIS.

3 | RESULTS

3.1 | Models and projections by environmental predictors

Summer SST returned the highest per cent gain contribution to the MAXENT models for 12 of the 15 species, and it was ranked second for one other species. In all but in one single species, GLMs and/or GAMs showed consensus with MAXENT in suggesting the significant effect of maximum temperature (Table 2). Species restricted to south-eastern Australia (*Macrocystis pyrifera*, *Durvillaea potatorum*,

Xiphophora chondrophylla and *Phyllospora comosa*) experience the coolest temperatures and the narrowest range of summer SST's (Figure 1a). The response functions linking the presence of these seaweeds with summer SST therefore reflected a narrow realized thermal niche centred in the low temperature range (Figure 2a,b and Appendix S2). Consequently, the models predicted substantial decrease in habitat suitability for these species under projected future ocean warming for 2100 (Figures 3a,b,c,d and 4a,b,c,d), potentially affecting >79% of their current distribution, and the four becoming extinct in Australia under the RCP 6.0 medium-emission levels scenario (Table 3). Moreover, projections for these species illustrate the overall lower habitat suitability for macroalgae at a given latitude in eastern than in western Australia, presumably due to the strong southward flow of the warm East Australian Current, which in contrast to the weaker Leeuwin Current, is most intense in summer (Coleman et al., 2011).

Summer SST was also the main predictor of distribution for two seaweeds distributed up along both the east and west coasts, namely *Cystophora retroflexa* and *Ecklonia radiata*. Model projections suggested a potential 71%–49% contraction of the distribution

TABLE 2 (Continued)

Environmental predictors	CRET	SDOR	SLIN	SSPI	PVER	SDER	XGLA
SST January (summer)	73.8**	59.4*	61.3**	41.7*	69.2**	0.1	16.3
SST July (winter)	3.9	1.3	0.0	0.3	29.3**	1.5	22.2*
Dissolved Nitrogen	7.4	27.6	5.1	22.6	0.4	37.3**	54.9**
Dissolved Phosphorus	0.7	0.0	0.1	0.4	0.2	8.4	0.2
Primary Productivity July	0.5	1.7	0.7	1.9	0.2	13.8	1.8
Primary Productivity October	0.2	0.1	0.1	3.3	0.0	28.8	1.5
Salinity	0.7	2**	26.4**	11.6**	0.6	7.2	3.0
Surface Currents October	0.0	3.9	0.5	8.0	0.2	1.3	0.0
Surface Currents April	12.8	4.1	5.8	10.3	0.0	1.6	0.2
Number of grid cells with presences (N)	63	60	59	43	69	46	26
AUC MAXENT	0.893	0.904	0.855	0.845	0.857	0.788	0.977
MEAN AUC 70% ^a MAXENT	0.903	0.912	0.859	0.846	0.863	0.788	0.978
AUC FINAL MODEL MAXENT	0.838	0.878	0.826	0.793	0.858	0.647	0.974
Sensitivity MAXENT	98.4	93.3	94.9	79.1	95.6	65.2	100.0
Specificity MAXENT	76.4	81.7	74.7	78.8	70.9	83.4	93.2
Kappa MAXENT	0.291	0.324	0.217	0.280	0.229	0.224	0.570
AUC simple GLM	0.892	0.897	0.864	0.831	0.873	0.796	0.988
Kappa simple GLM	0.250	0.243	0.202	0.142	0.212	0.163	0.535
AUC GAM	0.891	0.898	0.861	0.832	0.871	0.793	0.988
Kappa GAM	0.239	0.250	0.188	0.145	0.227	0.170	0.558

SPECIES CODES: MPYR—*Macrocystis pyrifera*, DPOT—*Durvillaea potatorum*, XCHO—*Xiphophora chondrophylla*, PCOM—*Phyllospora comosa*, CRER—*Cystophora retroflexa*, ERAD—*Ecklonia radiata*, CSUB—*Cystophora subfarinata*, PDEC—*Phyllotricha decipiens*, CRET—*Cystophora retorta*, SDOR—*Scytothalia dorycarpa*, SLIN—*Sargassum linearifolium*, SSPI—*Sargassum spinuligerum*, PVER—*Phyllotricha verruculosa*, SDER—*Sargassopsis decurrens*, XGLA—*Xiphophora gladiata*.

MAXENT per cent contribution scores $\geq 20\%$ in bold.

*Significant after GLM or GAM (BIOMOD2 software).

**Significant after GLM and GAM.

^aMean AUC values of 70% test data were based on 10 replicate data split (70%–30%) with associated standard errors (SE) ≤ 0.007 . AUC: 1–0.9 good, 0.9–0.8 fair, 0.8–0.7 poor, 0.7–0.6 fail, following Swets (1988).

Reported values are the area under the curve (AUC) of a receiver operating characteristic plot (ROC) calibrated on all data (AUC 100%) and on the test datasets generated after cross-validation (mean value after 10-fold cross-validation using 70–30% partitioning calculated with MAXENT) for the full models (all predictors) and the final reduced models. Sensitivity (ratio of corrected classified presences), Specificity (ratio of corrected classified absences) and Kappa coefficient (k).

along the east and west coasts for *E. radiata* and more broadly for *C. retroflexa* (95%–67%), in both cases including a western section of the south coast (Table 3, Figures 3e,f and 4e,f). Similar contractions in response to summer warming were predicted for a third group of seaweeds restricted to the west and south coast of Australia (*Cystophora subfarinata*, *Phyllotricha decipiens*, *Cystophora retorta* and *Scytothalia dorycarpa*, Figures 3g,h,i,j and 4g,h,i,j). Interestingly, the response functions suggest physiological tolerance ranges similar to those species that are present in eastern Australia (compare Figure 2b,c). The absences of these species from eastern Australia

do therefore not appear to be related to temperature conditions. Similarly, *P. comosa* does not occupy areas of temperatures within its tolerance range in western and south-western Australia. Summer SST was also the main predictor (Table 2) for the final group of widespread seaweeds with records in relatively warm tropical and subtropical waters (*Sargassum linearifolium*, *S. spinuligerum* and *Phyllotricha verruculosa*) (Figures 2d, 3k,l,m and 4k,l,m, Appendix S2). However, with few presence records reported from warmer relative to cooler areas, additional field records should be evaluated to increase confidence in the predicted responses of these species.

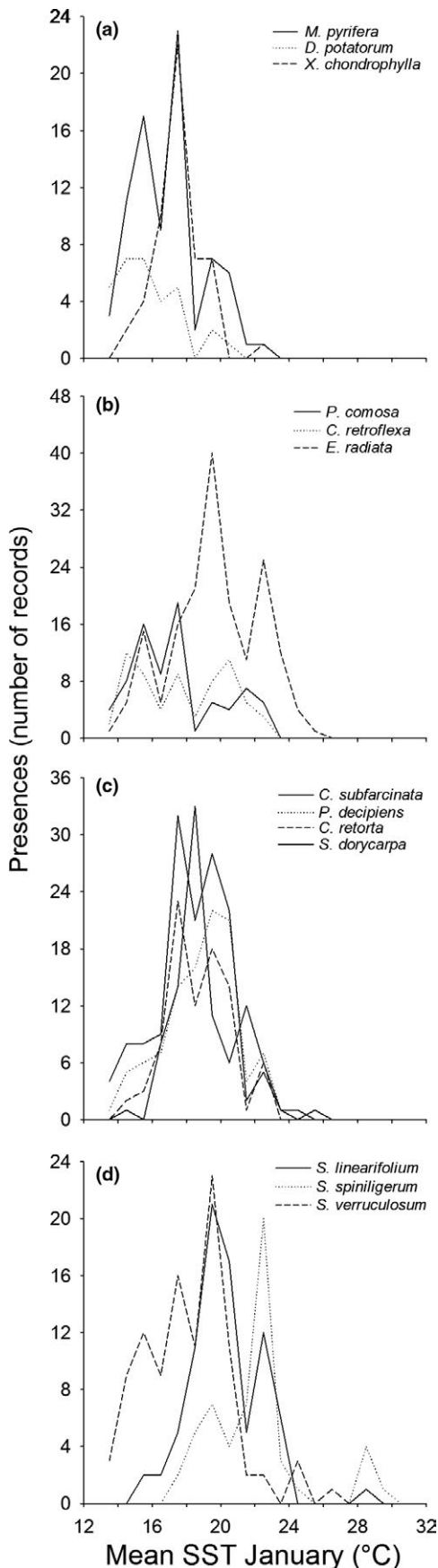


FIGURE 2 Frequency of grid cell presences of target seaweeds at different mean Sea Surface Temperature in January (SST January) of (a) *Macrocystis pyrifera*, *Durvillaea potatorum* and *Xiphophora chondrophylla*; (b) *Phyllospora comosa*, *Cystophora retroflexa* and *Ecklonia radiata*; (c) *Cystophora subfarcinata*, *Phyllotricha decipiens*, *Cystophora retorta* and *Scytothalia dorycarpa*; and (d) *Sargassum linearifolium*, *Sargassum spinuligerum* and *Phyllotricha verruculosa*. *Sargassopsis decurrens* and *Xiphophora gladiata* not shown as these species were not related to temperature (Table 2)

While relationships with summer SST's were strongest for most species, the contribution of temperature to the distribution of five species (*M. pyrifera*, *C. subfarcinata*, *P. decipiens*, *P. verruculosa* and *X. gladiata*) was further demonstrated by significant relationships with winter SST's (Table 2, Appendix S2). In particular, winter SST ranked highest in the models for *P. decipiens* (over summer SST, which was not significant using GLMs and GAMs). The influence of the warm Leeuwin Current, which is particularly intense during winter, can be seen in the projections for these species as low habitat suitability on the western temperate coast and towards the inner Great Australian Bight (see Figures 3a,g,h,m and 4a,g,h,m). For one species, *Xiphophora gladiata*, the distribution was significantly related to winter SST but not summer SST by both MAXENT and regression-like methods (Table 2, Appendix S2). *X. gladiata* is found within a narrow thermal tolerance window of low temperatures along a short coastal fringe in south-eastern Australia and Tasmania (Figure 5) where SST's vary little (Appendix S2).

Seawater nitrogen concentration was the variable most often selected among the non-climatic predictors considered in this study and the primary predictor for the distributions of *X. gladiata* and *Sargassopsis decurrens* (Table 2). As mentioned above, *X. gladiata* is restricted to the cold and nutrient-rich waters off Tasmania, whereas *S. decurrens* is most common in nutrient-poor tropical waters but is also found in temperate regions except Tasmania (Figure 5). Being present across broad temperature regimes *S. decurrens* can be considered a generalist with wide thermal tolerances. Seawater nitrogen concentration was also a significant predictor of the distribution of at least four other fucoiids, although ranked in a distant second position with few consensus among methods (Table 2). It is, however, uncertain if the relationships with seawater nitrogen are causal because with the exception of *X. gladiata*, responses curves suggested the species being favoured by low-nutrient availability or the existence of an optimal range (Appendix S2), contradicting the physiological responses expected for seaweed (Lobban & Harrison, 1994). For some species, the shape of the response curves changed significantly when the contribution of other predictors was accounted for (Appendix S2), suggesting residual variance in this parameter.

3.2 | Accuracy of models and projections

Overall, GLMs and GAMs were significant for climatic factors with high MAXENT scores (i.e., maximal and minimal temperatures)

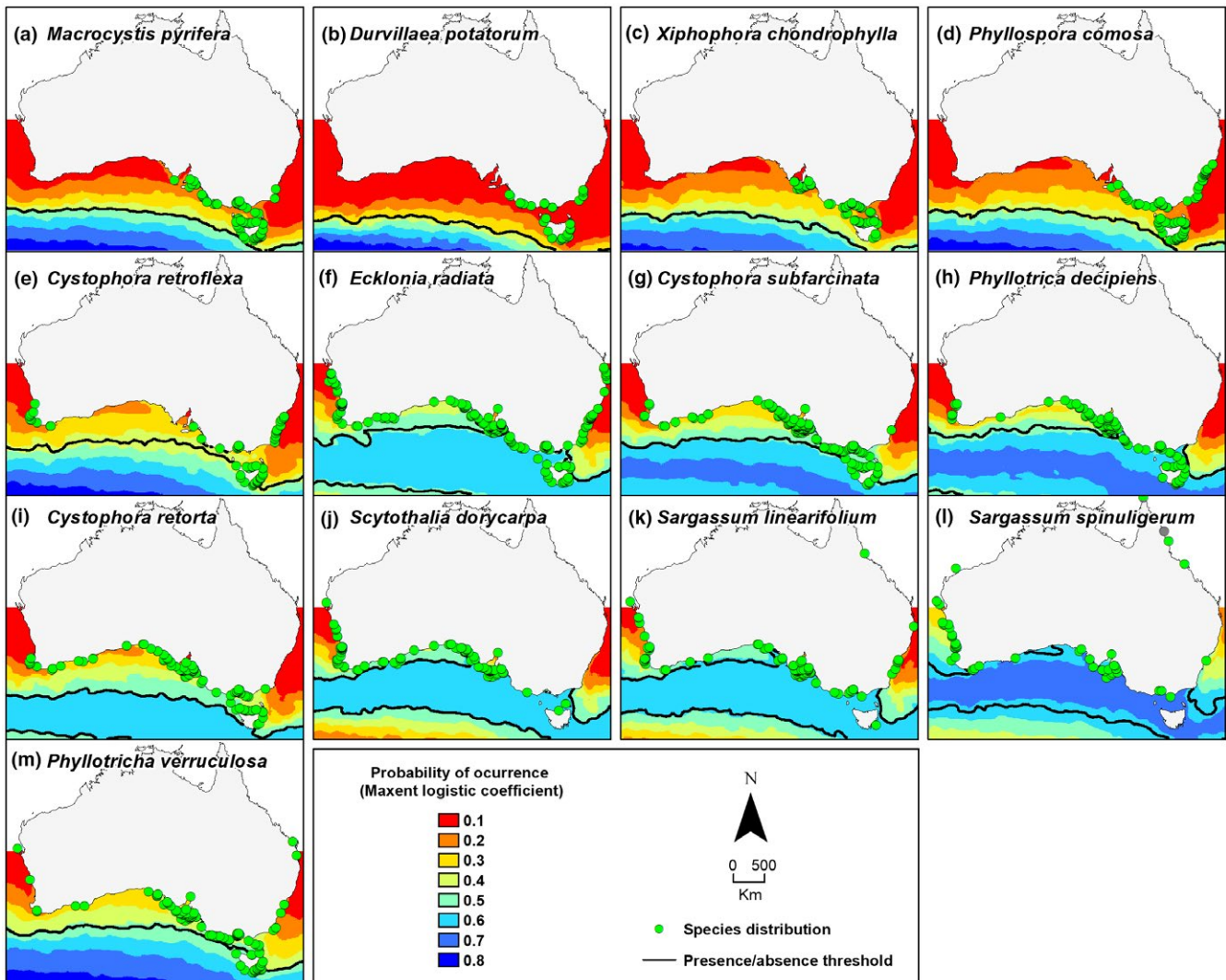


FIGURE 3 Projected maps showing the species distributional records lodged in the Australian Virtual Herbarium (green dots) and MAXENT logistic coefficients of habitat suitability of seaweed in temperate Australia using the projected RCP 6.0 warming scenario for 2100. Panels b, c, d, e, f, i, j, k, l based on SST in January (summer) and panels a, g, h, m based on both in SST January (summer) and in SST July (winter) (cf. results in Table 2). The threshold for presence/absence suggested by the “Equal Training Sensitivity and Specificity” criterion is shown as a black line. No projection maps are shown for *Sargassopsis decurrens* and *Xiphophora gladiata* as their distributions were not strongly related to SST (cf. Table 2, Figure 5) [Colour figure can be viewed at wileyonlinelibrary.com]

showing high degree of consensus among methods, but otherwise variable for non-climatic physical factors of large regional variation. The inclusion of seawater nutrient concentration and other factors of large regional variation, specifically salinity and surface currents, was dependent on the statistical method used and thus of high uncertainty, and therefore, projections based on these parameters were not reliable (not shown).

Projections under different climate change scenarios all resulted in similar spatial patterns of change in habitat suitability, although suggesting different magnitudes of likely contractions (compare Figures 3 and 4). As expected, the most conservative RCP 2.6 scenario resulted in less pessimistic poleward contractions than RCP 6.0 (Table 3).

Area under the curve values were highly consistent among MAXENT, GLMs and GAMs algorithms, suggesting good

performances of the SDMs for four species (>0.9), and high to fair discrimination ability (0.9–0.8) for another 10 (Table 2). Only the model of *Sargassopsis decurrens* had poor discrimination ability. Sensitivity and specificity values for MAXENT (Table 2) suggested correct classification of both presences and absences, and were similar to that observed when using GLMs and GAMs (not shown). The latter two regression-like algorithms did not differ in any of the measures of accuracy, Kappa values being similar between them, and somewhat lower than those observed for MAXENT (Table 2).

4 | DISCUSSION

Our SDMs demonstrated that summer ocean temperature is by far the strongest predictor of species distribution for habitat-forming

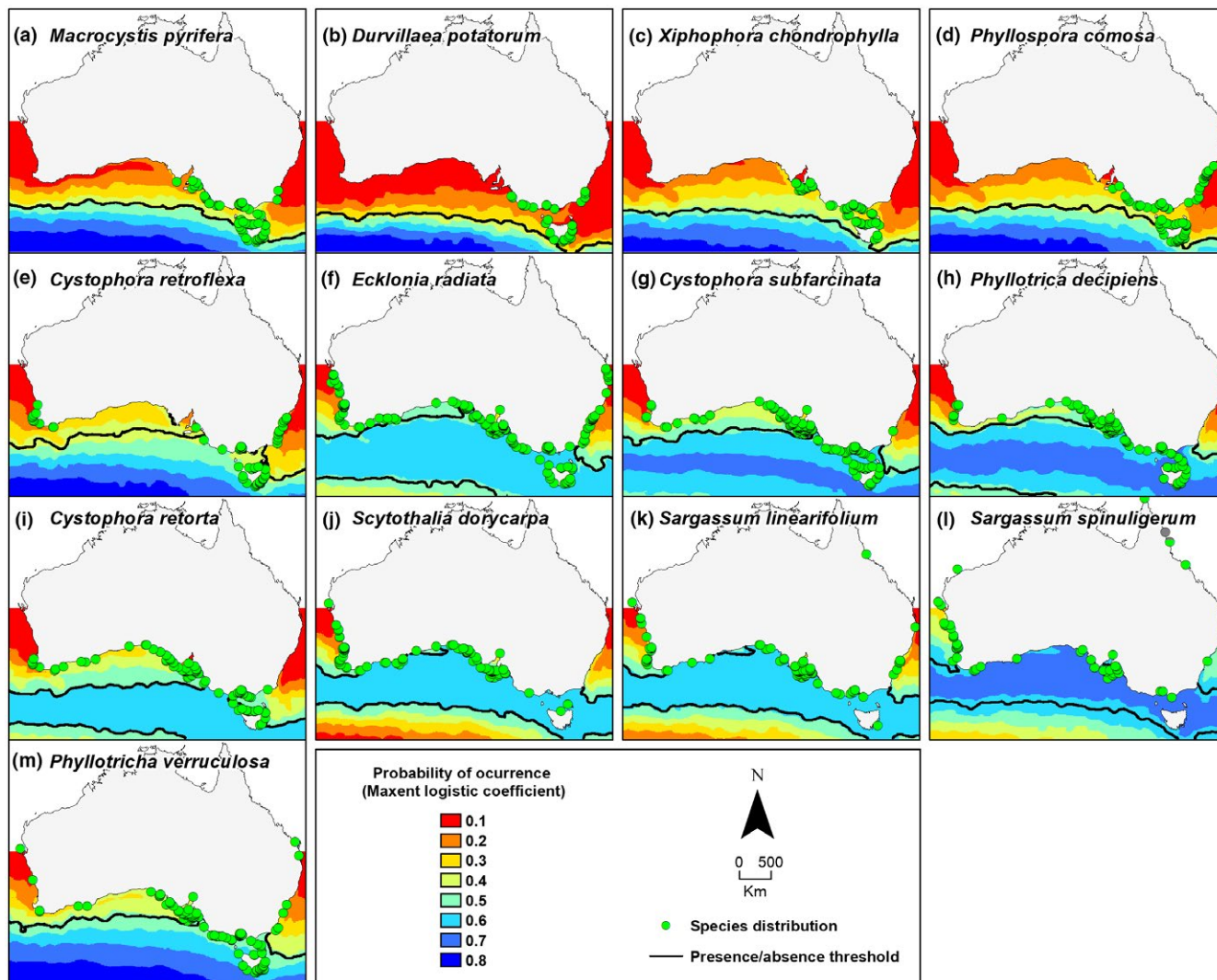


FIGURE 4 Projected maps showing the species distributional records lodged in the Australian Virtual Herbarium (green dots) and MAXENT logistic coefficients of habitat suitability of seaweed in temperate Australia using the projected RCP 2.6 warming scenario for 2100. Panels b, c, d, e, f, i, j, k, l based on SST in January (summer) and panels a, g, h, m based on both in SST January (summer) and in SST July (winter) (cf. results in Table 2). The threshold for presence/absence suggested by the “Equal Training Sensitivity and Specificity” criterion is shown as a black line. No projection maps are shown for *Sargassopsis decurrens* and *Xiphophora gladiata* as their distributions were not strongly related to SST (cf. Table 2, Figure 5) [Colour figure can be viewed at wileyonlinelibrary.com]

temperate seaweeds in Australia, and that projected future warming is likely to cause widespread contraction of these seaweeds. These climate-driven changes in distribution could potentially result in major impacts to ecosystem structure and function across large geographic areas (Wernberg, Bennett et al., 2016). Nine of the 15 species modelled were predicted to lose >70% of their current distribution by 2100, with the iconic giant kelp *Macrocystis pyrifera*, and three prominent fucooids, namely *Durvillaea potatorum*, *Xiphophora chondrophylla* and *Phyllospora comosa*, predicted to become extinct in Australia under the medium-emission levels scenario RCP 6.0. The northern boundary of the common kelp *Ecklonia radiata*, a dominant species of great ecological importance (Bennett et al., 2016), was predicted to shift southward along the western and eastern coastlines of the continent with the species losing almost 50% of its current distribution over the next 85 years. Independent statistical

modelling methods (MAXENT, GLM and GAM) showed consensus in ranking summer temperature as the most important predictor. Projections suggested virtually the same spatial patterns for all RCP scenarios, with relatively small differences in the magnitude of likely distributional changes. Finally, the predictions in this study are consistent with observations of recent declines of conspicuous seaweeds attributed to global warming around the world, including southern Australia (Johnson et al., 2011; Smale & Wernberg, 2013; Wernberg, Russell, Thomsen et al., 2011; Wernberg, Bennett et al., 2016), Japan (Tanaka et al., 2012), southern (e.g., Díez et al., 2012; Fernández, 2011; Nicastro et al., 2013) and northern (Moy & Christie, 2012) Europe, and eastern Canada (Filbee-Dexter et al., 2016).

The mean summer SST was the main predictor of the distribution of habitat-forming seaweeds in temperate Australia in most of our

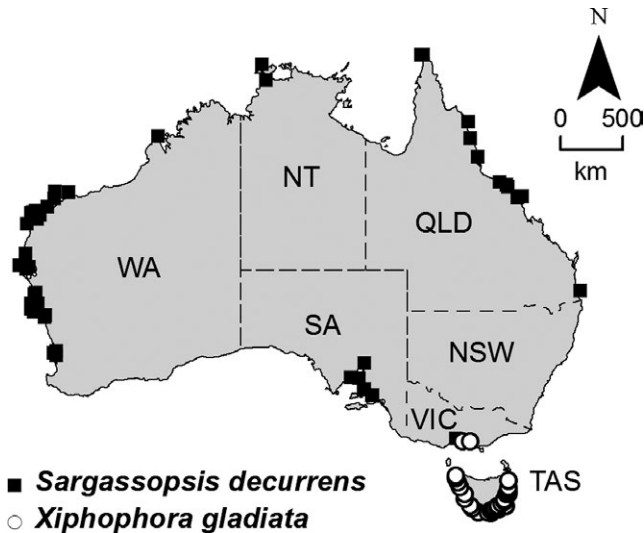


FIGURE 5 Map showing the species distributional records lodged in the Australian Virtual Herbarium of *Sargassopsis decurrens* and *Xiphophora gladiata*

models and with high consensus among statistical methods. Abiotic stress is known to limit the low-latitude distribution of many organisms (Clarke, 1993; Hampe & Petit, 2005; Hawkins, Porter, & Felizola Diniz-Filho, 2003; van den Hoek, 1982a). For temperate seaweeds, low-latitude boundaries have been linked to ocean summer isotherms above the maximum thermal thresholds for survival of a critical life-cycle phase (Breeman, 1988; Eggert, 2012; van den Hoek,

1982a; Lüning, 1990). Our results are consistent with this interpretation as well as the available physiological knowledge on tolerance thresholds. For example, *E. radiata* gametophytes cannot survive beyond 26–29°C (tom Dieck, 1993; Novaczek, 1984), and in our study, *E. radiata* was not observed at mean temperatures above 26°C. Moreover, the prevalence of *E. radiata* decreased in areas with mean temperatures higher than 20°C, consistent with experiments showing a negative relationship of growth of both microscopic (Mabin, Gribben, Fischer, & Wright, 2013; Moring, Kendrick, Wernberg, Rule, & Vanderklift, 2013) and macroscopic (Bearham, Vanderklift, & Gunson, 2013; Hatcher, Kirkman, & Wood, 1987; Xiao et al., 2015) sporophytes at temperatures above 20–22°C. Our distribution records for *M. pyrifera* also match its survival threshold for gametophytes (23–25°C (tom Dieck (Bartsch), 1993) and the poor growth of adult sporophytes at 20°C (Buschmann et al., 2004; Rothäusler et al., 2009). These results also align with experimental data demonstrating that temperature is the dominant factor limiting the performance and survival of *Phyllospora comosa*, *Scytothalia dorycarpa*, *Sargassum* spp. and *Ecklonia radiata* compared to non-climatic factors (Flukes, Wright, & Johnson, 2015; Mabin et al., 2013; Provost et al., 2017; Xiao et al., 2015). For example, Mabin et al. (2013) and Flukes et al. (2015) found no effects of nitrate but strong negative effects of current summer temperatures (22°C) on growth and survival of *E. radiata* and *P. comosa*, concluding that long-term warming would have severe population-level effects. Consequently, although physiological data are only available for very few of the modelled species, it appears they currently fill their thermal niches, at least within their

TABLE 3 Extent of historical and predicted future (2100) distribution under the RCP 6.0 and 2.6 climatic scenarios for 13 habitat-forming seaweeds in temperate Australia

Species	RCP 6.0				RCP 2.6		
	Historical distribution (km coastline)	Future distribution (km coastline)	Projected habitat loss (km coastline)	Projected habitat loss (% of current distribution)	Future distribution (km coastline)	Projected habitat loss (km coastline)	Projected habitat loss (% of current distribution)
<i>Macrocystis pyrifera</i>	6,343	0	6,343	100	1,306	5,036	79
<i>Durvillaea potatorum</i>	4,126	0	4,126	100	0	4,126	100
<i>Xiphophora chondrophylla</i>	5,014	0	5,014	100	261	4,753	95
<i>Phyllospora comosa</i>	5,547	0	5,547	100	744	4,802	87
<i>Cystophora retorta</i>	8,853	246	8,607	97	1,792	7,061	80
<i>Cystophora retroflexa</i>	9,790	666	9,124	93	3,196	6,594	67
<i>Phyllotricha verruculosa</i>	11,901	1,720	10,181	86	4,556	7,345	62
<i>Cystophora subfarinata</i>	9,493	1,542	7,951	84	4,433	5,060	53
<i>Ecklonia radiata</i>	11,462	3,365	8,097	71	5,842	5,620	49
<i>Sargassum linearifolium</i>	11,844	5,092	6,751	57	6,993	4,851	41
<i>Phyllotricha decipiens</i>	9,138	4,621	4,517	49	6,358	2,781	30
<i>Scytothalia dorycarpa</i>	10,300	5,522	4,778	46	7,089	3,211	31
<i>Sargassum spinuligerum</i>	11,190	7,209	3,981	36	8,150	3,040	27

Total length of temperate coastline was estimated to be 26,730 km. Note, projections could not be made for *Sargassopsis decurrens* and *Xiphophora gladiata* as the distributions of these species were not strongly related to temperature (Table 2, Figure 5).

biogeographic provinces (cf. Waters et al., 2010). This supports the broader notion that the present-day distribution patterns of temperate habitat-forming seaweeds are sensitive to warming, and that increases in mean and extreme temperatures are likely to cause rapid shifts in species distributions.

In contrast to summer temperatures, we found little support for an overall influence of winter temperatures on the biogeography of most temperate Australian seaweeds. The northern limits of the warm-temperate Australian provinces have previously been linked to winter isotherms, but this is more related to the southern dominance of corals (reviewed in Lüning, 1990). Nevertheless, winter heat did contribute significantly to explain the distribution of the giant kelp *M. pyrifera* and some canopy-forming fucooids. In New Zealand, 13°C is the upper temperature limit for *M. pyrifera* gametogenesis (Peters & Breeman, 1993). However, this value falls within the optimal temperature range for gametogenesis and gametophytes in other Southern Hemisphere populations (South Africa, reviewed in Bolton, 1986) and Australian populations extend to areas of higher mean winter temperatures (this study). This species displays large plasticity in growth and life-cycle patterns among geographic areas making generalizations difficult (Brown, Nyman, Keogh, & Chin, 1997). Both summer and winter ocean temperatures have been linked to the biogeography of this species (Hay, 1990; Lüning, 1990) supporting its sensitivity to warming irrespective of seasons, as confirmed in this study.

The response functions that link the presence of seaweeds with summer SST suggest that fucooids absent from eastern (e.g., *Scytothalia dorycarpa*) or western (e.g., *Phyllospora comosa*) Australia are currently not occupying all habitats with suitable environmental (temperature) conditions. The historic isolation by the palaeogeographic barrier maintained in the Pleistocene by the Bassian Isthmus, a land bridge which connected Tasmania with mainland Australia, could at least partially explain these absences (Waters, 2008; Waters et al., 2010). In addition, the southward flowing boundary currents (Wernberg, Thomsen et al., 2013) and complex currents and eddies in the transition area between the continent and Tasmania may also contribute to maintain the historic biogeographic isolation of the east coast as shown for diverse marine fauna (Waters, 2008). Other potential contributing mechanisms could include biotic interactions that differ between eastern and western Australia. For example, urchin-mediated barren areas dominated by encrusting coralline algae are common in eastern but not in western Australia (Connell & Irving, 2008; Waters et al., 2010). In any case, these biotic mechanisms did not influence, or were not captured by, our SDM's which forecasted similar range contractions for temperate seaweeds on both coasts. This illustrates the well-known limitation of SDMs in niche under filling situations by biotic constraints or limited connectivity between different geographic areas.

Our SDM's and overall predictions indicated lower habitat suitability at a given latitude for species on the east coast compared to the west coast. This likely reflects the flow of the warm East Australian Current, which in contrast to the west coast Leeuwin Current, is particularly intense in summer and also substantially stronger. Like

other western boundary currents (Wu et al., 2012), the EAC has strengthened and is expected to increase further (Poloczanska et al., 2007; Ridgway, 2007). The southward flow of both the EAC and the LC has been connected to range changes and tropicalization of Australia's temperate ecosystems (Hyndes et al., 2016; Vergés et al., 2014, 2016; Wernberg, Bennett et al., 2016). In eastern Tasmania, the increased influence of warm and nutrient-poor EAC has been associated with dramatic declines of giant kelp (*Macrocystis pyrifera*) forests (Johnson et al., 2011). As a consequence, in August 2012 the Australian giant kelp forests became the first marine community in Australia to be listed as endangered under the Environment Protection and Biodiversity Conservation Act (DEPNV 2012). Ecologists are currently gathering evidence for similar declines in *D. pottorum*, *P. comosa*, *E. radiata* and other fucooids on the east coast and in Tasmania. In addition to general warming, episodic extreme climatic events such as the 2011 marine heatwave in Western Australia have been linked to ocean currents and climate change (Hobday et al., 2016) and represent a substantial threat to temperate seaweeds (Wernberg, Smale et al., 2013; Wernberg, Bennett et al., 2016). Unfortunately, the consequences of such events are difficult to predict by SDMs because extremes and local variability are poorly resolved in projected scenarios of ocean warming. Furthermore, indirect effects associated with changing consumer pressure, for example, due to current-driven range-shifting tropical herbivores (Nakamura, Feary, Kanda, & Yamaoka, 2013; Wernberg, Bennett et al., 2016), are unaccounted for in climate projections but could accelerate the retreat of temperate seaweeds (Vergés et al., 2014, 2016; Zarco-Perello, Wernberg, Langlois, & Vanderklift, 2017). Thus, thermal anomalies driven by variation in mesoscale warm currents, episodic heatwaves and cascading biological responses add a layer of concern above the predicted declines based on forecasted increases in baseline temperatures (this study, but also see Molinos et al., 2015). It is unknown if adaptive responses could help decelerate or offset these changes (e.g., Hoffmann & Sgro, 2011). However, it seems unlikely (e.g., Wernberg, Coleman et al., 2018) due to the relatively long generation time (~1 year) of most habitat-forming seaweeds and the low selection pressure for resistance against rare extremes and novel species interactions.

At present, it remains unknown to which extent subtropical and tropical seaweed species will expand to higher latitudes and, in particular, whether these will provide similar ecological functions as contracting temperate species. While some shifts towards warm-affinity seaweeds have already been observed in Australia (Wernberg, Bennett et al., 2016) and Japan (Tanaka et al., 2012), and warm-water species in general are projected to expand (Molinos et al., 2015), there is little evidence to suggest that temperate habitat-forming seaweeds will be replaced by equally structurally complex habitat-forming warm-water species. Instead, the globally consistent pattern is that structurally complex habitat-forming species are replaced by small turf-forming species, resulting in habitat simplification with cascading impacts across the coastal ecosystem (reviewed in Filbee-Dexter & Wernberg, 2018). It is possible that more eurythermal species, such as the kelp *E. radiata* (Wernberg, de Bettignies, Bijo, & Finnegan, 2016),

initially could increase in abundance from competitive release following declines in more sensitive species especially within the centre of *E. radiata*'s current and future distribution. However, our projections clearly suggest that the distribution of *E. radiata* will eventually contract due to physiological constraints, causing a transition of current temperate marine communities in Australia into an alternative state of persistent turf dominated habitats of little complexity (Wernberg, Bennett et al., 2016). These range contractions predicted by SDMs will ultimately threaten numerous endemic seaweeds and seaweed-associated species, as well as species supporting valuable commercial and recreational activities (Bennett et al., 2016). The expansion of species of similar ecological functions relies on their potential to disperse and biotic dominance, and thus would be predicted with uncertainty by SDMs that are proxies of the realized tolerance to climatic and other physical factors.

5 | CONCLUSION

This study found strong relationships between ocean temperature, particularly in summer, and the historical and current distribution of habitat-forming seaweeds across temperate Australia, with other environmental conditions explaining relatively little. With high temperatures limiting the low-latitude distribution of temperate seaweeds, projections of changes in distribution of temperate habitat-forming seaweeds suggested substantial range contractions under the RCP scenarios of global warming. Nine of 15 species modelled were forecasted to lose >70% of their current distribution by 2100, and four prominent species, including the iconic giant kelp (*Macrocystis pyrifera*), were predicted to become extinct in Australia. Similar changes will likely occur in hundreds if not thousands of less conspicuous seaweed-associated species, many of which are endemic and found nowhere else in the world (Bennett et al., 2016). Moreover, future contractions are likely to also occur in other regions of the world, where evidence of decline of foundation seaweed is growing. While projections based on SDMs suffer from uncertainty thus representing crude estimates, they could be optimistic as they do not consider less conservative emission scenarios, for example, RCP 8.0, or the compounding influences of other human pressures, extreme events, ocean acidification, herbivory and other biological interactions, all of which are also increasing (Filbee-Dexter & Wernberg, 2018; Vergés et al., 2014; Wernberg, Russell, Moore et al., 2011). Unless replaced by functionally similar species, changes of the projected magnitude, for such a broad suite of habitat-forming species, would have catastrophic consequences for Australia's temperate marine ecosystems and the ecosystem services they support. Little is known about what species might replace the temperate habitat-formers, but increasing evidence suggests that small structurally simple turf-forming seaweeds will become more prominent features of temperate rocky coastlines (Filbee-Dexter & Wernberg, 2018). It therefore seems inevitable that the coming decades will see dramatic changes from what currently define temperate rocky coasts of Australia.

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BIOSKETCH

The authors represent a broad international group of marine focused scientists with expertise in conservation ecology, biogeography, ecophysiology, marine botany and spatial statistics.

Author contributions: TW, BM and CFDG conceived the research; CFDG and DF supplied data; BM, FC and BR analysed the data; BM and TW wrote the study. All authors discussed the research as it developed and edited the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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