Ecological interactions mediate projected loss of kelp biomass under climate change

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Abstract

Aim: Climate change has precipitated loss of kelp in temperate regions globally, with further losses projected in response to ocean warming. Projected climate-driven changes to kelp are commonly derived from responses to sea surface temperature and neglect the effects of important ecological interactions, such as herbivory. Here, we use a stacked species distribution model to project impacts of future climate scenarios on kelp distribution and biomass incorporating the effects of key ecological interactions.

Location: The eastern Australian coastline (28.0–37.5°S).

Methods: A stacked species distribution model, incorporating ecological interactions with urchins, was used to project future effects of climate change on kelp. This model incorporated key drivers of kelp occurrence and cover (habitat availability, light and in situ temperatures) that are rarely considered when projecting the effects of climate change on kelp.

Results: Consistent with previous research, we find range contractions of kelp (~275 km) at lower latitudes (<32°S), due to ocean warming under RCP 8.5 (~3.4°C) by 2100. However, in contrast to previous studies, we find range contractions will not occur under RCP 2.6 (~0.8°C), and only moderate contractions are projected (~55 km) under RCP 6.0 (~2.3°C). Instead, vertical migration of kelp, from shallow areas to cooler deep water refugia, is likely under future change. Interestingly, range contractions at lower latitudes are projected to be offset by increased kelp biomass at higher latitudes (32–37.5°S) resulting from reductions in urchin herbivory. Consequently, a net gain in kelp biomass is projected for mainland eastern Australia by 2100 under RCPs 2.6 and 6.0 (up to 29.4%), while relatively small net losses are projected under RCP 8.5 (~3.5%).

Main conclusions: Considering key ecological interactions when developing species distribution models can significantly change projections of habitat loss and must be integrated into assessments to accurately evaluate future change and enable evidence-based management.

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1 | INTRODUCTION

Climate change is causing rapid shifts in the distribution and biomass of marine species, including algae (Filbee-Dexter et al., 2020; Martínez et al., 2018; Vergés et al., 2016; Zarco-Perello et al., 2017), invertebrates (Nimbs et al., 2016; Scott et al., 2015) and fishes (Champion et al., 2021; Kumagai et al., 2018; Wernberg, Bennett, et al., 2016). These changes are causing novel species interactions (Vergés et al., 2019) and invasions (Ling et al., 2009) and are anticipated to lead to local species extinctions (Doney et al., 2012; Martínez et al., 2018). The ability to predict such change is vital for proactively managing and conserving marine habitats in future oceans.

Among the marine species most impacted by climate change are kelps, the underwater forests of temperate seas (Babcock et al., 2019). As a foundation species, kelp underpins vast ecosystem goods and services along temperate coasts, with an estimated value of ~$1 M per kilometre of coast per year for Australia alone (Bennett et al., 2016; Eger et al., 2021). Kelp forests provide substantial input to marine food webs (Wernberg et al., 2019), contribute to coastal food chains (Bishop et al., 2010; McLachlan, 1985) and to blue-carbon storage (Filbee-Dexter & Wernberg, 2020). These valuable ecosystem goods and services are threatened by climate change, with widespread losses of kelps projected for many regions globally (Assis et al., 2016; Filbee-Dexter et al., 2016; Martínez et al., 2018).

Australia’s coastal ocean is a recognized climate change hot spot, where ocean warming is occurring between 2 and 4 times faster than the global average (Hobday & Pecl, 2014). In response to these environmental changes, 198 species from Australian marine systems have been documented undergoing climate-driven range shifts (Gervais et al., 2021), with some of the most alarming shifts projected for temperate seaweeds (Martínez et al., 2018). For example, species distribution modelling (SDM) by Martínez et al. (2018) projected complete losses of many seaweed species from the Australian continent by 2100. Even Australia’s most temperature tolerant kelp *Ecklonia radiata* is projected to lose between 49 and 71% of its distribution around Australia by 2100 under RCPs 2.6 and 6.0, respectively, including loss from almost the entire eastern Australian coastline. Similarly, Castro et al. (2020) predict a large poleward range contraction of ~530 km for *E. radiata* in eastern Australia by 2100. These predictions were based primarily on extant and projected impacts of sea surface temperatures (SST) alone, with other factors important in structuring kelp forests neglected, including ecological interactions (herbivory), habitat availability and in situ environmental conditions (e.g. available light and water temperature at the seabed). Refining models to incorporate such factors will be vital in accurately predicting the impacts of climate change on kelp and developing proactive management plans to mitigate loss.

Unquantified biotic interactions (such as herbivory) can greatly alter outcomes of SDMs (Godsoe & Harmon, 2012), but can be incorporated by combining SDMs for multiple species (Lany et al., 2017). This is particularly important for kelp because biotic interactions, particularly herbivory, are strong determinants of their distribution (Johnson et al., 2011; Ling et al., 2009), particularly along eastern Australia (Davis et al., 2021). Herbivory by the urchin *Centrostephanus rodgersii* has been closely linked to kelp loss (Andrew & Underwood, 1989), with increasing urchin abundances and range expansions known to have devastating impacts on kelp forests (Ling, Johnson, Ridgway, et al., 2009). Incorporating urchin densities into SDMs, therefore, should be a key consideration when developing models that aim to yield accurate predictions about future kelp distributions (Davis et al., 2021). Moreover, models are most accurate when they also incorporate in situ data on factors such as habitat/reef availability and in situ environmental conditions to refine projections of future kelp distribution and biomass and inform management and conservation strategies. Specifically, since kelp experiences water temperatures at the seabed that are several degrees lower than SST, kelp may persist in deep water refugia with lower temperatures at the seabed (Davis et al., 2021; Graham et al., 2007; Marzinelli et al., 2015) which may not be apparent in models that use SST alone.

Here, we use novel stacked species distribution models (stacked-SDMs), developed for kelp and urchins to project future changes to kelp distribution and biomass in eastern Australia. We also account for the effects of variation in *in situ* temperature and light with depth and reef availability across 9.5° degrees of latitude. These detailed and more nuanced estimates of kelp distribution and biomass reveal that projections for kelp forests must consider ecological interactions to accurately understand change in future oceans.

2 | METHODS

2.1 | Study area

The spatial extent of this study encompasses the eastern coast of Australia, between 28.0 and 37.5°S (Figure 1). This region was selected to assess the role of ecological interactions in altering predictions of kelp distributions under climate change because detailed habitat data are available on the presence of consolidated reef substrate and SDMs are available for prediction of kelp cover (Figure 1a) and relative urchin densities (Figure 1b) (Davis et al., 2021). These data enable calculation of current and future distributions of kelp biomass. Within this region, the perennial *E. radiata* is the only laminarian kelp species, while *C. rodgersii* is the dominant urchin species, with ecological interactions between these two species creating
a patchwork of kelp forests and urchin barrens on shallow reefs (Underwood et al., 1991). We acknowledge that a complete picture of future changes in the spatial extent of kelp and urchins along Australia’s east coast would need to include Tasmania, where urchins are a new range expanding species and are responsible for significant kelp decline (Ling, Johnson, Ridgway, et al., 2009). However, extrapolation outside the latitudinal range of data used by Davis et al. (2021) (i.e. 28.0–37.5°S) to quantify kelp cover and urchin densities was not considered valid.

2.2 | Reef data

Kelp only occurs on submerged rocky reefs, due to kelp holdfasts requiring a hard substrate for attachment (Wernberg et al., 2019). Consequently, predicting kelp distributions requires a detailed knowledge of reef distributions as this varies significantly by latitude. Data on reef presence were assembled from NSW Department of Primary Industries (DPI) 2002 and 2013 marine habitat data. These data were obtained from the Seaman Australia data repository (seamapaustralia.org, 2002 data source: NSW—Marine habitats 2002, type = Reef and shoal; 2013 data source: NSW—Seabed habitat state waters, type = Reef). Data on reef presence originating from a combination of multibeam sonar, LIDAR (LADS), aerial photographs and nautical charts. Where reef data were unavailable in these DPI data sets, reef presence was obtained from 2017 nearshore data, obtained from the NSW SEED data repository (datasets.seed.nsw.gov.au), which was digitized from aerial imagery, using standardized methodology. This method is well suited to distinguishing between consolidated and unconsolidated substrates, in clear shallow waters, with these data accounting for ~5% of the total reef area mapped. Additionally, any remaining gaps in reef presence data were filled by
manually digitizing reef extent, at a resolution of 1:10,000, using the 2018 LiDAR data set available from NSW SEED data repository. All reef data were combined into a single data set using ArcGIS (ESRI, 2021). To enable calculation of total kelp biomass along the eastern Australian coast, reef polygons from 28.0 to 37.5°S were divided into 0.083° latitudinal increments to match the resolution of environmental predictors of kelp cover and biomass. Reef polygons in each latitudinal increment were then further subdivided into 5 m depth classes from 0 to 40 m. Area of reef (ha) was calculated for each subdivided reef polygon, within these latitude and depth divisions, with a total of 77,720 ha of consolidated reef identified (~11.2% of total seabed). The distribution of this consolidated reef varied substantially with depth and latitude along the coast (Figure 1d).

### 2.3 | Species distribution model development

Modelling of kelp and urchin distributions was conducted using the stacked-SDM recently developed by Davis et al. (2021). The stacked-SDM consists of two submodels, a kelp SDM and an urchin SDM, that are integrated to ultimately estimate the distribution of kelp biomass throughout the study extent. The stacked-SDM was constructed using kelp percentage cover data and data on relative densities of the urchin C. rodgersii, from 143 randomly positioned 200 m transects, spread across 23 sites along the eastern Australian coastline (Figure 1). Transects covered the full range of different habitats present, including urchin barrens and areas with differing kelp covers. The kelp SDM was developed by matching kelp percentage cover data (binomial response variable) to a suite of satellite-derived environmental data of likely importance to kelp persistence and data on relative urchin densities, as urchins are known to strongly affect the distribution of kelp through the study region (Andrew & Underwood, 1993). Explanatory variables for the kelp SDM were selected by trialling explanatory variable combinations in a generalized additive mixed effects modelling (GAMM) framework, with the most parsimonious kelp SDM (optimal model) selected using the Akaike information criteria (AIC). The optimal model predicts the spatial distribution of kelp cover (Figure 1a) as a function of: (1) summer maximum temperatures at the seabed (Figure 2a), (2) average photosynthetically available radiation (PAR) at the seabed (Figure 2b), and (3) the density of urchins (Figure 2c), with these variables all found to be significant predictors of kelp occurrence off eastern Australia (see Appendix S1). Summer maximum temperatures were chosen as these were found to provide a stronger predictor of kelp distributions in model development, when compared against average annual temperatures. We note that the kelp SDM could potentially be improved by including a more detailed relationships between urchin densities, rates of grazing and kelp loss, to more accurately reflect the complex temperature- and density-dependent nature of urchin consumption of kelp.

Relative urchin densities utilized in the kelp SDM were calculated from the urchin SDM. This quantified the abundance of urchins throughout the spatial extent of the study for incorporation into the kelp SDM, which is dependent on information on urchin densities to accurately estimate kelp cover. To develop the urchin SDM, data on relative urchin densities from 200 m transects were matched to a suite of potential explanatory variables that are likely to be important predictors of urchin density. Urchin density was modelled using GAMMs fitted using a negative-binomial distribution. The most parsimonious urchin SDM from our set of exploratory models was selected using AIC. This model predicts the spatial distribution of relative urchin densities using two explanatory variables: (1) summer maximum temperatures at the seabed (Figure 2d), and (2) water depth (Figure 2e), with these variables found to be significant predictors of relative urchin densities (see Appendix S2). A full description of the methodology used to develop and evaluate these SDMs is provided in Davis et al. (2021) and included in Appendices S1–S3.

### 2.4 | Kelp distribution and biomass

The current distribution of kelp biomass in the study area was estimated in 0.083° latitudinal increments, from 28.0 to 37.5°S, and for 5 m depth classes from 0 to 40 m (Figure 1c). Estimates were made using satellite-derived historical data, for summer maximum temperatures and average photosynthetically available radiation, at the seabed (see Appendix S3). Biomass for subdivided reef polygons ($B_{ij}$ kg), at latitude (i) and depth (j), was calculated using the relationship: $B_{ij} = M \times A_{ij} \times C_{ij}$ where: $M =$ average biomass (wt. weight) of kelp per square metre at 100% cover, $A_{ij} =$ area of reef in subdivided reef polygon (Figure 1d) and $C_{ij} =$ kelp SDM predictions for kelp percentage cover (Figure 1a). The average wet weight of kelp per square metre ($M = 11.50 \text{ kg.m}^{-2}$) was quantified using 6–9 replicate 0.25 m² kelp samples, collected across a range of depths (3-15m) from six sites along the NSW coast (see Appendix S4).

Total kelp biomass ($B = 1.5 \text{ Mt}$) was calculated by summing the biomass for all subdivided reef polygons across the full range of latitudes and depths being considered: $B = \sum B_{ij} ($kg$). The greatest concentration of kelp biomass (~0.96 Mt°⁻¹) was predicted to currently occur at ~33.75°S, where relatively high kelp cover (Figure 1a) coincides with extensive areas of consolidated reef (Figure 1d).

### 2.5 | Climate change projections

Projections for kelp distributions and total biomass were made for the period 2090–2100 under representative concentration pathway scenarios 2.6, 6.0 and 8.5 (IPCC, 2014), with the latter most closely align with current climate trends (Schwalm et al., 2020). Projections required information about future changes to the key explanatory variables. It was assumed that these changes would impact both relative urchin densities and kelp, with changes in urchin densities, in turn, influencing kelp distributions. However, given the indirect nature of these ecological interactions with urchins, future distributions of kelp biomass were calculated both with and without urchin interaction effects. It should be noted though that the inclusion of
ecological interactions with urchins markedly improves model accuracy (Davis et al., 2021). Loss of kelp from the coast was projected to occur at those latitudes where kelp biomass was predicted to fall below 5% of current biomass levels under future climate change scenarios.

For future projections, future water temperatures at the seabed (Figure 3b–d) were calculated by applying temperature differences, between nominal present-day (2002–2009) and future (2090–2100) summer maximum SST (Figure 3a), as increments to current summer maximum temperatures at the seabed. Future temperature data were extracted from the Bio-ORACLE model (Tyberghein et al., 2012), for climate change scenarios RCP 2.6, RCP 6.0 and RCP 8.5, at 0.083° latitudinal increments along the coast, with coastal water temperatures in eastern Australia projected to increase by an average of 0.8, 2.3 and 3.4°C under RCPs 2.6, 6.0 and 8.5 respectively. Future average PAR levels were assumed to be unchanged from current levels, with projections utilizing a historical average encompassing the period (2009–2018) for this predictor. The effects of future changes to ocean mixing and vertical stratification, on seabed temperatures and PAR, were not included in modelling.

3 | RESULTS

The stacked-SDM revealed that substantial shifts in distributions of kelp and urchins are likely to occur along the NSW coast by 2100, with the magnitude of these responses varying among climate change scenarios (Figures 4 and 5). Reductions in relative urchin densities are projected to occur at high latitudes under all climate change scenarios (Figure 5). Projections for total kelp biomass, from 28.0 to 37.5°S, indicated that net gains in kelp biomass are expected under RCP 2.6 by 2100, both when biological interactions are considered (+18.5%) and when these are ignored (+3.7%; Figure 6). Similarly, for RCP 6.0, a substantial increase in kelp biomass (+29.4%) is projected when considering biological interactions, whereas a small reduction (−4.0%) is projected where these are ignored. Contrastingly, for RCP 8.5, losses in kelp biomass are projected, although these losses are much more moderate when biological interactions are considered (−3.5%) compared to when they are ignored (−35.2%).

When examining patterns of change in kelp biomass latitudinally, all models forced under all RCP scenarios projected substantial losses of kelp biomass at low latitudes by 2100 (<−33°S, Figure 4b),
with temperatures at the seabed above −26°C associated with an absence of kelp cover. These losses are projected predominantly for shallow–intermediate depth reefs (i.e. <20 m) where the majority of current kelp biomass is concentrated (Figure 1c). No latitudinal range contractions were projected for kelp under RCP 2.6, with kelp projected to persist on deeper reefs (>20 m) at low latitudes under this scenario. Contrastingly, under RCP 6.0 and RCP 8.5, kelp is projected to be unable to persist on many deeper reefs at low latitudes, resulting in range contractions of 55 and 276 km of coastline, respectively.

It is projected that biomass losses at low latitudes will be offset by increases in kelp biomass at high latitudes (≥33°S) by 2100 as well as an increase in kelp at greater depths in mid-latitudes. The magnitude of these increases is highly dependent on biological interactions, latitude, water depth and climate change scenario. For RCP 2.6, increases in kelp biomass at high latitudes are projected across the entire depth range, whereas for RCP 8.5, increases are generally restricted to deeper reefs (>20 m; Figure 4b). To tease apart the relative influence of temperature (Figure 4a) versus grazing in promoting kelp biomass increases at high latitudes, we examine each independently and identified that these increases result from a combination of both temperature and grazing (Figure 4b). Increases in kelp biomass, from temperature effects alone (Figure 4a), will occur where temperatures increase from sub-optimal conditions into the optimal range for promoting high kelp cover and biomass (i.e. −22–24°C; predicted from our models), with the contribution of increasing temperatures, to changes in kelp biomass at high latitudes, ranging from +50.8% for RCP 2.6 to −3.7% for RCP 8.5, whereas increases in kelp biomass due to biological interactions alone will occur due to substantial projected reductions in relative urchin densities at high latitudes under climate change (Figure 5), likely resulting in reductions in grazing on kelp. The contribution of biological interactions, to changes in kelp biomass at high latitudes, is projected to range from +49.2% for RCP 2.6 to +103.7% for RCP 8.5.

4 | DISCUSSION

Stacked-SDM modelling highlighted the importance of considering ecological interactions and environmental conditions at the seabed to generate accurate predictions of future kelp distribution and biomass. Incorporating ecological interactions with urchins reduced projected losses of kelp biomass by 14.8–33.4%. Similarly, considering variation in water temperatures with depth also substantially reduced (−48% to −66%) previous projected range contractions for kelp (Castro et al., 2020; Martínez et al., 2018). Furthermore, our consideration of temperature variation with depth identified that vertical redistributions in kelp biomass are likely to occur, with kelp expected to migrate into cooler deeper water refugia as oceans warm into the future.

4.1 | Effects of ecological interactions on future kelp biomass

Ecological interactions with the urchin C. rodgersii had a profound influence on projected future kelp biomass in eastern Australia. Incorporating this key ecological interaction into future projections reduced projected kelp biomass loss by 14.8%, 33.4% and 31.7% under RCPs 2.6, 6.0 and 8.5, respectively. This highlights the considerable effect that biotic interactions can have on SDM predictions.
Indeed, when considering ecological interactions, only small net losses in kelp biomass (−3.5%) were seen under the most severe RCP8.5 scenario. In eastern Australia grazing by the urchin *C. rodgersii* creates extensive urchin barrens devoid of kelp (Davis et al., 2020; Ling, Johnson, Frusher, et al., 2009) with experimental removal of urchins resulting in rapid increases in kelp cover and biomass (Andrew...
Consequently, climate-induced reductions in urchin densities at higher latitudes will likely lead to reduced grazing on kelp and consequent increases in kelp biomass. Interestingly, this study did not account for the decreased future transport of urchin larvae equatorward of latitudes 36°S (Coleman et al., 2017) which may further reduce urchin densities and enhance kelp biomass along much of this coastline under future climate change scenarios.

4.2 | Changes to total kelp biomass and geographical distribution

Coastal water temperatures in eastern Australia are projected to increase by an average of 0.8, 2.3 and 3.4°C under RCPs 2.6, 6.0 and 8.5, respectively (Tyberghein et al., 2012). These changes are projected to cause extensive impacts on urchin densities and kelp
biodiversity, with stacked-SDM predictions shedding new light on the future for *E. radiata* in eastern Australia. Net kelp biomass is projected to increase under RCP 2.6 and RCP 6.0, by 18.5% and 29.4%, while even under the more severe RCP 8.5 "business-as-usual" scenario only small biomass losses (~3.5%) are projected to occur by 2100. Additionally, no latitudinal range retraction for kelp are projected to occur by 2100 for RCP 2.6, while relatively small (55 km, ~5% loss) to moderate (275 km, ~27% loss) range contractions are projected by 2100 under RCP 6.0 and RCP 8.5.

These predictions are more optimistic than previous predictions by Martínez et al. (2018), who concluded that losses of 49% and 71% would occur for *E. radiata*, across Australia by 2100, under climate change scenarios RCP 2.6 and RCP 6.0, respectively. Our predictions for 2100, under RCP 8.5, are also more optimistic than those by Castro et al. (2020), who predict a 530 km range contraction for kelp in eastern Australia by 2100. These contrasting findings are predominantly due to three factors not fully considered in previous modelling, but incorporated into the current study: (1) kelp cover is strongly impacted by ecological interactions with the urchin *C. rodgersii*, with these urchins also experiencing concomitant effects from climate change; (2) kelp distributions are influenced by water temperatures at the seabed, which are substantially lower than SST; and (3) kelp distributions are influenced by the availability of suitable reef habitat, which varies substantially with latitude and depth. However, this study did not account for the effects of marine heatwaves, which are projected to increase in frequency and severity (Oliver et al., 2018), and which cause lasting negative impacts for kelp communities (Wernberg, 2021). Future modelling efforts could be further refined by considering additional factors known to influence kelp such as heatwaves and herbivory by range extending tropical fishes and urchins at low latitudes, although these herbivory effects are often secondary impacts that prevent kelp recovery following loss from direct impacts from temperature increases (Vergés et al., 2016; Wernberg, Bennett, et al., 2016).

### 4.3 | Latitudinal redistributions of kelp biomass

While at a regional scale our projected changes to net kelp biomass are generally positive under future climate scenarios, at a local scale there is more cause for concern. Notably, projected changes do not occur uniformly across the latitudinal range examined. Rather, extensive kelp biomass losses are projected to occur on reefs at low latitudes (<33°S), while these losses are offset by biomass gains, which are generally restricted to reefs at high latitudes (>33°S). This latitudinal redistribution will result from temperature having varying impacts on urchin densities, kelp survival and a range of kelp physiological processes including reproduction, photosynthesis and respiration (Wernberg et al., 2019).

While *E. radiata* occupies a niche in which temperatures range from 8 to 26°C (Bolton & Anderson, 1987), conditions towards the upper end of this niche (~24°C) are nominally optimal for kelp growth (Wernberg et al., 2019), while temperatures above ~26°C are generally unsuitable for *E. radiata* survival and reproduction (Bolton & Anderson, 1987). Therefore, projected increases in water temperatures on low latitude reefs, where temperatures are currently near the upper thermal limit for kelp (i.e. 26°C), will lead to increased kelp mortality and reduced kelp biomass on reefs. Consequently, the upper thermal limit for kelp survival will impose the future northern limit on the distribution of *E. radiata* in eastern Australia and temperature increases at the seabed, above this threshold, will cause the poleward range contractions for kelp projected under the more severe future climate scenarios examined (RCPs 6.0 and 8.5).

Conversely, for higher latitude reefs, increases in water temperatures are projected to improve conditions for kelp growth, generally causing increases in kelp biomass. Indeed, net photosynthesis of *E. radiata* increases with increasing temperature up to an optimum at ~24°C before falling sharply above this temperature (Wernberg et al., 2016). Consequently, temperature increases on reefs where summer temperatures are currently <24°C will tend to improve conditions for kelp photosynthesis, promoting increased kelp cover and biomass. Temperature increases on the south coast are also projected to cause reductions in urchin densities, resulting in reduced grazing, thereby enhancing kelp biomass. Consequently, temperature influences kelp cover both directly, through kelp’s thermal sensitivity, and indirectly, through temperature’s effects on urchin densities. Therefore, we predict that reduced urchin predation, acting in concert with enhanced temperatures for growth, will lead to substantial local increases in kelp biomass on high latitude reefs in mainland eastern Australia by 2100, even under the severe business-as-usual scenario RCP 8.5.

### 4.4 | Vertical redistributions in kelp biomass

Interestingly, our modelling indicates that the effects of reduced grazing and rising water temperatures will interact to lead to a vertical redistribution in kelp biomass at intermediate latitudes, particularly under RCP 8.5. At these latitudes, kelp is expected to undergo substantial declines on shallow reefs, due to temperatures often exceeding kelp thermal tolerances, while simultaneously increasing on cooler, deeper reefs, due to reduced urchin predation and temperatures remaining within the optimal range for growth.

These projected vertical migrations for kelp mimic those of terrestrial plant and animal species in mountainous areas, where cold-adapted species are being forced to retreat to higher altitudes, where temperatures are cooler, as global air temperatures rise (Dirnböck et al., 2011; Trivedi et al., 2008). Similar retractions of kelp, to colder deep waters, are believed to have occurred in previous geological periods, with deeper water acting as refugia during past periods of ocean warming (Assis et al., 2016; Graham et al., 2007). The general trend for lower temperatures to occur in deeper waters means that deeper reefs in eastern Australia also have the potential to provide future refugia for kelp (Davis et al., 2021). This is already evident in deep waters off Moreton Island (27°S), where SST currently exceeds kelp thermal tolerance levels, yet kelp persists at depths
>20 m (Marzinelli et al., 2015) and even as deep as 80 m (Richmond & Stevens, 2014). Our modelling suggests that, by 2100, only deeper reefs at low latitudes in eastern Australia will harbour kelp, while shallow reefs will, most-likely, transition to alternate tropical states as temperatures increase beyond the thermal limit for kelp survival (Vergés et al., 2019).

This vertical stratification will occur predominantly due to the substantial decline in temperature that occurs as depth increases off eastern Australia, with average summer water temperatures typically falling by ~5°C (at 28.0°S) as depth increases from 0 to 40 m. These depth-related reductions in water temperature are of comparable magnitude to the typical latitudinal variations in water temperature that occurs along the entire east Australian coastline (~6°C from 28.0 to 37.5°S). Therefore, depth will play a key role in determining the future distributions of kelp and other marine species as climate changes. Consequently, consideration of water temperatures at the seabed, rather than SST, as well as the availability of reef habitat, is imperative when modelling the redistribution of marine species.

5 | CONCLUSION

Our findings highlight the importance of incorporating key ecological interactions and biologically relevant environmental data (e.g. temperature at the seabed) when projecting changes to the distribution and biomass of marine species. Specifically, we provide valuable new insights into current and future distributions of kelp biomass along the coast of eastern Australia. Modelling indicates that future distributions of kelp will change by 2100, due to the impacts of climate change-induced ocean warming. Kelp is expected to contract at the northern limit of its range and to migrate to deeper waters, due to ocean warming exceeding kelp tolerance limits. However, future losses of kelp biomass at low latitudes are projected to be offset by increases in biomass at high latitudes and at depth, due to reduced urchin predation and temperatures shifting into a more optimal range. We suggest that careful parameterization of species distribution models with environmental and biotic variables known to drive species distributions and abundance is paramount for generating accurate predictions and meaningfully informing future conservation of key habitat-forming species such as kelp.

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CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Dryad data set: https://doi.org/10.5061/dryad.r4xgd2dm.

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BIOSKETCH

The authors are focussed on research examining the impacts of climate change on marine habitats and species. Research includes investigation of current and future impacts of climate change on kelp forests, marine ecosystems and important commercial and recreationally targeted fish species.

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SUPPORTING INFORMATION

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