

Article

Impacts of Climate Change on Densities of the Urchin *Centrostephanus rodgersii* Vary among Marine Regions in Eastern Australia

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Abstract: The urchin *Centrostephanus rodgersii* is expanding its range southward in eastern Australia, which has been associated with negative ecological impacts, including shifts from kelp forests to barrens. However, limited analyses are available that examine the factors influencing its abundance and distribution across the entirety of this range. Here, we utilise data from 13,085 underwater visual census surveys, from 1992 to 2022, to develop an urchin density model for *C. rodgersii* across its historical and extending geographical range. We apply this model to examine whether *C. rodgersii* densities are increasing and to project future urchin densities by 2100 under IPCC climate scenario RCP 8.5. Significant increases in *C. rodgersii* densities were detected in data for the South-east marine region of Australia, which encompasses Tasmania, Victoria, and the far south coast of New South Wales (NSW) over the last 30 years. In the Temperate East marine region (encompassing Queensland and NSW waters to 36.6° S), however, no significant increases in densities were observed. Future projections indicated that further substantial increases in *C. rodgersii* densities are likely to occur in the South-east marine region and substantial reductions in most of the Temperate East marine region by 2100. Importantly, results indicate that current and future changes to *C. rodgersii* densities in Australia vary among marine regions. Therefore, the future ecological impacts of urchins on temperate ecosystems, including the formation of barrens, will also vary among regions. Consequently, management actions will need to differ among these regions, with the South-east marine region requiring mitigation of the impacts of increasing *C. rodgersii* densities, whereas the Temperate East marine region may need actions to preserve declining *C. rodgersii* populations.

Keywords: echinoderm; range expansion; species distribution model



Citation: Davis, T.R.; Knott, N.A.; Champion, C.; Przeslawski, R. Impacts of Climate Change on Densities of the Urchin *Centrostephanus rodgersii* Vary among Marine Regions in Eastern Australia. *Diversity* **2023**, *15*, 419. <https://doi.org/10.3390/d15030419>

Academic Editor: Michel Baguette

Received: 13 February 2023

Revised: 8 March 2023

Accepted: 9 March 2023

Published: 13 March 2023



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1. Introduction

There is heightened public awareness about the negative effects of climate change on marine environments, driven by factors including rising ocean temperatures, ocean acidification, and species range shifts [1,2]. Amongst these, species range shifts by sea urchins have been linked to the loss of kelp and the formation of urchin barrens (barrens), resulting in dramatic changes to temperate ecosystems [3–5].

The long-spined sea urchin *Centrostephanus rodgersii* is a native species to the warm-temperate east coast of mainland Australia [6], which is known to contribute to the formation and persistence of barrens [7,8]. Historically, the distribution of *C. rodgersii* in Australia stretched from Southern Queensland to the Bass Strait, with the species absent in Tasmania [9]. However, *C. rodgersii* has recently extended its range into Tasmania, with this range expansion understood to be related to climate-driven ocean warming [5] and the thermal tolerances of its larvae [10]. This range expansion has created extensive new areas

of barrens, with an associated loss of kelp forests and the ecosystems these support [11]. Consequently, in Tasmania, *C. rodgersii* is considered a pest species, and there is heightened public concern about the role that *C. rodgersii* has played in the loss of kelp forests [5].

This concern has also become prevalent in regions within the urchin's natural range. Furthermore, the realisation that extensive barrens exist in these regions has led to fears that these areas may have also been affected by urchin overgrazing. However, an alternative model is that these barrens may be a natural part of marine ecosystems along the east coast of Australia, where they are known to have been stable for many decades [12]. Therefore, an understanding of how *C. rodgersii* urchin distributions and densities may have changed through time and may change in the future is needed to help inform this current debate and management actions.

Within the historic distributional range of *C. rodgersii*, barrens are considered part of the natural mosaic of habitats along with the kelp *Ecklonia radiata* [8,13]. Early studies found that *C. rodgersii* do not have consistent abundance patterns spatially [14], whereas more recent studies indicate that *C. rodgersii* urchin abundances vary greatly with latitude, water depth and proximity to estuaries [15,16]. Temporal studies have shown that NSW *C. rodgersii* populations are stable over years [17], but small-scale reductions have been observed in response to low-salinity nearshore waters [18]. Findings from NSW contrast with those from recent studies examining *C. rodgersii* populations in Tasmania, where the species has undergone significant population growth due to range extensions [19]. Currently, limited data are available examining the factors influencing the densities of *C. rodgersii* across its entire newly expanded range. Therefore, further investigation is needed to examine the drivers of variation in *C. rodgersii* densities across this range and to verify whether observed shifts in urchin densities are comparable among different Australian marine regions, as defined by Richardson et al. [20].

Here, we utilise data on *C. rodgersii* densities spanning 30 years from the Reef Life Survey (RLS) and Australian Temperate Reef Collaboration (ATRC) programs to examine changes in *C. rodgersii* densities throughout the species' current eastern Australian distribution and identify the influence of explanatory factors on urchin densities. It was hypothesised that climate change has caused increases in densities on higher latitude reefs, in the South-east marine region, due to recent ocean warming (~ 0.21 °C decade⁻¹, [21]) facilitating species range extensions, but is unlikely to have caused substantial changes to densities in the Temperate East marine region, as *C. rodgersii* populations are already well established within this region. Models developed to explain the past and current distributional patterns in *C. rodgersii* densities were then applied to project future changes to urchin densities by 2100, with these projections needed to inform future management actions. Future projections were made for representative concentration pathway scenario 8.5 (RCP 8.5) [22], as this scenario most closely aligns with the current trajectory of climate change [23].

2. Materials and Methods

2.1. Study Area and Data Collection Methods

This study examined *C. rodgersii* density data from two research programs. RLS is a citizen science program that collects high-quality underwater visual census data in close collaboration with university ecologists [24]. ATRC is a long-term university and government collaboration with professional ecologists sampling specific sites [25]. The RLS methodology includes underwater visual censuses on 50 m transects set on hard reefs along a depth contour (generally at depths < 20 m). Divers undertake three survey methods along each transect to capture the majority of large biota that can be surveyed visually: fishes (method 1), mobile invertebrates and cryptic fishes (method 2), and photoquadrats of the substrate (method 3). ATRC data are collected using similar methods as for RLS, but with 200 m transects. Data on *C. rodgersii* presence/absence and abundances were obtained from the RLS and ATRC method 2 data from 1992 to 2022. Surveys quantified all large mobile invertebrates (echinoderms, molluscs, and crustaceans > 2.5 cm) in duplicate

1 m wide belts on either side of transects for RLS surveys and in a single 1 m-wide belt for ATRC surveys. Urchin absence was inferred when method 2 surveys were conducted and no urchins were recorded. Abundance data were divided by the area surveyed to quantify *C. rodgersii* density. Details of RLS survey methods, diver training and data quality assessment are described in [26,27].

Only data from sites within the geographical bounds where the presence of *C. rodgersii* had been recorded were included in the modelling, resulting in a study area spanning from southeast Queensland (153.63° E, 27.3° S) to eastern Victoria and Tasmania (145.92° E, 43.36° S, Figure 1a). Data from surveys outside this area were excluded from modelling, as recommended by Zuur et al. [28], to avoid zero inflation through the inclusion of data from regions where *C. rodgersii* has never been found. Screening resulted in the selection of data from 13,085 standardised surveys at depths ranging between 1 and 40 m. These surveys were undertaken at 573 locations by RLS divers between 2008 and 2022, and at 335 locations by ATRC between 1992 and 2022 [25]. All data were obtained from the Australian Open Data Network (AODN) web portal (portal.aodn.org.au, accessed on 22 November 2022).

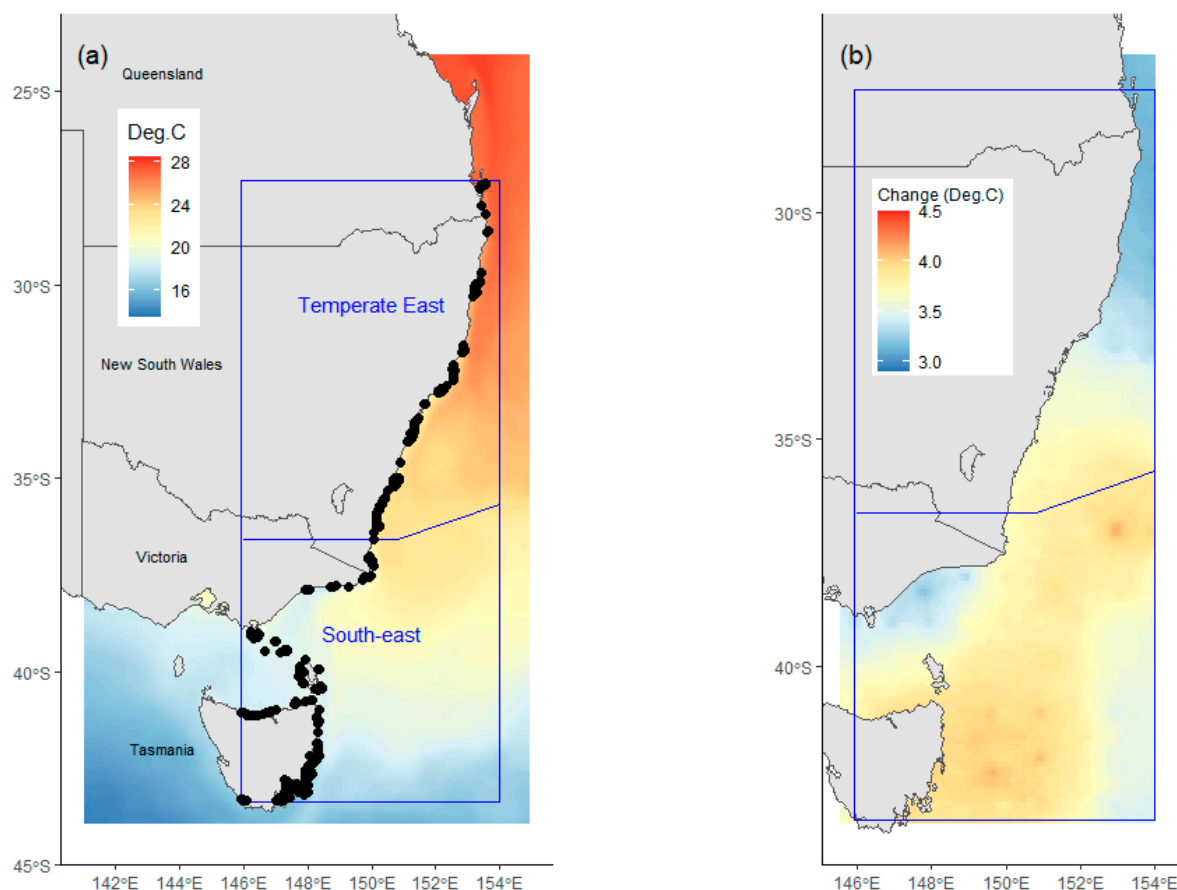


Figure 1. (a) Study area in Australia separated into marine regions (blue rectangles) showing (a) sampling locations (dots) and average February (i.e., summer) water temperature (2002–2009) at a depth of 0.5m. (b) Projected change in sea surface temperatures by 2100 under RCP 8.5. Future temperature data are from the Bio-ORACLE model [29].

2.2. *Centrostephanus rodgersii* (Urchin) Density Modelling

Centrostephanus rodgersii densities were modelled using a generalised additive mixed effect model (GAMM) framework using a negative binomial distribution. Urchin density data were square-root transformed prior to modelling to reduce skewness. Urchin data were aggregated so that all data from surveys conducted at the same site, in the same month, and in the same depth range (within 5 m) were averaged. Averaging was applied to reduce

overfitting models to the data, due to autocorrelation among samples with close spatial and temporal proximities [30]. Models were parameterised using the *mgcv* package [31] in R [32].

Models were developed using selected explanatory variables of physiological importance to *C. rodgersii*, with the contributions of each explanatory variable to the model explored through backward stepwise selection; i.e., successively removing individual variables that explained the least amount of variance. The optimal model was selected based on the Akaike information criteria (AIC). The explanatory variables examined were:

1. Water temperature at the sampling depth (Tz). Water temperature at depth was selected as a potential explanatory variable, rather than sea surface temperature (SST), as substantial variations in temperature occur with depth within the depth range where urchins are present [16]. Temperature is a key driver of *C. rodgersii* biological processes, including reproduction and larval survival [33,34]. Water temperatures (Tz) for model development were calculated as the mean of average monthly temperatures in February (i.e., summer maximum) over the period of 2002–2009. Summer temperatures were used as these have been shown to be a more powerful predictor of *C. rodgersii* densities than annual average temperatures [16]. Water temperatures at sampling depths were extracted from the E.U. Copernicus Marine Service (<http://marine.copernicus.eu> (accessed on 2 December 2022)), using the Global Ocean Physics Reanalysis monthly mean product (PHY_001_030). Data at the sampling depths were extracted at the closest depth available in the oceanographic re-analysis product;
2. Water depth at the sampling site (Depth). Depth was selected as a potential explanatory variable as depth influences a range of factors including pressure, light, and wave exposure and is correlated to *C. rodgersii* densities [16]. Depth was recorded at each transect;
3. Sampling date (Date). Date was included as a potential explanatory variable to allow the investigation of whether changes in *C. rodgersii* densities occurred over time. Date was incorporated as Julian day numbers throughout the study period;
4. Australian marine region (Region). The region was included as a potential explanatory variable to test the hypothesis that changes in *C. rodgersii* densities over time varied among distinct marine regions. To achieve this, the effects of Date on urchin densities were examined separately in each of the marine regions present. The study area encompassed sections of two distinct marine regions, the Temperate East region and South-east region (Figure 1a), as defined by Richardson et al. [20].

2.3. Historical *C. rodgersii* Urchin Density Predictions and Climate Change Projections

Following the development of the optimal *C. rodgersii* density model, historical predictions and future projections of urchin densities were made throughout the study area for three scenarios:

1. Predictions for past *C. rodgersii* densities were made using average summer temperatures at depth (1–40 m), using data from the aforementioned oceanographic reanalysis product for the period 1990–2000;
2. Predictions for nominal current *C. rodgersii* densities were made based on average summer temperatures at depth, using data from the same oceanographic reanalysis product for the period 2010–2020;
3. Projections for future *C. rodgersii* densities, under RCP 8.5, were made using projected future average summer temperature at depth, for the period 2090–2100.

For projections, future temperatures were calculated by adding projected changes to ocean temperatures, between the periods 2002–2009 and 2090–2100, obtained from the Bio-ORACLE model [29] (Figure 1b), to average summer temperature at depth values for the period 2002–2009, from the oceanographic reanalysis product. The use of Bio-ORACLE SST data to derive future summer temperatures at depth was an approximation necessitated by a lack of available future projections for temperatures at depth. This approximation was deemed to be acceptable as future changes to vertical temperature stratification are likely to be small compared to future changes in SST. Furthermore, the addition of ocean

temperature change values obtained from the Bio-ORACLE model to historical data from the oceanographic reanalysis produce improves comparability between past, nominal current, and future estimates of *C. rodgersii* densities.

3. Results

3.1. Reef Life Survey and ATRC Urchin Data

Presences of *C. rodgersii* were recorded in data from Moreton Bay in Queensland (27.39° S) to the Derwent River in Tasmania (43.35° S, Figure 2). Very low urchin densities were recorded at the northern and southern extremes of this distribution, as was to be expected with these data encompassing the entire realised niche for the species. A maximum density of 24.1 urchins.m⁻² was recorded at Jervis Bay (35.05° S) in March 2009, with an average density of 0.89 ± 0.02 urchins.m⁻² across the entire current distribution.

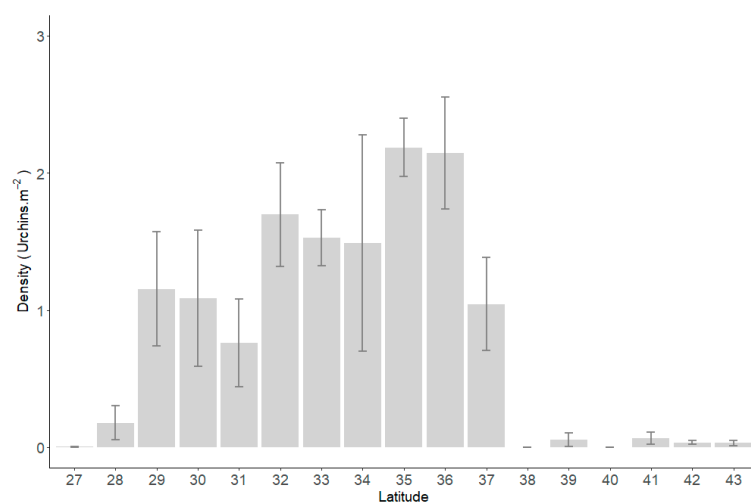


Figure 2. Average density of *Centrostephanus rodgersii* urchins on Reef Life Survey transects for one-degree latitudinal bins eastern Australia. Averaging conducted for all sites in each bin, across all survey dates (1992–2022) and depths (1–40 m). Error bars \pm Standard Error.

3.2. Key Drivers of *C. rodgersii* Density Variations

Modelling to determine the significance of factors influencing *C. rodgersii* densities found that temperature (Tz), Depth, Date and Region were all significant factors in the optimal model developed (i.e., lowest AIC, Table 1). This optimal model explained 44.3% of the variation in urchin densities, with all explanatory variables making significant contributions to the model, although Date only made a significant contribution to the model in the South-east region (Table 2).

Table 1. Backward stepwise selection of explanatory variables for models to explain *C. rodgersii* urchin densities at sites in Australia. Tz = average from 2002 to 2009 of the summer monthly (February) temperature at depth (z). Depth = average survey depth (m). Date:Region = survey date by region (East, South-east).

Model	Variables	AIC	Δ AIC	Deviance Explained
1	Date:Region + Depth + Tz	20,276.8	0.0	44.3%
2	Depth + Tz	20,436.9	160.1	42.2%
3	Tz	20,704.1	427.3	38.9%

Table 2. Contribution of variables to the optimal model for describing *C. rodgersii* urchin density variations across sites in Australia. Tz = average from 2002 to 2009 of the summer monthly (February) temperature at depth (z). Depth = average survey depth (m). Date:Region = survey date by region (Temperate East, South-east).

Variables	Effective Degrees of Freedom	p-Value
Tz	4.948	<0.001
Depth	4.828	<0.001
Date:Region (Temperate East)	1.012	0.496
Date:Region (South-east)	4.234	<0.001

Of the explanatory variables, temperature provided the greatest explanatory power, explaining 38.9% of the variation when considered in isolation. The effect of temperature on *C. rodgersii* densities was non-linear, with low densities occurring at temperatures of 17–19 °C, densities increasing to a plateau from ~21 to 24 °C and densities then rapidly decreasing as temperatures approached 26 °C (Figure 3a). In relation to depth, urchin densities gradually increased with increased depth from 10 to 20 m and then rapidly decreased with depth as this approached 40 m (Figure 3b). Changes over time (as Date) differed between marine regions. In the Temperate East region, there were no significant changes in densities over time (Table 2, Figure 3c). Contrastingly, in the South-east region, there were significant changes over time (Table 2), due to a significant increase in *C. rodgersii* densities over time ($p < 0.001$, Figure 3d).

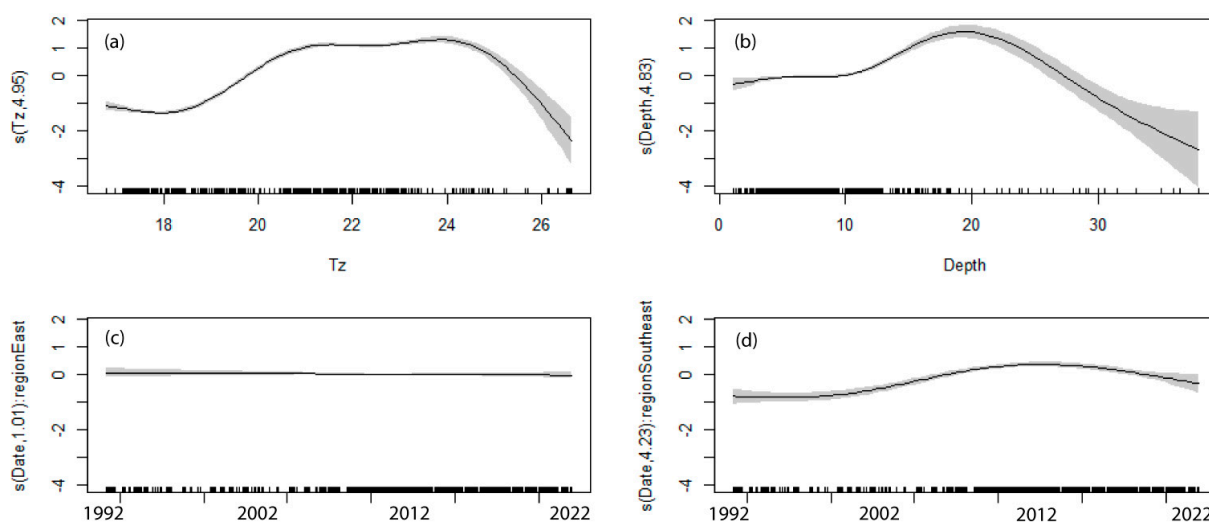


Figure 3. Effects of explanatory variables on *C. rodgersii* urchin densities for the optimal explanatory model developed for Australia. Solid lines show average predicted values with shaded areas showing standard errors and small vertical marks along the x-axis show data points. (a) Effect of summer water temperature at depth (Tz), (b) effect of depth, (c) effect of survey date in Temperate East region, and (d) effect of survey date in South-east region.

3.3. Predicted and Projected *C. rodgersii* Densities

Model predictions for historic *C. rodgersii* densities, from 1990 to 2000 (Figure 4a) reflect the high abundances of urchins through the Temperate East region (the native range) with low densities into the South-East region. Model predictions for nominal current *C. rodgersii* densities (2010–2020) reflect the significant increase in densities in the South-east region that has occurred as part of the urchin range expansion (Figure 4b). Simultaneously, predictions indicate declines in *C. rodgersii* densities in the north of the Temperate East region in 2010–2020, when compared to 1990–2000 (Figure 4a,b).

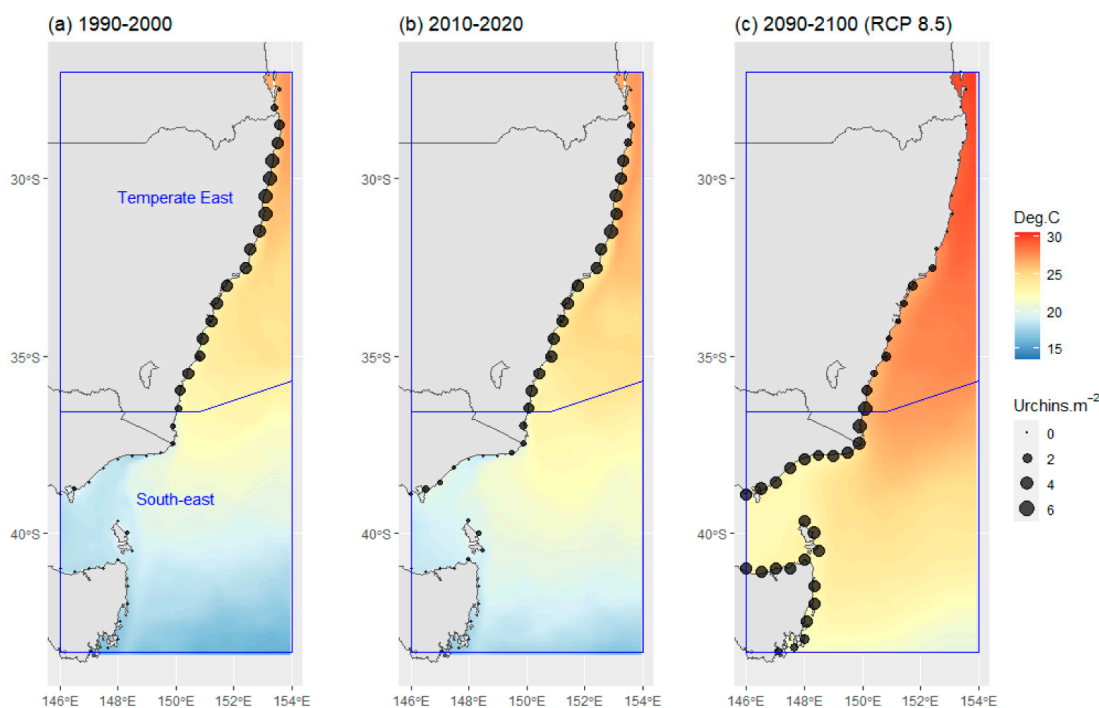


Figure 4. *Centrostephanus rodgersii* urchin density predictions and projections made using the optimal explanatory model developed for Australia. (a) Predictions for average densities from 1990 to 2000, (b) predictions for average densities from 2010 to 2020, (c) projections for average densities under climate change scenario RCP 8.5 for the period 2090–2100. Contours show average summer maximum (February) temperatures for the reference period. Blue boxes indicate distinct marine regions in Australia as shown in Figure 1a [20].

Application of the model to future projections of *C. rodgersii* densities (2090–2100), under RCP 8.5, indicated that there could be a dramatic southward shift in the distribution of urchin densities by 2100 (Figure 4c). Large increases in *C. rodgersii* densities are projected across the South-east region by 2100, with these increases balanced by substantial reductions in urchin densities throughout much of the Temperate East region, particularly at lower latitudes (Figure 4c).

4. Discussion

This study demonstrates that *C. rodgersii* densities are changing differently in different marine regions in Australia and indicates that densities are not consistently increasing throughout the species' range. Our results support the hypothesis that ocean warming has driven increases in densities on higher latitude reefs in the South-east region and indicate that warming has not caused substantial changes to *C. rodgersii* densities in the Temperate East region, although modelling suggests that declines in the north of the Temperate East region may be occurring. Findings are consistent with the previously documented range expansion of *C. rodgersii* into Tasmania, with significant increases in its abundance occurring in the South-east region [5,19] and with studies from NSW that have identified that *C. rodgersii* is a stable feature of ecosystems in the Temperate East region [12,35].

Future projections, based on IPCC scenario RCP 8.5, indicate that there will be marked changes in the distribution of *C. rodgersii* across south-eastern Australia. Substantial shifts in the distributions and densities of *C. rodgersii* are projected by 2100, with changes expected to differ markedly among regions. Substantial increases in densities are projected in the South-east region, whereas range contractions are projected in the north in the Temperate East region, accompanied by considerable declines in densities across most of the region. Projections for the Temperate East region are generally in agreement with those made by

Davis et al. [36], who also projected substantial declines in *C. rodgersii* densities in NSW by 2100 under RCP8.5. However, Davis et al. [36] projected that these declines would occur throughout NSW, whereas our modelling indicates that declines will be concentrated in northern and central NSW, with increases in *C. rodgersii* densities possible on the southern NSW coast. The differences between these model projections are most probably due to variations in the geographical and temporal extent and quality of the urchin data used for model construction. The Davis et al. [36] study was based on towed video surveys conducted in NSW in 2020, whereas the current study was based on underwater visual census (UVC) data collected over 30 years across the entire geographical distribution of *C. rodgersii* in Australia. Therefore, we argue that the current study is likely to provide a more reliable projection of changes, particularly for southern NSW which is at the boundary of the Davis et al. [36] model. Long-term datasets such as the one used in this study are crucial to confidently monitor range shifts and changes in abundance. The early identification and understanding of ecological shifts and the potential issues that may occur then provide the opportunity to tailor appropriate management actions for population conservation or reduction, as required.

It should be noted that future shifts to urchin densities and distributions will be influenced by a range of other unquantified factors, which were not examined in this study. These unquantified factors include physical and hydrological barriers to larval dispersal, changes to ocean mixing and vertical stratification, ocean acidification, and the development of novel ecological interactions. As adult *C. rodgersii* are relatively immobile, larval dispersal will play a key role in future range expansions [37], with the successful range expansion of immobile marine species dependent on conditions at a new location being suitable for larval settlement and long-term survival, and on the supply of competent larvae [38]. In eastern Australia, the larval supply for *C. rodgersii* is facilitated by strong poleward flows of the East Australian Current (EAC), which enables the long-range dispersal of pelagic larvae [37], with the EAC linked to the recent range expansion of *C. rodgersii* into Tasmania [5]. Consequently, the projected future poleward shifts in densities for *C. rodgersii* are unlikely to be limited by larval dispersal but are more likely to be limited by the prevalence of suitable conditions for larval settlement and persistence.

Modelling identified significant non-linear relationships between *C. rodgersii* densities and summer bottom water temperatures. Urchin densities were low in locations where summer bottom temperatures were in the range of 17–19 °C, high for locations at 21–24 °C, and low for locations with temperatures > 26 °C. This pattern closely matches the experimentally measured range for successful larval development of *C. rodgersii* (17.2–24.5 °C) as reported by Pecorino et al. [33] but does not compare as well against the optimal thermal range for *C. rodgersii* larvae (14.1–21.3 °C), within which, 90% of echinoplutei larvae survived, as determined by Byrne et al. [10]. These differences may reflect varying larval thermal tolerances among northern and southern populations of *C. rodgersii*. Regardless, the larval development of ectotherms is closely linked to the realised niche of adults [39] and likely imposes constraints on the distribution of *C. rodgersii* at both high and low latitudes.

The results also revealed a non-linear relationship between *C. rodgersii* densities and depth, with densities increasing up to depths of ~20 m and then decreasing with depth. This is similar to relationships reported between *C. rodgersii* densities and depth in NSW, where urchins are generally abundant from 2 to 20 m and then decrease with depth [9,40], whereas, in Tasmania, *C. rodgersii* generally occur in deeper waters (10–25 m, [9]). Given that declines in *C. rodgersii* densities are projected in the Temperate East region over the coming decades, deeper and therefore cooler offshore waters have the potential to act as refugia for urchins in this region, with these waters also expected to provide refugia for kelp against warming oceans in this region [16].

5. Conclusions

It was found that *C. rodgersii* densities are not responding to ocean warming equally across its complete current distributional range in Australia, with densities only found to be

increasing significantly in the South-east region. Future projections indicate that increases in *C. rodgersii* densities in this region will accelerate over the coming decades under the RCP 8.5 climate change scenario. Consequently, the ecological impacts of *C. rodgersii*, including the formation of barrens, are likely to increase within the South-east region by 2100. The significance of these predicted changes means that potential mitigation strategies will need to be considered, as the increases in urchin abundances are likely to place enormous pressures on kelp habitats in this region, in addition to the pressures already placed on kelp by warming waters. Contrastingly, *C. rodgersii* densities are projected to decline in the Temperate East region over the same period, with a concomitant reduction in the ecological influence of urchins on ecosystems. In this region, conservation actions to preserve declining *C. rodgersii* urchin stocks may be required. Our results support other recommendations to consider different management approaches between NSW and other regions [41].

Author Contributions: Conceptualization, T.R.D. and R.P.; Data curation, N.A.K.; Formal analysis, T.R.D. and C.C.; Funding acquisition, R.P.; Investigation, T.R.D. and N.A.K.; Methodology, T.R.D., N.A.K. and C.C.; Project administration, T.R.D.; Software, T.R.D.; Supervision, R.P.; Validation, C.C.; Visualization, T.R.D.; Writing—original draft, T.R.D. and R.P.; Writing—review and editing, N.A.K., C.C. and R.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the NSW Marine Estate Management Strategy, Initiative 3.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Publicly available datasets were analysed in this study. Water temperatures at sampling depths can be extracted from the E.U. Copernicus Marine Service (<http://marine.copernicus.eu> (accessed on 2 December 2022)). Future temperature projections can be extracted from the Bio-ORACLE portal at: <https://www.bio-oracle.org> (accessed on 15 December 2022). RLS and ATRC survey data can be obtained from the Australian Open Data Network (AODN) web portal at: <http://portal.aodn.org.au> (accessed on 22 November 2022).

Acknowledgments: We thank the enormous number of volunteer RLS divers and scientists (RLS and ATRC) who have collected data over large spatial scales and long periods of time—especially Graham Edgar, Neville Barrett, Rick Stuart-Smith, Toni Cooper, and Lizzie Oh. Thanks also to Rowan Chick for his valuable feedback which greatly improved the final manuscript. Data were sourced from Australia’s Integrated Marine Observing System (IMOS)—IMOS is enabled by the National Collaborative Research Infrastructure Strategy (NCRIS).

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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