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Research article

Climate-driven trans-Tasman population increase of the habitat-modifying, range extending sea urchin *Centrostephanus rodgersii*

Sterling B. Tebbett [a,b,*], Graham J. Edgar [a], Celia A. Balemi [c], John P. Keane [a], Nick T. Shears [c], Arie J.P. Spyksma [c], Rick D. Stuart-Smith [a], Scott D. Ling [a]

[a] *Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, 7001, Australia*
[b] *College of Science and Engineering, James Cook University, Townsville, Queensland, 4811, Australia*
[c] *Leigh Marine Laboratory, Institute of Marine Science, University of Auckland, Leigh, Aotearoa New Zealand*

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ABSTRACT

Global climate change is shifting thermal gradients in the world's oceans, resulting in the redistribution of species and thermophilisation of reefs. In the Southwest Pacific, warming has underpinned the range extension and population increase of the habitat-modifying sea urchin, *Centrostephanus rodgersii*. Eastern Tasmania and Northeastern Aotearoa New Zealand (NZ) lie at the forefront of these changes, with increases in *C. rodgersii* driving declines in kelp in these regions. However, the extent of *C. rodgersii* increases in both regions remains unclear, although given well-established thermal limits of *C. rodgersii* there appears greater potential for increases in the warmer waters of NZ than in the cooler waters of Tasmania. Here we leverage a combination of broad spatial scale data and region-specific depth-stratified data to examine regional *C. rodgersii* abundance changes in recent decades and their relation to minimum sea surface temperature (SST). The abundance of *C. rodgersii* increased 1.7-fold between 2001/02 and 2016/17 for Tasmania and 3.3-fold between 2012 and 2024 for NZ. Larger *C. rodgersii* abundance changes in NZ align with predictions based on their modelled abundance against SST. Moreover, modelled estimates suggest *C. rodgersii* abundance in NZ have the potential to increase further into the future (by ~2.7-fold at 8.1 m). While the increase in Tasmania has been well documented, these findings demonstrate a greater increase in population density in Northeastern NZ and potential for further increases. Ultimately, increase in *C. rodgersii* abundance in both regions call for the establishment, or ramping up, of management programs to curb population increases.

1. Introduction

Global climate change is reshaping the distribution of species on Earth (Parmesan and Yohe, 2003). The thermal boundaries that previously limited species ranges are being redrawn as the planet warms, allowing species to extend their ranges into new geographic areas (Chen et al., 2011). Changing temperature regimes can also mean that species within their native ranges exist closer to, or further from, their thermal optima, which can have profound effects on their population dynamics and ultimately community composition (Deutsch et al., 2008). Alterations in community composition have been particularly pronounced in the marine realm as oceans warm (Lenoir et al., 2020) and some poleward flowing currents strengthen (e.g. Ridgway and Ling, 2023). Notably, climate-driven species redistributions and population increases have already had marked ecological effects on many subtropical and temperate reefs (Vergés et al., 2014), especially when the 'thermophilisation' (*sensu* Gottfried et al., 2012) of these reef systems involves the increasing abundance of highly influential habitat-modifying species.

Sea urchins are renowned for their capacity to modify habitat structure when their populations increase (Steneck, 2013; Filbee-Dexter and Scheibling, 2014). A litany of examples exist in which sea urchins have driven large-scale temperate reef ecosystem collapse from kelp-beds to overgrazed urchin barrens (e.g. Norderhaug and Christie, 2009; Filbee-Dexter and Scheibling, 2014; Kerr et al., 2025; Ling and Keane, 2024). An example of this phenomenon is currently playing out on the temperate reefs of the Southwest Pacific, involving the diadematid sea urchin, *Centrostephanus rodgersii* (Fig. 1c). Despite being native to a geographic region encompassing the south-east coast of mainland Australia (chiefly New South Wales) east to the Kermadec Islands (Fell, 1975; Byrne and Andrew, 2013; Przeslawski et al., 2025),

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[*] Corresponding author. Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, 7001, Australia.
E-mail address: sterling.tebbett@utas.edu.au (S.B. Tebbett).

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C. rodgersii populations have increased in some areas within this native geographic range (Balemi and Shears, 2023; Davis et al., 2023). In addition, ocean warming has also facilitated *C. rodgersii* range extension poleward (Ling et al., 2009b) (see Fig. 1a for the current geographic range based on survey data). The mechanistic basis behind this warming-mediated range extension appears to lie, at least in part, in the larval biology of this species (Ling et al., 2008; Pecorino et al., 2013a). Development of the planktotrophic larvae of *C. rodgersii*, which spend a minimum of 1 month in the water column (Mos and Dworjanyn, 2016), is closely tied to sea temperature with poor development below 12 °C evidently constraining the historic distribution of this species in Eastern Australia to the mainland (Ling et al., 2008; Byrne et al., 2022). However, with continued ocean warming, this temperature is now readily exceeded outside the historical native range of *C. rodgersii*, facilitating its range extension (Ling et al., 2009b; Byrne et al., 2022).

The geographic regions of Northeastern Aotearoa New Zealand (hereafter NZ) and Eastern Tasmania (hereafter Tasmania) lie at the forefront of *C. rodgersii* climate driven invasion and/or population increase. *Centrostephanus rodgersii* is considered a native species in NZ and has been documented in this region since at least 1897 (Fell, 1949). However, this species historically occurred at low densities (i.e. it was rarely observed) and was not recorded shallower than 20 m (Choat and Schiel, 1982). Yet recent studies have suggested *C. rodgersii* populations in NZ are significantly increasing, with links to ocean warming (likely facilitating larval dispersal) and greater self-recruitment over the past quarter century (Thomas et al., 2021; Balemi and Shears, 2023). In contrast, *C. rodgersii* is not considered a native species in Tasmania, with this species first reported on the Tasmanian mainland in 1978 (Edgar, 1997). Initially, the species was observed sporadically, however, it is now well established (Ling and Keane, 2024). Notably, it has also been reported that the depth distribution of *C. rodgersii* in Tasmania diverges from that documented across its native range (Perkins et al., 2015). This suggests that enhanced understanding of *C. rodgersii* abundance-depth relationships is warranted when evaluating early-stage population increases in this species.

In both NZ and Tasmania, *C. rodgersii* is a growing ecological problem, underpinning the formation of extensive barrens and, in turn, driving the loss of biodiversity and fisheries resources associated with kelp (Johnson et al., 2005; Ling, 2008; Balemi and Shears, 2023). For example, the cover of urchin barrens on open coasts has increased from 3 % to 15 % between 2001/02 and 2016/17 in Tasmania, because of increasing *C. rodgersii* abundance (Ling and Keane, 2024). Despite *C. rodgersii* being a key habitat-modifying species, the extent of similarities or differences in population increases in Tasmania versus NZ, as well as how these increases are being shaped by the geographic location of each region relative to the broader distribution of *C. rodgersii*, is currently unclear. In this respect, Tasmania is situated at a higher latitude with colder waters than NZ. Based on these temperature differences and the established thermal limitations to *C. rodgersii* biology (Ling et al., 2008; Byrne et al., 2022), one could reasonably expect that population increases are playing out differently between regions.

The aim of this study was to compare regional change in *C. rodgersii*

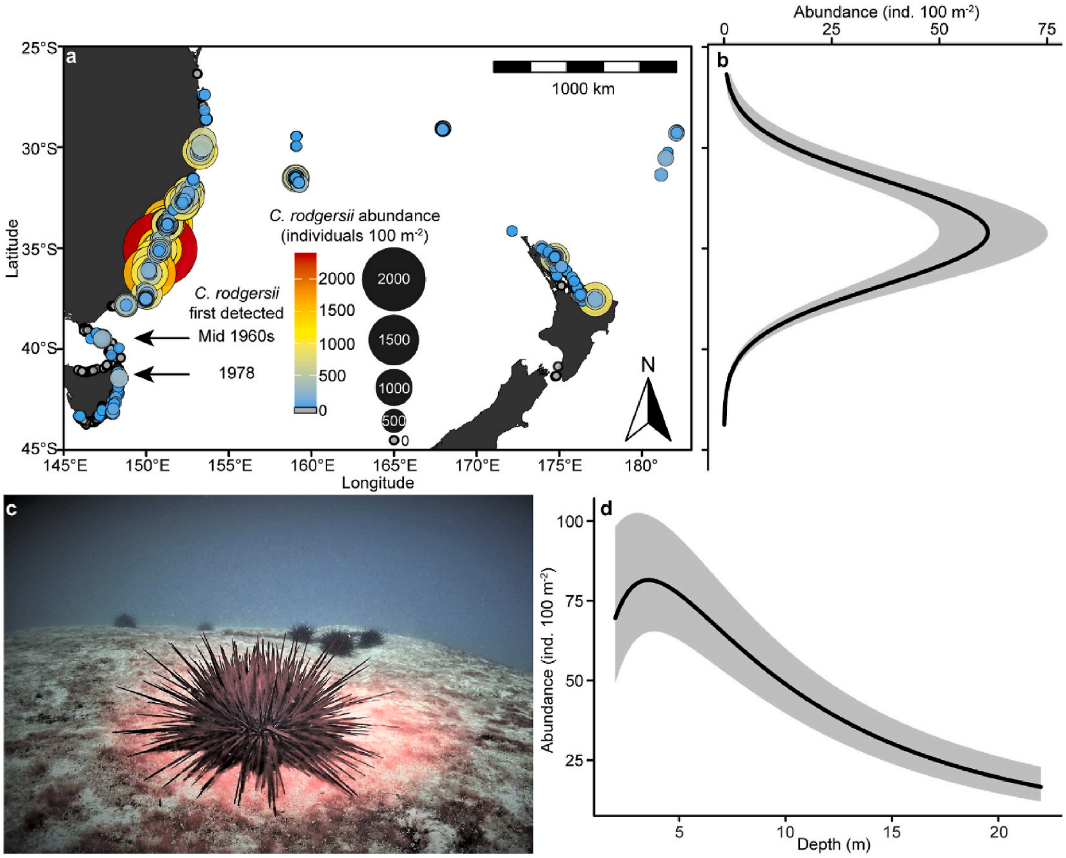

Fig. 1. The spatial distribution of *Centrostephanus rodgersii*. (a) Location of survey sites (coloured points) analysed within the distribution of *C. rodgersii*. The colour and size of points denotes the abundance of *C. rodgersii* averaged across adjacent surveys (time period considered = 2006–2024). The arrows show when *C. rodgersii* was first detected at specific locations (i.e. the Kent Group in the Bass Strait in the mid-1960s, and Eastern Tasmania in 1978 [Edgar, 1997; Johnson et al., 2005]). (b) The relationship between *C. rodgersii* abundance and latitude, while depth was held at the mean of 7.7 m. (c) *Centrostephanus rodgersii* in an urchin barren at St. Helens, Tasmania (photograph SD Ling). (d) The relationship between *C. rodgersii* abundance and depth, while latitude was held at 34.2°S (the latitude where abundance peaked). In (b) and (d) the solid black line denotes the mean predicted fit from a generalised linear mixed effects model and the grey shaded area denotes the 95 % confidence intervals (n = 3456).

abundance through time and across depth in Tasmania and NZ during distinct temporal periods that encompassed reported ‘ramping-up’ of *C. rodgersii* abundances (e.g. Johnson et al., 2011; Balemi and Shears, 2023). In addition, we specifically, consider how regional patterns in abundance align with expectations based on the geographic distribution of *C. rodgersii* in relation to sea surface temperature. To explore such large spatio-temporal patterns, we leverage broadscale datasets, which have quantified *C. rodgersii* abundance throughout its geographic distribution over recent decades, as well as detailed region-specific depth-stratified data. Assuming realised *C. rodgersii* abundance across its broader geographic distribution peaks in the central part of its thermal range (Waldock et al., 2019), and the warmer temperatures of NZ relative to Tasmania, we hypothesised that the magnitude of change in *C. rodgersii* abundance was larger, towards a higher maximum abundance, in NZ than in Tasmania.

2. Methods

2.1. Broadscale geographic distribution patterns

To explore broad scale geographic distribution patterns of *C. rodgersii* abundance, we used the publicly available mobile macroinvertebrate abundance data from the National Reef Monitoring Network, which includes data from the Reef Life Survey program (RLS) (https://reeflifesurvey.com) and Australian Temperate Reef Collaboration (ATRC) (https://atrc.au) (downloaded August 05, 2024). This dataset was used as it has broad spatial coverage spanning the entire distribution of *C. rodgersii* from southeast Australia to Aotearoa NZ, including the Kermadec, Norfolk, and Lord Howe Islands (Fig. 1a). From 2006 to 2024 RLS and ATRC data has been collected on a regular basis within this geographic range, with sampling frequency and time being relatively haphazard across specific sites. Detailed survey level information, including date of sampling, can be found in the publicly available dataset available on the Australian Ocean Data Network (https://portal.aodn.org.au/search). The RLS program is based on a standard method, with all mobile macroinvertebrates >2.5 cm in length recorded in two adjoining 50 m^2 ‘blocks’ (measuring 50 × 1 m) either side of a transect line (Edgar et al., 2020). The ATRC program is based on quantifying all mobile macroinvertebrates >2.5 cm in length along four 50 × 1 m transects laid end-to-end. In all cases, we averaged *C. rodgersii* abundance across surveys for the same depth at the same site due to the lack of spatial independence, with all *C. rodgersii* abundances standardised to the number of individuals 100 m^{-2} for analysis to facilitate comparison with previous studies.

The broad scale data were collected over nearly two decades (2006–2024) and were filtered to include all transects conducted between the depths of 2–22 m, the latitudes of 26°S-43.8°S, and the longitudes of 145.85°E and 177.85°W ($n = 3456$ site and depth-level averages [see below for regional information]) (Fig. 1a). The broad temporal bounds ensured we focused on recent abundance patterns of *C. rodgersii* while minimising the inclusion of data from earlier years when the spatial distribution of sampling was limited. The spatial bounds ensured we retained all transect data collected within the distribution of *C. rodgersii*, while minimising the inclusion of data from outside of their current geographic range, or from areas where data were sparse (e.g. at depths >22 m). An overview of the data is provided in Fig. S1.

Initially, we explored the latitudinal and depth distribution of *C. rodgersii* across the entire geographic dataset to provide an overview of its distribution using a generalised linear mixed effects model (GLMM) (package: *glmmTMB* [Brooks et al., 2017]) in R (version 4.4.1; R Core Team, 2024). We treated *C. rodgersii* abundance as the response variable, and latitude and depth (logged) as continuous fixed effects with an interaction between them. A degree of non-linearity was detected in the relationships between *C. rodgersii* abundance and both latitude and depth, therefore, these factors were fitted with second-order polynomial terms to account for this non-linearity. Additionally, we treated site identity as a random effect to account for any lack of spatial independence. The GLMM was based on a Tweedie distribution with a log-link function. Model fit and assumptions were evaluated using standard residual plots and simulation-based model checking (QQ plot, residual versus predicted plot; based on $n = 250$ simulations) which were satisfactory in all cases (package: *DHARMa* [Hartig, 2020]).

2.2. Population changes and depth distribution in northeastern New Zealand

Examination of the relationship between the abundance of *C. rodgersii* and depth in two distinct time periods was possible using RLS data from NZ. Virtually all RLS sampling in this region was confined to two years (2012 and 2024), because of two distinct survey campaigns (Fig. S2a). In both campaigns, many of the same sites were surveyed and a broad range of depths sampled (Fig. S2b). Therefore, we were able to compare relationships between *C. rodgersii* abundance with depth at two time periods (i.e. surveys from 2012 to 2024) at the same sites using RLS survey data.

Initially, RLS data from NZ were filtered to retain surveys conducted between 2 and 22 m (i.e. the same depth range as the geographic analysis) and only from sites quantified in both time periods ($n = 129$ transects in 2012 and $n = 117$ transects in 2024). Using this filtered subset of survey data, we explored the relationship between *C. rodgersii* abundance and depth in both time periods using a GLMM with a Tweedie distribution and log-link function. We treated *C. rodgersii* abundance as the response variable, time period as a fixed categorical effect with two levels (2012 and 2024) and depth as a fixed continuous variable. A degree of non-linearity was detected in the relationship between *C. rodgersii* and depth. Therefore, we fitted depth with a second-order polynomial term and considered models with and without an interaction term between fixed effects. The most parsimonious model was subsequently selected based on the corrected Akaike Information Criterion (AICc) (package: *AICcmodavg* [Mazerolle, 2017]) (Table S1). The best model was considered the model with the lowest AICc, however, models within two AICc units were considered equivalent (in which case the simpler model was used). Site identity was also fitted as a random effect in models to account for the repeated measures sampling design. All other model fitting and checking procedures followed those outlined in section 2.1.

2.3. Population changes and depth distribution in Eastern Tasmania

RLS sampling was not conducted in Tasmania in the same manner as in NZ; that is sampling was not conducted with a broad, relatively well distributed, spread of surveys across depth in each of two distinct periods. This limited the use of the RLS dataset for exploring depth-related patterns of *C. rodgersii* in Tasmania between time periods. Therefore, to facilitate a comparison of variation in *C. rodgersii* abundance across depth in each region we sourced published data from Ling and Keane (2024). These data were suited to this comparison as they were collected in two distinct sampling periods (2001/02, and 2016/2017), across a similar depth range as that examined in NZ (for full sampling methods refer to Ling and Keane [2024]). In addition, the total area surveyed in each period (~10,000 m^{-2}) was similar to that surveyed in NZ using RLS surveys in each period (11,700–12,900 m^{-2}).

It should be specifically acknowledged here that the need to include data from Ling and Keane (2024) means that different temporal periods were examined in Tasmania (2001/02 and 2016/17) compared to NZ (2012 and 2024). However, it is important to note that these temporal periods in each region encompass an initial ‘ramping-up’ of *C. rodgersii* abundance, thereby facilitating cross-region comparisons at this early stage of population increase. In addition, the length of time between sampling periods differs slightly between Tasmania (~15 years) and NZ (12 years). However, this difference is unlikely to have a major influence on our inferences as *C. rodgersii* abundance does not appear to be increasing linearly (e.g. Balemi and Shears, 2023). Nevertheless, as we only have two sampling periods for each region, we avoid discussion of 'temporal trends' from these data.

It is also important to highlight that given the contextual differences between the two regions (i.e. *C. rodgersii* is native to NZ but not Tasmania, and minimum sea surface temperatures are ∼2 °C warmer in NZ than Tasmania [with this difference apparent for a long period of time, see Fig. S3]) examining change in *C. rodgersii* abundance during the exact same temporal period would not necessarily be more meaningful. Indeed, examination of the same temporal period does not account for long-term differences in thermal regimes or population dynamics. While a comparison that accounts for these contextual differences is not logistically possible, examination of two distinct time periods in each region that have encompassed the reported period of 'ramping up' of *C. rodgersii* in each respective region is possible (e.g. Johnson et al., 2011; Balemi and Shears, 2023; Sweatman et al., 2025). Leveraging these two datasets to make broad-scale temporal comparisons also addresses problems with the lack of broad scale temporal data on *C. rodgersii* in NZ (as recently highlighted as a key issue by Sweatman et al., 2025). Despite the mismatched temporal periods, we can ask a) to what extent have *C. rodgersii* abundances increased in both regions in these respective ramp-up periods? b) how do any increases align with depth in each region? and c) how do any increases align with expectations based on the longer-term abundance of *C. rodgersii* across its distribution relative to sea surface temperature? From a management perspective, answering such questions is informative because despite the inherent contextual differences of both regions, we can begin to place a problem playing out in two countries into a similar framework based on thermal regimes.

Despite ongoing warming in Tasmania (Ridgway and Ling, 2023), inclusion of more recent survey data in this temporal comparison would have also biased inferences due to the growing harvest of the *C. rodgersii* fishery in Tasmania (such a fishery is not currently operating in NZ). Indeed, since the 2016/2017 sampling period, the impact of the fishery in Tasmania has grown significantly, potentially decreasing the abundance of *C. rodgersii* by up to 53 % in some areas (Cresswell et al., 2025). Therefore, these fishery effects have likely modified abundance patterns in more recent years and acted as a confounding effect (which is minimised by focusing on data from earlier years).

For this study we retained all data from Ling and Keane (2024) collected within our Tasmanian region of interest (i.e. from the north-eastern tip of Tasmania to the end of the Tasman Peninsula). This region included nine sampling sites, with three subsites in each region, and four transects in each subsite. Unlike RLS sampling, transects were laid perpendicular to the shore to a maximum depth of ∼18 m and averaged ∼50 m in length. Along each side of the transect a contiguous quadrat size of 5 m^2 (1 m wide × 5 m long section of transect – with quadrats continuously defined along a transect) was examined. Divers recorded the number of *C. rodgersii* and the depth. The abundance of *C. rodgersii* across each pair of adjacent quadrat areas were subsequently averaged due to the lack of spatial independence ($n = 1034$ quadrats in 2001/02 and $n = 1033$ quadrats in 2016/17). In each sampling period, the same transects were quantified, with relocation based on GPS coordinates.

We explored the relationship between *C. rodgersii* abundance and depth in both sampling periods in Tasmania using a GLMM with a Tweedie distribution and log-link function. The GLMM was based on the same fixed effects (i.e. time period and depth [with a second order polynomial term]) as for the NZ model, however, in this case we include site, subsite, and transect identity as nested random effects to account for the repeated measures sampling design and any lack of spatial independence. Note this random effects structure differs to that used for the NZ model due to the clear nested structure of this sampling design (i.e. the same transect locations, in the same subsites, in the same sites) relative to the RLS sampling (i.e. the same sites – with transect location haphazard within a site). All other model fitting, selection, and checking procedures followed those outlined in section 2.1.

2.4. *Observed changes versus expectations based on sea surface temperature*

To explore the relationship between *C. rodgersii* abundance changes and sea surface temperature, we used the same broadscale geographic dataset based on RLS and ATRC surveys as in section 2.1. However, for this analysis we replaced latitude with the mean minimum long-term sea surface temperature (SST) for each sampling location. We used the mean minimum SST as the distribution of *C. rodgersii* has previously been linked to minimum sea temperatures (Ling et al., 2008; Byrne et al., 2022). These SST data were sourced from the 2010–2020 surface raster layer in Bio-Oracle V3 (Assis et al., 2024) and based on the mean minimum SST value in a 15 km radius buffer around each survey site (i.e. the values across grid cells that intersected with this buffer were averaged yielding mean minimum SST). We refit the same GLMM as described in section 2.1 for the broadscale geographic data (i.e. using all the same model fitting and checking procedures) but with SST substituted for latitude. In addition, given the limited occurrence of *C. rodgersii* across the northern coast of Tasmania (Fig. 1a), likely due to limited larval dispersal into this region due to increased distance from the East Australian Current (Ling et al., 2009b), we refit the model as above after excluding all data west of 147.89°E. This limited the data to the eastern coast of Tasmania and allowed us to evaluate if our inferences were shaped by the inclusion of a high number of zero observations close to the southern limit of *C. rodgersii*.

Ultimately, we wanted to explore how the observed regional patterns in *C. rodgersii* change aligned with expectations based on its abundance across its thermal distribution, such as higher abundances in the middle of its thermal range. To do this, we used the GLMM above to predict the 'expected' relationship between *C. rodgersii* abundance and depth in Tasmania and NZ, based on the average mean minimum SST across sampling sites in each region between 2010 and 2020 (12.23 °C and 14.87 °C in Tasmania and NZ, respectively). These minimum SST values from Bio-Oracle closely align with minimum SST values recorded in-situ in each region during this time at a smaller spatial scale (Ling and Keane, 2024; Shears et al., 2024) (Fig. S3). Assuming mean minimum SST had increased by 0.5 °C in each region from a baseline value (i.e. using a baseline of 11.73 °C and 14.37 °C in Tasmania and NZ, respectively), we also predicted how much *C. rodgersii* abundance may have increased in each region based on this standardised magnitude of SST change. We calculated these increases for the depth at which *C. rodgersii* abundance peaked across the broadscale data at the latitude of peak abundance and at the regional scale. We used 0.5 °C as this represented a consistent comparison, allowing us to place our observed regional changes into context with the broader distribution of *C. rodgersii*.

3. Results

3.1. *Broadscale geographic distribution patterns*

The abundance of *C. rodgersii* follows a unimodal distribution pattern across its geographic range (Fig. 1b; Table S2). At a depth of 7.7 m (the mean across the broadscale dataset examined) the GLMM demonstrated that *C. rodgersii* average abundance peaks at over 61.26 individuals 100 m^{-2} at 34.2°S (Fig. 1b); a latitude that aligns with a region slightly south of Sydney Harbour on Australia's east coast (i.e. between Sydney and Wollongong), and approximately the northernmost tip of New Zealand's North Island (i.e. North Cape). The highest *C. rodgersii* abundance recorded in the dataset (averaged across adjacent survey blocks) was 2408 individuals 100 m^{-2} (Fig. 1a). Within this geographic range, the average abundance of *C. rodgersii* was not uniformly distributed across depth, with the GLMM demonstrating that abundance followed a second order polynomial relationship with depth, although the nature of this relationship was dependent on the latitude in question (Table S2). At the latitude where *Centrostephanus rodgersii* abundance peaked (i.e. 34.2°S), abundance was low at the shallowest depths surveyed but increased to a peak average abundance at 3.5 m, before declining with depth (Fig. 1d).

3.2. Regional population changes and depth distributions

In both Tasmania (2001/01–2016/17) and NZ (2012–2024), the abundance of *C. rodgersii* increased substantially (Fig. 2; Table S2). The GLMM demonstrated that *C. rodgersii* abundance increased by 1.7-fold, on average, in Tasmania (Fig. 2a–c), and 3.3-fold, on average, in NZ (Fig. 2b–d). Although *C. rodgersii* abundance increased in both regions, the nature of these increases differed across depth (Fig. 2). In both Tasmania and NZ, the interaction between depth and time period was not influential (Table S1) with *C. rodgersii* abundance following a second-order polynomial relationship across the depth gradient ($p < 0.05$; Table S2). However, in Tasmania, *C. rodgersii* were rarely observed at shallow depths, especially <5 m, with their abundance peaking at a depth of 13.5 m, with a mean of 7.5 ± 3.8 individuals 100 m^{-2} in 2016/17 (Fig. 2c). In contrast, in NZ, *C. rodgersii* abundance peaked at a depth of 8.1 m, with a mean of 14.5 ± 6.6 individuals 100 m^{-2} in 2024 (Fig. 2d).

3.3. Expected versus observed changes based on sea surface temperature

Across the geographic distribution of *C. rodgersii*, the GLMM demonstrated that their abundance peaked at a mean minimum SST of 16.7 °C when depth was held at its mean of 7.7 m (Fig. 3; Table S2). Based on this modelled relationship, and the SST in Tasmania and NZ, we predicted the 'expected' relationship between *C. rodgersii* abundance and depth. In Tasmania, the abundance of *C. rodgersii* surveyed in 2016/17 closely aligned with expectations and was 1.47-fold higher at 3.5 m depth (i.e. the depth where *C. rodgersii* abundance peaks at their peak abundance) (Fig. 3c). However, at 13.5 m depth, where *C. rodgersii* abundance peaks in Tasmania, surveyed abundance was 3.97-fold higher than expectations (Fig. 3c). The situation differed in NZ in that *C. rodgersii* abundance was substantially lower, by 5.44-fold and 2.71-fold, than expectations at both 3.5 m and 8.1 m (i.e. the depth where *C. rodgersii* abundance peaks in NZ), respectively (Fig. 3d).

Based on the relationship between C. *rodgersii* abundance and SST we also predicted the absolute change in *C. rodgersii* abundance given a 0.5 °C increase in SST. These predictions suggested the maximum potential for increase is lower in Tasmania than in NZ, with an increase of 0.97 urchins 100 m^{-2} (0.89 ± 0.24 to 1.85 ± 0.41; mean ± SE) versus 14.48 urchins 100 m^{-2} (24.69 ± 2.96 to 39.17 ± 4.78) on average,

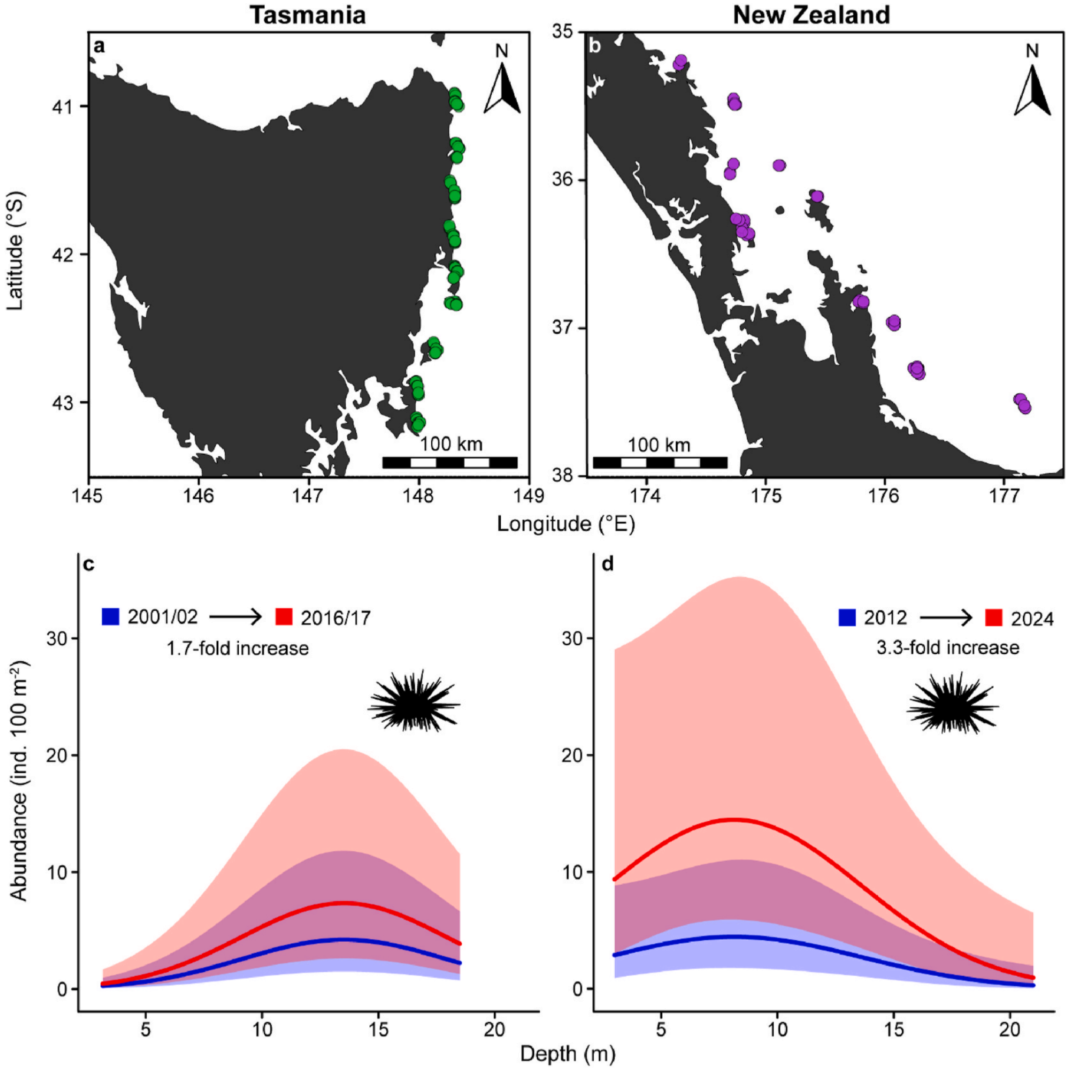

Fig. 2. Patterns of increasing *Centrostephanus rodgersii* abundance in Eastern Tasmania and Northeastern New Zealand (NZ). The sampling sites (coloured dots) where *C. rodgersii* abundance was quantified in (a) Tasmania (n = 1034 quadrats in 2001/02 and n = 1033 quadrats in 2016/17), and (b) NZ (n = 129 transects in 2012 and n = 117 transects in 2024). The abundance of *C. rodgersii* across depth gradients in two sampling periods at the same sites in (c) Tasmania, and (d) NZ. The coloured lines show the mean predicted fit from generalised linear mixed effects models (GLMMs), while the coloured ribbons denote the 95 % confidence intervals.

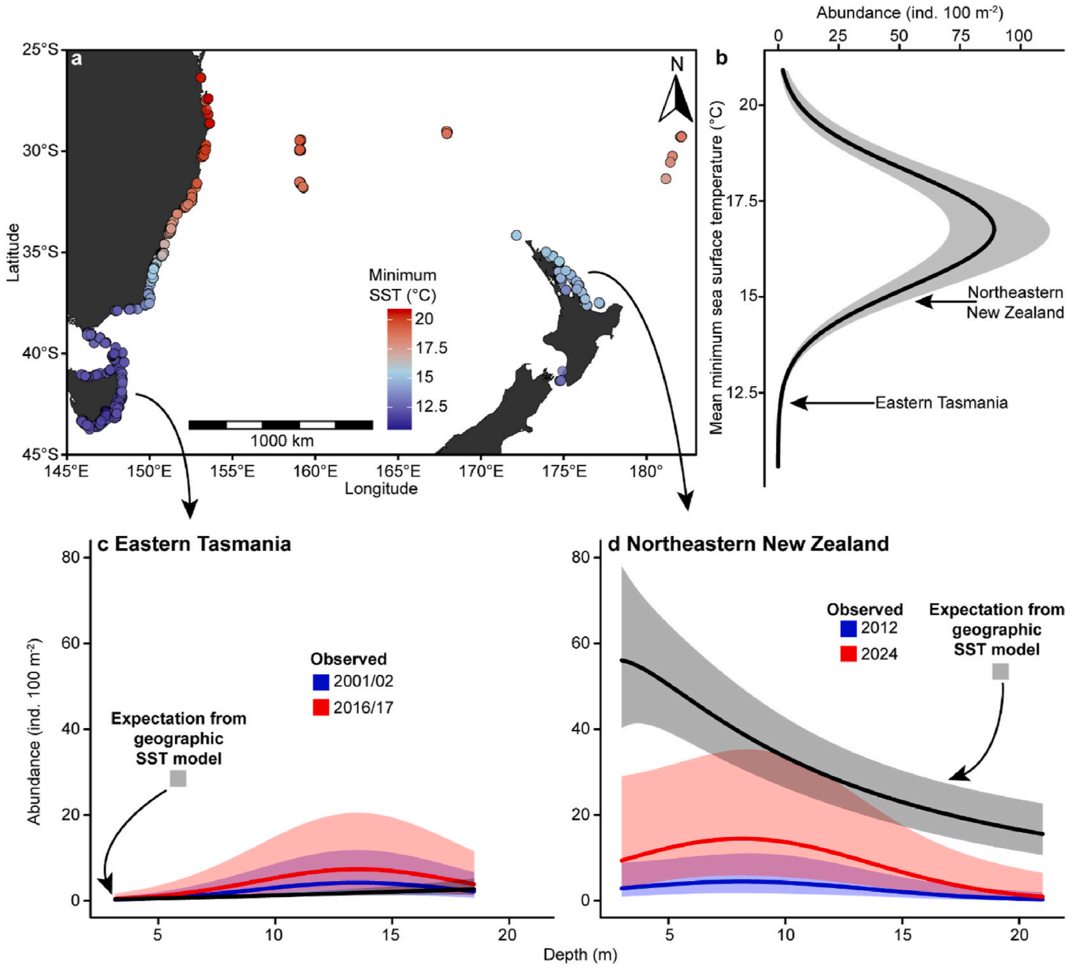

Fig. 3. The spatial distribution of *Centrostephanus rodgersii* in relation to minimum sea surface temperature. (a) Location of survey sites (coloured points) analysed within the distribution of *C. rodgersii*. The colour of points denotes the mean minimum sea surface temperature (SST) between 2010 and 2020 from BioOracle V3.0 (Assis et al., 2024). (b) The relationship between *C. rodgersii* abundance and mean minimum SST, while depth was held at the mean of 7.7 m (n = 3456). Observed as well as expected abundance versus depth relationships for *C. rodgersii* in (c) Eastern Tasmania (n = 1034 quadrats in 2001/02 and n = 1033 quadrats in 2016/17) and (d) Northeastern New Zealand (n = 129 transects in 2012 and n = 117 transects in 2024) based on the data presented in Fig. 2 and predicted from the broadscale relationship in (b) (arrows in panel b show the position of each region in the thermal abundance curve). In (b–d) the solid lines denote the mean predicted fit from generalised linear mixed effects models and the shaded areas denote the 95 % confidence intervals.

respectively, for an equivalent amount of warming. These expectations aligned with observations in that the maximum absolute *C. rodgersii* abundance increase was lower in Tasmania (an increase of 3.1 urchins 100 m^{-2} between 2001/02–2016/17) compared to NZ (an increase of 10.1 urchins 100 m^{-2} between 2012 and 2024).

The general inferences outlined above were robust to the exclusion of western data distributed through the Bass Strait and across Northern Tasmania where *C. rodgersii* was largely absent (Fig. S4). However, the magnitude of differences between observed and expected *C. rodgersii* abundance did change slightly based on predictions from the SST model after excluding the western data. For example, based on this model, at 13.5 m in Tasmania the surveyed abundance of *C. rodgersii* in 2016/17 was only 1.18-fold higher than expectations, with observations and expectations therefore aligning closely after the exclusion of western data (Fig. S4c and S5a). In contrast, exclusion of the western data meant that the magnitude of the difference between observations and expectations increased in NZ, with surveyed *C. rodgersii* abundance at 8.1 m in 2024 being 3.06-fold lower than expectations (Figs. S4d and S5b). Based on this model, a 0.5 °C increase in temperature predicted an increase of 2.24 and 12.56 urchins 100 m^{-2} in Tasmania and NZ, respectively.

4. Discussion

The sea urchin *C. rodgersii* represents a habitat-modifying species that has benefited from recent ocean warming, including clear evidence of temperature driven range extension and/or increased abundance (Balemi and Shears, 2023; Ling and Keane, 2024). The thermophilising regions of Tasmania and NZ lie at the forefront of these changes (Soler et al., 2022; Middleton et al., 2023), with our study revealing the extent of significant *C. rodgersii* abundance increases in both regions. Larger absolute changes in *C. rodgersii* abundance in NZ compared to Tasmania align with expectations based on the SST of both regions. However, given contemporary SST in NZ, there appears to be potential for substantial further increases in *C. rodgersii* abundance to match levels that might be expected based on the thermal abundance curve (i.e. to match the abundances recorded along the south coast of New South Wales [Przeslawski et al., 2025]). While the magnitude of *C. rodgersii* abundance increase appears lower in Tasmania, abundances in this region peak at depths far deeper than at the latitudes of peak *C. rodgersii* abundance. Beyond temperature, key differences between regions in respect to the magnitude of *C. rodgersii* increase and depth distribution may also relate to other factors, such as predation, hydrodynamics, and stock recruitment relationships (discussed below). Given the evidence of significant *C. rodgersii* abundance increases in both regions, and the potential for marked ecological consequences as a result of such increases (Johnson et al., 2005; Ling, 2008), these increases represent an ongoing and worsening management issue in both regions.

The large-scale patterns in *C. rodgersii* abundance described herein directly align with previous studies which show the high abundance and ecological dominance of *C. rodgersii* on rocky reefs within a latitudinal band of ~31–37°S (Glasby and Gibson, 2020; Davis et al., 2023; Blount et al., 2024). These abundance patterns suggest that latitudinal variability in abiotic and biotic factors have shaped *C. rodgersii* distribution and abundance, with optimal conditions at these central latitudes. One key variable appears to be sea temperature as this relates strongly with *C. rodgersii* abundance across this range and has direct links with their larval biology (Ling et al., 2008; Pecorino et al., 2013b; Byrne et al., 2022). Indeed, evidence suggests that the optimal thermal range (~14–22 °C) for *C. rodgersii* larvae, based on 90 % survival at 72 h, closely aligns with the thermal range of peak adult abundance (Byrne et al., 2022). Based on such links between SST and *C. rodgersii*, our results aligned with expectations of a greater increase in *C. rodgersii* abundance in the warmer NZ region.

While the nature of *C. rodgersii* increases in Tasmania and NZ were broadly in line with expectations based on temperature and broader geographic distribution patterns, the increases appear to have diverged from predictions in some key respects. Firstly, based on contemporary patterns of abundance across its entire geographic range, *C. rodgersii* abundance is currently far lower than expectations in NZ across the depth range examined. Secondly, in Tasmania abundances peak on deeper reefs. These divergences raise three key questions. Firstly, given that *C. rodgersii* have been present in the NZ region for well over a century (Fell, 1949), and during this period minimum sea temperatures are likely to have been above the 12 °C threshold needed for *C. rodgersii* larval survival (Ling et al., 2008; Byrne et al., 2022; Shears et al., 2024), why is abundance well below expectations and only increasing significantly in recent decades? Secondly, given that the thermal regime of more southerly parts of NZ align with that of Tasmania, is it just a matter of time until *C. rodgersii* extend further south in NZ? Thirdly, why does *C. rodgersii* abundance peak deeper in Tasmania? Below we explore these questions.

In the case of NZ, part of the explanation to the questions above could lie in stock-recruitment relationships. Historical low C. *rodgersii* population densities (Choat and Schiel, 1982; Cole, 1993) may have resulted in recruitment limitations across the region and maintained populations lower than the expected abundances modelled here. For example, as Pecorino et al. (2013a) suggest, low *C. rodgersii* densities and the potential for a skewed sex ratio at such densities, could have previously limited fertilization success in NZ populations, constraining the potential for large population increases. However, if *C. rodgersii* populations have slowly increased, adult densities may have surpassed a key threshold where it is theoretically possible for dramatic increases in fertilization success and subsequent increases in population to occur (Young et al., 1992). Indeed, exponential population growth following a period of low abundances has recently been observed in another diadematid sea urchin, *Diadema setosum*, within its invaded range in the Mediterranean Sea (Zirler et al., 2023), highlighting the potential for some urchin populations to rapidly increase in size.

Key factors related to life history characteristics and dispersal of *C. rodgersii* larvae may have underpinned a recent population build-up of this species in NZ. Genetic evidence suggests *C. rodgersii* in NZ are closely linked to *C. rodgersii* in New South Wales, especially from Port Stephens and areas further north (Banks et al., 2007; Thomas et al., 2021). Notably, while 12 °C represents the minimum temperature for full larval development and survival in this species (Ling et al., 2008; Byrne et al., 2022), it has been suggested that more northerly populations, including those in NZ, may be adapted to warmer waters with a minimum temperature threshold for larval development to the plutei stage of 15 °C (Pecorino et al., 2013b). If this is the case, this may explain why *C. rodgersii* populations have only increased substantially in recent years with sustained warming in NZ towards this 15 °C threshold (Fig. S3; Shears et al., 2024). Although, it is important to note that even for *C. rodgersii* populations in Tasmania it takes ~7 days for larvae to reach the plutei stage at 12 °C (Ling et al., 2008), and the study by (Pecorino et al. (2013b) only assessed larval development to the plutei stage at 3 days. When the same window of time (i.e. <3 days) is considered in both studies, *C. rodgersii* larvae from NZ and Tasmania were both found to reach the gastrula stage at ~12 °C after ~2 days, suggesting that larvae from NZ were on a similar developmental trajectory to those in Tasmania (Ling et al., 2008; Pecorino et al., 2013b). Therefore, the extent to which any temperature related differences in larval development are shaping patterns of population increase in NZ are currently equivocal.

Beyond larval development, changes to recruitment may have shaped recent population trajectories. Historically, the low abundances of *C. rodgersii* in NZ may have been sustained by sporadic larval supply and recruitment from Australian populations in New South Wales, as evidenced by the strong genetic links between these two areas (Banks et al., 2007; Thomas et al., 2021). However, levels of self-recruitment have now increased in NZ, with this potentially leading to more regular recruitment, underpinning increased population sizes (Thomas et al., 2021). Indeed, examination of size structure in this region is now indicative of regular recruitment (Pecorino et al., 2012; Balemi and Shears, 2023; Sweatman et al., 2025). Such regular recruitment, combined with the fact that *C. rodgersii* is long-lived (>20 years) (Ling et al., 2009b), has increased potential for reproductive output with size (Byrne et al., 1998), and has a relatively long breeding period in NZ when compared to Tasmania (Pecorino et al., 2013a) may all be contributing factors to rapid increases in population size. Given these life history characteristics, a relatively small increase in the stock size of *C. rodgersii* could indeed have the potential to fundamentally reshape the nature of stock-recruitment relationships and lead to large increases in *C. rodgersii* abundance. Whether enhanced larval supply will result in range extension further south in NZ is currently unclear. Considering that more southerly areas in NZ may be suitable from a temperature perspective (Fig. 3a), the main factor hindering *C. rodgersii* expansion further south may be ocean currents and associated larval dispersal constraints (see Michie et al., 2024).

In the case of Tasmania, our finding that *C. rodgersii* abundance peaks on deeper reef areas compared to its native range aligns with the conclusions of a previous study (Perkins et al., 2015). This result also aligns with reports of a deeper depth distributions for the range extending *D. setosum* within its invaded Mediterranean range (Zirler et al., 2023). However, the factors which are driving this different depth distribution in both species of range extending urchin are currently unclear (Perkins et al., 2015; Zirler et al., 2023). In the case of *C. rodgersii*, given that its range extension was historically limited by colder temperatures, one may expect it to be found in shallow warmer waters at its cooler range edge in Tasmania (although strong vertical mixing in coastal waters off Tasmania result in limited temperature depth-stratification undermining this suggestion Ridgway and Ling [2023]). Beyond temperature, high wave energy negatively affects the distribution of sea urchins (Kawamata, 2010; Rinde et al., 2014), potentially explaining why their abundance was relatively low in the shallowest reef areas surveyed, especially in Tasmania. The effect of wave energy is also magnified when it interacts with algae in exposed areas to generate a strong 'whiplash' effect that clears the surrounding reef area (Konar, 2000; Ling and Johnson, 2009). In Tasmania a large intact belt of robust algal species, such as *Durvillaea potatorum* and *Phyllospora comosa*, exists in the shallows on open coasts where the surveys were conducted (Edgar, 1984). The whiplash effect generated by these algae can break the spines of sea urchins and exclude *C. rodgersii* from shallow exposed areas (Ling and Johnson, 2009).

Consideration of wave action and macroalgal whiplash may also explain why *C. rodgersii* in NZ peak at shallower depths on average than in Tasmania. Specifically, the presence and population expansion of

C. rodgersii in shallower areas in NZ could have been facilitated by another sea urchin species, *Evechinus chloroticus*. In the shallow reef areas of our study sites in NZ, *E. chloroticus* is highly abundant (Text S1, Fig. S6). Given the potential for high wave energy to constrain the depth distribution of sea urchins (Kawamata, 2010; Rinde et al., 2014), including *E. chloroticus* (Shears et al., 2008) the high abundance of *E. chloroticus* in shallow areas at NZ survey sites suggests the wave action may have been lower than in Tasmania.

Evechinus chloroticus is also well known for its capacity to overgraze kelp and generate extensive urchin barrens in shallow areas (Andrew, 1988; Kerr et al., 2025), thereby removing any macroalgal whiplash effects. As such, the high abundance of *E. chloroticus* could have helped pave the way for *C. rodgersii* to rapidly expand into shallow reef areas from deeper areas, where it was historically documented in the late 1970s (Choat and Schiel, 1982). Indeed, *C. rodgersii* has now been observed directly recruiting into *E. chloroticus* barrens (*Pers*. *Obs*. AJPS). This observation was supported by supplemental analysis which explored the relationship between *C. rodgersii* abundance in NZ relative to key predators and the potential competitor *E. chloroticus* (Text S2). This analysis revealed that *C. rodgersii* abundance was positively related to *E. chloroticus* abundance in 2012, but this relationship approached a flat line in 2024 (Fig. S7). This suggests that high abundance of *E. chloroticus*, known to have been facilitated by lack of predators (Shears and Babcock, 2002), may have cascaded to initially facilitate higher abundance of *C. rodgersii*, but as *C. rodgersii* populations have become more established any potential facilitative mechanism has weakened. Indeed, it is also important to note that *E. chloroticus* abundance remained stable between the two surveys despite large increases in *C. rodgersii* (Fig. S6), suggesting that *C. rodgersii* was not displacing or outcompeting *E. chloroticus*. Instead, it is likely that *C. rodgersii* is now expanding the overall area of urchin barrens in NZ rather than just occupying existing barrens.

Beyond water temperatures and potential facilitative mechanisms, predation pressure is a key factor often linked to increases in sea urchin populations (Filbee-Dexter and Scheibling, 2014). Indeed, it could be hypothesised that the lower-than-expected *C. rodgersii* abundances in NZ, and the slightly higher than expected abundances in Tasmania, may partly be a result of differences in predation pressure between the two regions. In warmer waters across the distribution of *C. rodgersii* there is a more diverse guild of urchin predators composed of both fishes and invertebrates, such as the blue groper *Achoerodus viridis*, and *Heterodontus sharks* in New South Wales (Gillanders, 1995; Day et al., 2024), and the snapper *Chrysophrys auratus*, and southern rock lobster *Jasus edwardsii* in New Zealand (Andrew and MacDiarmid, 1991; Shears and Babcock, 2002). In contrast, the southern rock lobster, *Jasus edwardsii* is the only significant predator of larger *C. rodgersii* in Tasmania (Ling et al., 2009a). Nevertheless, despite these differences in predator guilds, studies that have examined predation pressure via tethering experiments have reported similar rates of urchin predation across both regions, with higher rates of predation inside compared to outside marine reserves (Shears and Babcock, 2002; Ling and Johnson, 2012).

In both NZ and Tasmania, key urchin predators have been heavily overfished for long periods of time (Willis et al., 2003; Lyle et al., 2020; Nessia et al., 2024), which potentially modifies predator-prey dynamics across both regions. For example, in Tasmania, *J. edwardsii* populations dropped below 10 % of unfished biomass prior to management interventions in 2013 (Lyle et al., 2020). Such low predator abundances in general, can alter relationships with urchin abundance and curtail the capacity of predators to impact high density urchin populations. In this respect, while previous examination of the Tasmanian data analysed herein revealed a negative, but weak, relationship between *C. rodgersii* and *J. edwardsii* abundance (Ling and Keane, 2024), supplemental analysis of the NZ dataset examined herein did not detect a relationship between either key predator (snapper or lobsters) and *C. rodgersii* abundance (see Text S2). Clear relationships between predators and urchins have been described previously for this NZ region (e.g. Shears and Babcock, 2002; Edgar, 2017), with the lack of a clear relationship in our case likely due to the low overall abundance of predators on surveys (e.g. lobsters were not detected on 82.5 % of transects), constraining our ability to detect any meaningful patterns at the scale examined. Moreover, while evidence suggests that restoring predator populations through marine protected areas can limit *C. rodgersii* increases (Ling et al., 2009a), these effects appear to be context dependent. For example, rebuilding of *J. edwardsii* populations in Tasmania was found to limit *C. rodgersii* populations at low densities in incipient barrens but had limited potential to control high densities of *C. rodgersii* on extensive barrens (Ling and Keane, 2021). At high urchin densities, other management interventions, such as targeted commercial harvesting or culling (e.g. Miller et al., 2022, 2024) may be required, in addition to rebuilding predator populations, to limit the ecological impact of *C. rodgersii* increases (Tracey et al., 2015; Keane et al., 2024; Cresswell et al., 2025).

Early management action of *C. rodgersii* is vital to prevent the species from reaching high densities and forming extensive barrens, which are much more difficult and more costly to reverse than smaller incipient barrens (Tracey et al., 2015; Ling and Keane, 2021; Keane et al., 2024). In Tasmania, the fact *C. rodgersii* represents a jurisdictionally invasive species (via range extension) underpinned early identification of this species' potential ecological and economic impact in the region, with establishment and ramping up of management efforts (Johnson et al., 2005; Keane et al., 2024). Direct removal of urchins by divers was recognised as a viable management strategy for controlling *C. rodgersii* abundances in Tasmania (Ling and Keane, 2021; Westcott et al., 2022; Keane et al., 2024). As such, plans for further upscaling and refining of management efforts, including development and expansion of a *C. rodgersii* fishery, are already underway (Tracey et al., 2015; Keane and Ling, 2022; Westcott et al., 2022; Cresswell et al., 2025).

In contrast to Tasmania, early warning signals were less apparent in NZ, in part because *C. rodgersii* is native within this region. Yet, the greater absolute increases in *C. rodgersii* abundance in NZ and scope for significant further increases based on SST, mean that ecological thresholds may be surpassed quicker in this region compared to Tasmania. A local *C. rodgersii* density of ~2.2 individuals m^{-2} represents the critical ecological threshold leading to overgrazing and barrens formation, while reduction in *C. rodgersii* densities to as low as ~0.36 individuals m^{-2} is required for kelp recovery to occur (Ling et al., 2015). Although urchin densities that trigger management intervention are yet to be determined, if the goal of management is to prevent extensive barrens, then *C. rodgersii* densities substantially lower than 2.2 m^{-2} will be needed as a trigger point. Nevertheless, a trade-off invariably exists between management of *C. rodgersii* densities to a desired level of ecological/economic/social/cultural impact and the cost/effort of management interventions, with the strength of these trade-offs likely to vary under different contexts (Keane et al., 2024). Therefore, depending on the management goals associated with a specific area, this is likely to necessitate the need for context-specific target management densities of *C. rodgersii* (Keane et al., 2024).

Relative to Tasmania, management of *C. rodgersii* in NZ likely needs to be applied faster and harder to curtail rapid and large-scale population increases given the far higher potential for future population growth based on relationships with SST. The development of a *C. rodgersii* fishery has been a vital means of applying the brakes in Tasmania (Cresswell et al., 2025), but the feasibility of developing a fishery for this species in NZ is unknown. In NZ, a multi-pronged management plan is needed that aims to rebuild key predator populations at large scales in addition to implementing active removal and/or harvest programs in key areas. This endeavour would be supported by a detailed, fine spatial scale, evaluation of *C. rodgersii* population sizes in the NZ region to identify key sites and appropriate approaches for management.

Several additional considerations and potential limitations of our study should be highlighted. Survey locations in both Tasmania, and NZ largely focused on areas of the open coast/offshore islands, where *C. rodgersii* often reach their highest abundance and are generally found deeper (*Pers. Obs.* SDL). As such, examination of more sheltered/nearshore sites is likely to result in lower abundances and potentially a shallower depth of peak abundance than we report for each region. Additionally, it is important to acknowledge that the methods and scale of the surveys used to quantify *C. rodgersii* in Tasmania (5 m^2) differed from that in NZ (50 m^2), and only data collected at the scale of 50 m^2 surveys (i.e. RLS and ATRC data) were included in the thermal abundance curve (to ensure a consistent method was used in this broad-scale analysis). Given this difference in methods, it is notable how closely the observed abundances of *C. rodgersii* in Tasmania (quantified at the 5 m^2 scale) aligned with those predicted from the thermal abundance curve, especially after the western data in the Bass Strait and across northern Tasmania were excluded (Fig. S4). However, the opposite appears to apply to NZ. Indeed, as data from NZ RLS surveys were included in the thermal abundance curve analysis, this means the 'expected' abundances for this region could be conservative, with the potential that the thermal regime in NZ may support even higher *C. rodgersii* abundance than we predict.

Overall, our study revealed that in both Northeastern NZ and Eastern Tasmania there have been significant increases of *C. rodgersii* populations in recent decades. However, in the warmer NZ region, *C. rodgersii* has rapidly attained higher abundance than in Tasmania, with substantial scope for ongoing population increases. Such increases represent a burgeoning ecological problem as the intensively grazing *C. rodgersii* forms extensive urchin barrens, with concomitant impacts on local biodiversity (Ling, 2008) and fisheries resources (Johnson et al., 2005). With ongoing warming there is an urgent need to ramp-up or implement ecosystem-based management to control *C. rodgersii* populations and increase resilience of remaining kelp beds, both in Tasmania, and NZ. Without such measures, both areas are poised for ongoing *C. rodgersii* increase and overgrazing of kelp ecosystems over increasingly large areas.

CRediT authorship contribution statement

Sterling B. Tebbett: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Graham J. Edgar:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Celia A. Balemi:** Writing – review & editing, Conceptualization. **John P. Keane:** Writing – review & editing, Investigation, Conceptualization. **Nick T. Shears:** Writing – review & editing, Conceptualization. **Arie J.P. Spyksma:** Writing – review & editing, Conceptualization. **Rick D. Stuart-Smith:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Scott D. Ling:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126842.

Data availability

All data analysed in this study are publicly available from https://portal.aodn.org.au/search and https://doi.org/10.1038/s41467-023-44543-x.

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