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Combined mechanistic modelling predicts changes in species distribution and increased co-occurrence of a tropical urchin herbivore and a habitat-forming temperate kelp

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Abstract

Aim: Identify climate change impacts on spawning and settlement of a tropical herbivore (*Tripneustes*), optimal habitat of a temperate kelp (*Ecklonia*) and implications for these species regions of interaction under future climate.

Location: Along eastern Australia and into the Tasman Sea including Lord Howe Island (LHI).

Time period: A contemporary scenario (2006–2015) and future "business as usual" RCP 8.5 climate change scenario (2090–2100).

Major taxa studied: The tropical sea urchin, *Tripneustes gratilla*, and the temperate kelp, *Ecklonia radiata*.

Methods: We combined mechanistic models to create a predictive map of *Ecklonia* and *Tripneustes* distributions, and their future potential to co-occur. We use 3D velocity and temperature fields produced with a state-of-the-art configuration of the Ocean Forecasting Model version 3 that simulates the contemporary oceanic environment and projects it under an RCP 8.5 climate change scenario. We map the contemporary and future *Ecklonia*'s realized and fundamental thermal niche; and simulate *Tripneustes* larval dispersal under both climate scenarios.

Results: Based on the thermal affinity of kelp and increases in projected temperatures, we predict a poleward range contraction of ~530 km by 2100 for kelp on Australia's east coast. Climate-driven changes in dispersal of *Tripneustes* lead to its range expansion into Bass Strait and poleward, ~340–650 km further into *Ecklonia*'s habitat range inducing new areas of co-occurrence in the future. We find warming decreases spawning and settlement of *Tripneustes* in the tropics by 43%, and causes significant connectivity changes for LHI with future reliance on self-recruitment.

Major conclusions: We predict novel regions of co-occurrence between a temperate *Ecklonia* and tropical *Tripneustes* species which may lead to greater loss of kelp. Our results provide a new modelling approach for predicting species range shifts that is transferable to other marine ecosystems; it considers species response to abiotic change, predicts spatial spread and anticipates new regions for species interactions.

KEYWORDS

climate change, dispersal, *Ecklonia radiata*, herbivory, kelp, Lagrangian particle-tracking, mechanistic model, species distribution model, species range shifts, *Tripneustes gratilla*, tropicalization

1 | INTRODUCTION

Globally, a large proportion of terrestrial and marine species are responding to climate change by undergoing range redistributions (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Poloczanska et al., 2013), with effects on biodiversity and ecosystem structure (Pecl et al., 2017). Warming is one of the primary causes leading to species range shifts (Chen et al., 2011; Poloczanska et al., 2013). All species have an optimal thermal range where they best function; outside of this range, performance decreases and extreme temperatures lead to demise (Angilletta, 2009; Pörtner & Knust, 2007). Ocean isotherms are shifting at an equal or faster rate than terrestrial isotherms, resulting in a greater range shift for marine species, as they move to new areas that encompass their thermal range (Burrows et al., 2011; Poloczanska et al., 2013; Sen Gupta et al., 2015).

Dispersal is a central process in distributional shifts (García Molinos, Burrows, & Poloczanska, 2017; Travis et al., 2013); it is particularly important for marine organisms as most species rely on the release of reproductive propagules into the water column where they are then carried by ocean currents (Kinland & Gaines, 2003) to replenish populations across their biogeographical range. Oceanic conditions strongly influence dispersal, as temperature often triggers reproduction and spawning events (Fincham, Rijinsdorp, & Engelhard, 2013; Yang & Rudolf, 2010) and ocean currents determine propagule trajectories influencing settlement patterns (Werner, Cowen, & Paris, 2007). Thus, diagnosing the impact of climate-driven circulation changes on larval dispersal is important to anticipate changes in species ranges (e.g. Cetina-Heredia, Roughan, van Sebille, Feng, & Coleman, 2015).

The Biotic–Abiotic–Mobility (BAM) framework highlights the three key factors that should be considered when predicting species range shifts in response to climate change (Peterson, Papeş, & Soberón, 2015). However, changes in species distributions are commonly predicted using correlative models such as species distribution models (SDMs; Peterson et al., 2015), which focus mostly on abiotic factors, by statistically relating known occurrence data of a species to environmental variables in order to predict a species range (Guisan & Zimmermann, 2000). Differently, mechanistic models use a biophysical approach to associate population processes with abiotic conditions. For instance, Rodríguez, García, Carreño, and Martínez (2019) forecasted *Millepora alcicornis* future habitat constructing a physio-climatic predictor which combined the coral maximal quantum yield of photosynthesis with sea surface temperatures (SSTs) into a raster reflecting coral optimal conditions. Nonetheless, there are other evolutionary and ecological processes which determine species distribution, such as reproduction and dispersal (i.e. mobility; Leroux et al., 2013), which are often lacking or simplified in correlative or mechanistic approaches (Robinson et al., 2011). Leroux et al. (2013) modelled the impact of climate change for North American butterflies, through a reaction-diffusion framework, which considered the population growth rate (which depends on both abiotic conditions and biological interactions), climate envelope (i.e. abiotic conditions) and diffusion rate (i.e. rate of movement) for the butterflies. Though Leroux et al. (2013) integrated all three factors of the BAM framework in the model, the research highlighted the need to also consider changes to species interactions which are often not considered but can be fundamental in determining ecosystem function and structure (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013).

Tropicalization offers a striking example of how distribution shifts of tropical species into temperate habitats can create novel biotic interactions, with consequences cascading throughout entire ecosystems (Vergés, Steinberg, et al., 2014). Tropicalization has been seen along Western Boundary Currents (WBC) such as the East Australian Current (EAC), whose climate-driven intensification (Wu et al., 2012) contributes to the greater transport of warm tropical water and larvae being carried into temperate ecosystems (Vergés, Steinberg, et al., 2014). Globally, this has resulted in new herbivore–algae interactions that have led to phase shifts, as areas once inhabited by dense kelp forests turn into turf algae dominated reefs, with tropical consumers preventing the re-establishment of temperate kelp (Bennett, Wernberg, Harvey, Santana-Garcon, & Saunders, 2015; Vergés et al., 2016, 2019; Vergés, Tomas, et al., 2014). This example highlights the importance of understanding and identifying climate-mediated changes in species interactions to understand future ecosystem composition and enable adaptive management decisions (Koehn, Hobday, Prachett, & Gillanders, 2011).

We develop a new combined mechanistic modelling approach to predict distributional range shifts and changes in regions of co-occurrence that allow for biotic interactions under climate change. We use a case study that forecasts future range shifts of a tropical herbivore, the tropical sea urchin *Tripneustes gratilla* (hereafter *Tripneustes*) and a temperate habitat-forming kelp *Ecklonia radiata* (hereafter “*Ecklonia*”). *Ecklonia* forms ecologically and economically important kelp forests that support a high diversity of organisms along 8,000 km of Australia's temperate reefs, from 27.7°S on the west coast to 27°S on the east coast (Bennett et al., 2016; Wernberg et al., 2019). *Tripneustes* is an important herbivore that preferentially consumes *Ecklonia* when a range of seaweeds are on offer, as demonstrated through both aquaria assays (Dworjanyn, Pirozzi, & Liu, 2007) and field experiments (Vergés et al., 2016). Further, *Tripneustes* is able to overgraze seagrass and macroalgae forests when present in high densities, as was seen in east Africa and Lord Howe Island (LHI), respectively (Eklöf et al., 2008; Valentine & Edgar, 2010). To develop our model, first, we characterize the fundamental niche and the realized niche (sensu Hutchinson (Vandermeer, 1972)) of thermal tolerance of *Ecklonia*. We then use temperature predictions under future Representative Concentration Pathway 8.5 (RCP 8.5) carbon emissions scenario to predict its distribution in the future. RCP 8.5 is a "business as usual" scenario where emissions and the population continue to grow throughout the 21st century (van Vurren et al., 2011). Second, we model the impact of a changing climate on the dispersal and geographical patterns of settlement of *Tripneustes* using the Connectivity Modelling System (CMS; Paris, Helgers, van Sebille, & Srinivasan, 2013). CMS is a Lagrangian-tracking algorithm that allows implementing organism's life traits to simulate the advection of particles such as larvae by ocean currents. Finally, we combine these results to determine the new overlapping areas where biotic interactions are likely to occur under this future climate scenario.

Through this case study approach, we seek to answer the following two questions: (a) how will spawning and settlement of *Tripneustes* larvae change in the future along the east coast of Australia? And (b) could *Tripneustes* pose an increased threat to *Ecklonia* in the future by increasing the overlap, and therefore the potential to interact, between these two species?

2 | METHODS

2.1 | Model details

The oceanographic data used to forecast the impact of climate change on the dispersal of *Tripneusteus* and distribution of *Ecklonia* came from the Ocean Forecasting Australian Model version 3 (OFAM3; Oke et al., 2013) configured to downscale and project future climate as detailed in Feng, Zhang, Sloyan, and Chamberlain (2017) and Zhang et al. (2016). The climate projection includes changes in temperature and circulation. OFAM3 is an eddy-resolving ocean model (1/10° spatial resolution) that has been thoroughly validated in the study region of eastern Australia (Oke et al., 2013). This configuration of OFAM downscales climate models with spatial resolution of 1° to a much finer grid (i.e. 1/10°) and daily temporal resolution. Using a downscaled model is of paramount importance, because it captures circulation features with spatial scales in the order of 10's km such as mesoscale eddies that are key drivers of larval transport along the east coast of Australia (Cetina-Heredia, Roughan, Liggins, Coleman, & Jeffs, 2019; Cetina-Heredia, Roughan, van Sebille, Keating, & Brassington, 2019; Malan et al., 2020; Roughan, Macdonald, Baird, & Glasby, 2011; Wilson et al., 2016). Due to the complexity of the systems represented in climate models, some physical processes are parameterized; such parameterizations can lead to biases or spurious trends denominated climate drift (Sen Gupta et al., 2012). An advantage of the OFAM3 configuration is that it reduces model drift by using non-adaptive relaxation (Zhang et al., 2016). Relaxation is a forcing term that prevents the modelled fields to diverge from a known climatology; in the OFAM3 configuration such forcing does not depend on differences between the climatology and the model state; thus, climate change signals are not masked (Zhang et al., 2016). Additionally, the climate signal used to force this OFAM3 configuration is an ensemble of climatologies from 17 CMIP5 climate models (Feng et al., 2017), averaging out non-systematic biases of individual climate models, and therefore avoiding the introduction of errors associated with a specific climate model. As such, the configuration of OFAM3 used in this study is a state-of-the-art product used to examine impacts of climate change on dispersal. We compare outputs for 10 years of contemporary (2006–2015) and 11 years of future (2090–2100) circulation to reduce the potential influence of interannual variability that can weaken significant results (Coleman et al., 2017).

2.2 | Optimal temperature range distribution of *Ecklonia*

Ecklonia is distributed throughout temperate Australia and its northern range edge lies within the temperate–tropical transition zone, where further expansion equatorward is mostly limited by temperature (Lüning, 1990; Martínez et al., 2018). On the east coast of Australia, the northern distribution of shallow (<25 m) *Ecklonia* forests stretches to Brunswick Heads (28.6°S; A. Vergés, personal communication). The northern limit of distribution, however, is in southern Queensland around Henderson (27°S), where deep *Ecklonia* forests (25–60 m) are present (Marzinelli et al., 2015; Richmond & Stevens, 2014). The poleward limit of distribution of *Ecklonia* in south-eastern Australia is the southern end of Tasmania (43.6°S; Wernberg et al., 2019).

We characterized the realized thermal niche of *Ecklonia*: its actual distribution with respect to temperature by using the mean temperature range of its present habitat in eastern Australia. Specifically, we use depth-averaged (surface to the 75 m isobath) temperatures from the contemporary scenario (2006–2015) to calculate the temperature mean and standard deviation (*SD*) at Brunswick Heads (28.6°S) and at the southernmost point of Tasmania (43.6°S) over this 10-year period. The mean temperature + *SD* (23.9°C + 1.7°C) at Brunswick Heads was identified as the upper temperature threshold where presently *Ecklonia* survives at all depths (i.e. surface to 75 m). Similarly, the mean temperature − *SD* (14.4–1.3°C) in southern Tasmania was identified as the lower temperature threshold for *Ecklonia*'s present habitat range. We then mapped the proportion of time (%) that daily depth-averaged temperature fell within this range in both contemporary and future scenarios. We found that at the northernmost location where *Ecklonia* is still observed at depth (>25 m in Henderson), these temperature conditions were met 70% of the time. We then used the 70% contour in the future scenario to infer the equatorial limit of *Ecklonia*'s distribution in the future. We did not focus on changes in the poleward limit of their distribution because future temperatures in those regions are not projected to shift outside of *Ecklonia*'s optimal thermal range (Martínez et al., 2018), and poleward expansion is indeed limited by the continental shelf.

We then characterized the fundamental thermal niche of *Ecklonia* by compiling reported upper survival threshold from the literature. Tolerance to high temperatures, usually experienced during summer (Lüning, 1984; Martínez et al., 2018), also affects habitat range. This climate envelope determines the potential niche (sensu Grinnell; Vandermeer, 1972), that is, the potential geographical distribution considering temperature as the only limiting factor. Wernberg, de Bettignies, Joy, and Finnegan (2016) found that *Ecklonia* could tolerate short-term temperatures of up to 26.5°C for ~45 min, after which net photosynthetic rate, an indicator of stress (Hurd, Harrison, Bischof, & Lobban, 2014), significantly decreased. We constructed maps of the proportion of time that the daily depth-averaged (surface −75 m isobath) temperature was >26.5°C for both the contemporary and future scenarios. At *Ecklonia*'s northernmost location (i.e. Henderson), the daily depth-averaged temperature was >26.5°C in a contemporary scenario, <20% of the time. Therefore, the 20% contour in the future scenario was used to predict the equatorial limit of *Ecklonia*'s distribution based on tolerance to maximum temperatures. We then superimposed the realized thermal niche onto these maps and compared the output of distribution models based on the two different niche indicators.

In order to explore changes to overlap between *Ecklonia* and *Tripneustes* and determine new areas of interactions in the future, we created a figure encompassing *Ecklonia* and *Tripneustes*' present and predicted future distributions, based on isothermal shifts for *Ecklonia* and: (a) suitability of spawning habitat for *Tripneustes* based on temperature; and (b) simulated dispersal and settlement of *Tripneustes*.

2.3 | Spawning and settlement behaviour of *Tripneustes*

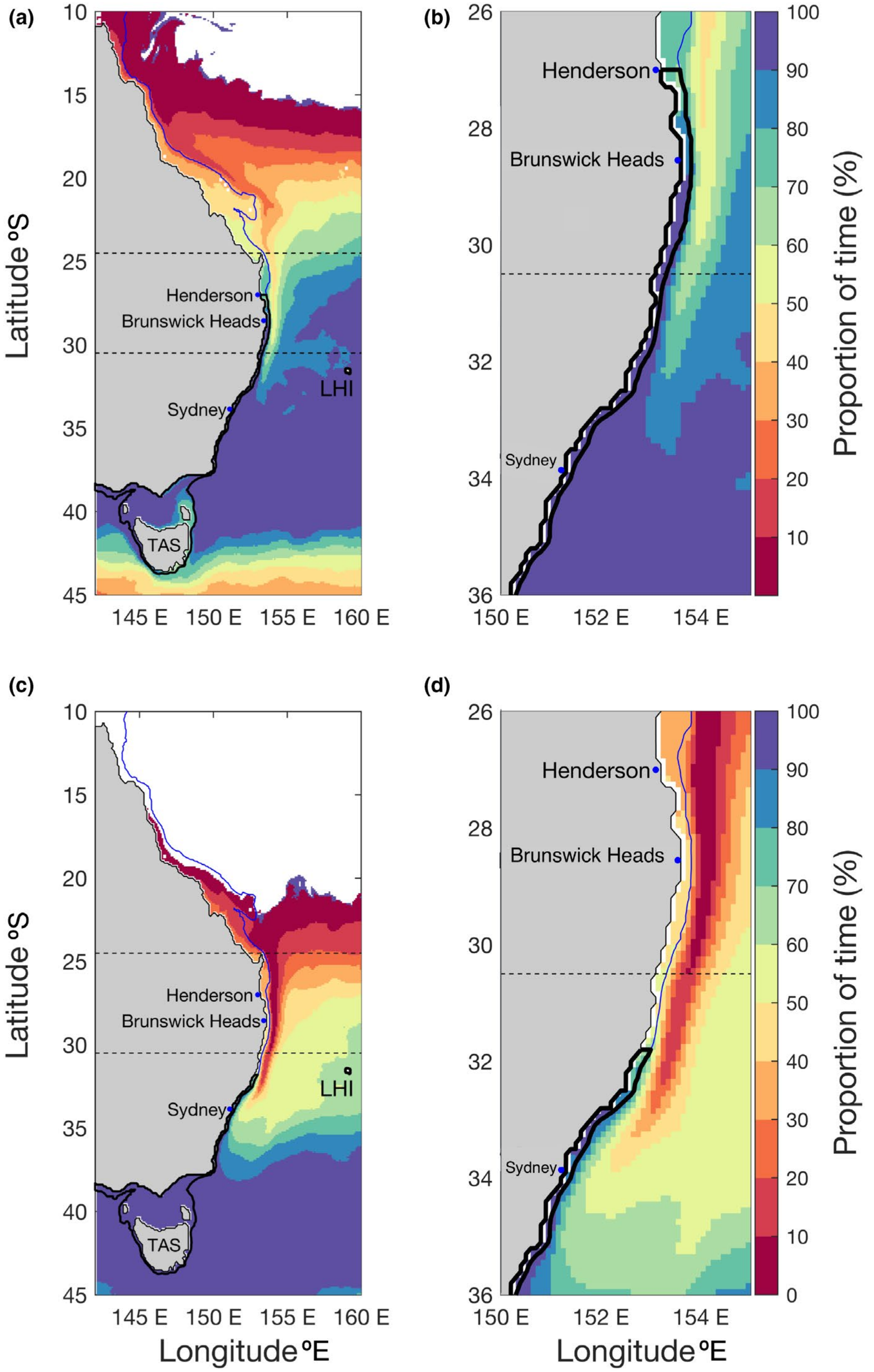
A Lagrangian framework, which uses as reference the position of a particle over time, is ideal to study the transport of larvae by ocean currents. We used the CMS (Paris et al., 2013) to simulate the dispersal of virtual *Tripneustes* sea urchin larvae. CMS is a Lagrangian algorithm that allows simulating the advection of particles by ocean currents while incorporating species-specific life traits. In this study, larvae are advected with 3-dimensional velocity fields produced by the ocean model (OFAM3), that is with ocean current vectors defined by north–south, east–west and up-down components, which are used to advect larvae both horizontally and vertically. In addition to advection by the velocity fields, diffusion is implemented following Cetina-Heredia et al. (2015, 2019). Spawning and settlement criteria are dictated by *Tripneustes* reproductive behaviour and larval development. *Tripneustes* is a fast-growing sea urchin commonly found in tropical/subtropical regions globally (Lawrence & Agatsuma, 2013). To simulate contemporary and predict future dispersal of *Tripneustes* larvae, we based our particle releases on known biological spawning behaviours of adult *Tripneustes* and simulated advection over a time period that corresponds to its pelagic larval duration (PLD). The conditions that enable spawning of *Tripneustes* are temperature-dependent (Chang-Po & Kun-Hsiung, 1981). Mos, Cowden, Nielsen, and Dworjanyn (2011) describe that *Tripneustes* could be consistently induced to spawn every 4–6 weeks when kept at a constant 25°C and fed an abundance of macroalgae. Rahman, Tsuchiya, and Uehara (2009) found that healthy embryonic development of *Tripneustes* occurred at temperatures between 22 and 29°C. *Tripneustes* has been found up to a depth of 75 m (Lane, Marsh, VandenSpiegel, & Rowe, 2000). We combined these conditions and allowed the daily release of particles, from the surface up to the 75 m isobath at all model grid-cell locations, if the mean temperature fell within 22–29°C over the past 6 weeks. A maximum of one particle could be released per day at any location (given by latitude, longitude and depth). As we had no larval supply or adult population data for specific locations (Everett et al., 2017), we could not include this information. Hence, spawning was based on empirical data of temperature suitability for spawning, which also appeared to reflect present distribution and abundance of *Tripneustes*. For instance, in our model *Tripneustes* was able to spawn all year round in the tropics as has been suggested by Malay, Juinio-Menez, and Villanoy (2000), with less spawning in temperate regions where abundance is very low (Williamson, 2015). Hence, spawning in our model reflected only "potential spawning" of larvae.

Tripneustes has a PLD of 15–52 days (Scholtz, Bolton, & Macey, 2013). Therefore, we considered virtual larvae could settle after 15 days and up to 52 days if they came close to the coast (i.e. anywhere between the coastline and the 75 m isobath). No other settlement conditions were considered due to lack of information or model resolution, and hence, we only consider "potential settlement."

2.4 | Data analysis of spawning and settlement across regions and seasons

To understand changes to potential spawning and settlement in both contemporary and future scenarios, we looked at differences in the total yearly number of virtual larvae released or settled within subtropical, tropical and temperate regions, as well as into downstream regions (Tasmania and LHI; Figure S1). Understanding shifts between these regions can help determine whether *Tripneustes* is likely to contribute to the tropicalization of temperate Australia in the future (i.e. an increase in the proportion of *Tripneustes* inhabiting temperate ecosystems and a poleward shift in *Tripneustes* distribution). It also enabled us to target specific areas of interest, such as LHI, where a population outbreak of *Tripneustes* in the past caused significant loss of canopy seaweeds (Valentine & Edgar, 2010). In addition, we investigated monthly differences in total number of larvae spawned and settled within regions. We also recorded the PLD and distance (km) that larvae travelled before settling.

FIGURE 1 Maps showing proportion of time that temperature falls within *Ecklonia*'s current temperature range on the east coast of Australia at two spatial scales. (a) and (b) represent a contemporary scenario (2006–2015). (c) and (d) represent a future RCP 8.5 scenario (2090–2100). The subtropical region lies between the dotted lines, north is the tropical, and south is the temperate region. Thin blue line indicates the 75 m isobath and the thick black line encompasses *Ecklonia*'s current and predicted distribution. White indicates 0% of time. RCP, Representative Concentration Pathway



Tropical and subtropical regions were classified according to the IMCRA 4.0: Provincial Bioregions (Commonwealth of Australia, 2006). Tropical-temperate transition zone was determined as subtropical (Figure S1), with areas north (>24.5°S) considered tropical and areas south (<30.5°S), temperate. The temperate region originally included a section that combined mainland south-eastern Australia and Tasmania, since the maximum depth within the Bass Strait (between mainland Australia and Tasmania) is mostly shallower than 75 m. These two regions were subsequently split into two using shallower 50 m isobaths in this region, with each settlement region extending roughly halfway into Bass Strait (Figure S1). These regions remained the same for contemporary and future scenarios. Larval trajectories were analysed using MATLAB (version R2018a) to quantify spawning, settlement and determine changes in connectivity between sources and sinks.

Changes to potential spawning and settlement within specific regions were analysed using the statistical platform R version 3.4.4. (R Core Team, 2018). To determine statistical differences between the total number of particles spawned and settled within a specific region, an unpaired two-sample Wilcoxon test was used with contemporary and future scenarios as the arguments and the number of years within each scenario as the replicates. To ensure years were independent samples, we corroborated autocorrelations of total spawning and settlement for each region across years. These were not strongly autocorrelated, and therefore, assumptions of independent sample units were met.

3 | RESULTS

3.1 | Temperature as a predictor of *Ecklonia*'s future distribution

In the future scenario, *Ecklonia*'s northern distribution experiences a poleward contraction of ~530 km (from 27°S to 31.8°S) based on shifts in its realized thermal niche (Figures 1 and 2). This range contraction is supported by forecasts based on changes in its fundamental thermal niche, that is high temperatures (>26.5°C) above *Ecklonia*'s maximum thermal tolerance threshold (Figure S2). In most northern areas of *Ecklonia*'s predicted new range, high temperatures are expected to be experienced 0%–20% of the time (Figure S2c,d), as is presently experienced in *Ecklonia*'s northern distribution (Figure S2a,b, around Henderson and Brunswick Heads). The only exception is the northernmost point at 31.8°S, where in future predicted conditions high temperatures will be reached 20%–30% of the time (Figure S2d).

3.2 | Changes in potential spawning and settlement of *Tripneustes*

Modelled spawning potential in a contemporary scenario adequately reflected present *Tripneustes* occurrence. In the contemporary scenario, greatest spawning of *Tripneustes* occurred in its usual habitat range (the tropics and subtropics). Spawning then gradually decreased towards Sydney, where *Tripneustes* is still found but in low abundances (Williamson, 2015). No spawning occurred south of 35.8°S, which is close to Merimbula, the furthest point where *Tripneustes* has been recorded (Williamson, 2015). Hence, temperature-based spawning in the model appears to appropriately reflect *Tripneustes*' broad present distribution (Figure 3a), suggesting this is a suitable abiotic driver to predict future spawning grounds and range shifts.

Temperate regions experienced a 3.6-fold increase in potential spawning of *Tripneustes* (Figure 4a; Table S1). In a contemporary scenario, potential spawning within temperate regions typically occurs less than 40% of the time, never exceeds 70%, and no spawning occurs poleward of 35.8°S (Figure 3). In a future scenario, spawning potential in temperate regions increased dramatically, with areas suitable for spawning 50%–100% of the time stretching from 30.5–35.8°S and with the southernmost possible spawning location predicted in Tasmania at 42.5°S (Figure 3). This equates to a ~650 km poleward range expansion in suitable spawning grounds (Figure 2). Temperatures within the subtropics also became more suited to enable spawning (Figure 3), resulting in an 8.1% increase in future spawning (Figure 4a; Table S1). Conversely, the model predicts the tropics will become less suitable for the spawning of *Tripneustes*, which decreases by 43% in the future (Figure 4a; Table S1). In a contemporary scenario, temperatures are suitable for spawning 40%–100% of the time in the tropics, while temperatures are only suitable for spawning 10%–70% of the time in the future (Figure 3). LHI experienced a significant 47.8% increase in spawning potential of *Tripneustes* (Figure 4a; Table S1), evidenced by a change in the occurrence of suitable temperature for spawning from 60%–70% to 90%–100% (Figure 3).

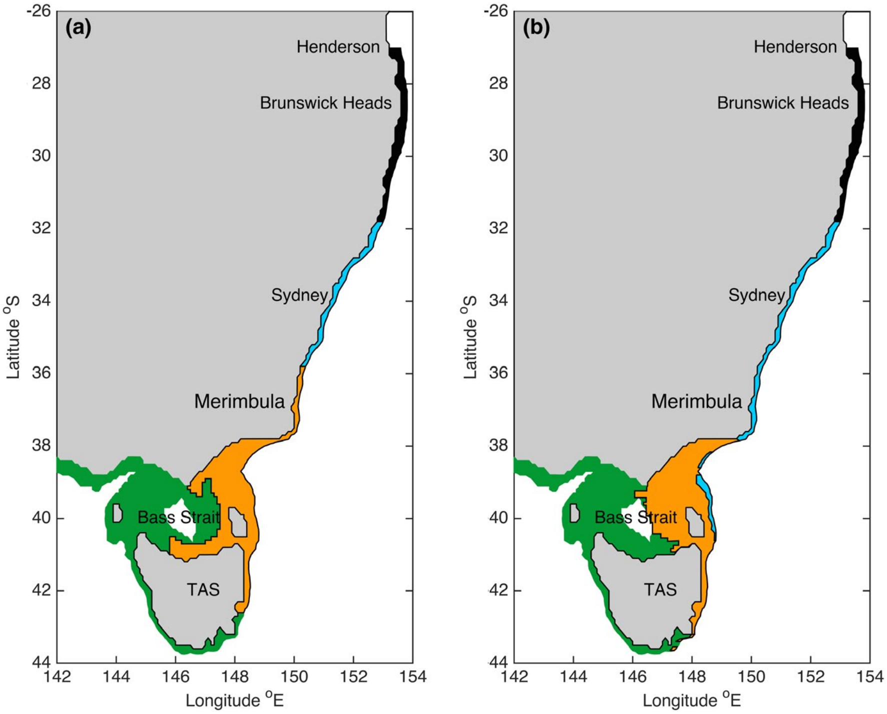


FIGURE 2 Maps of change in the distribution of *Ecklonia* and *Tripneustes*. The black region indicates the area where *Ecklonia* will be lost according to changes in temperature. The blue outlines areas where *Ecklonia* and *Tripneustes* presently co-exist and will continue to co-occur in the future based on model simulations for (a) potential spawning and (b) potential settlement of *Tripneustes* larvae. Merimbula denotes the present southernmost recorded location of *Tripneustes* (Williamson, 2015). The orange indicates areas where *Ecklonia* and *Tripneustes* may co-exist in the future only based on model simulations for (a) potential spawning and (b) potential settlement of *Tripneustes* larvae. The green indicates areas where *Ecklonia* will exist in the future but will likely not interact with *Tripneustes*

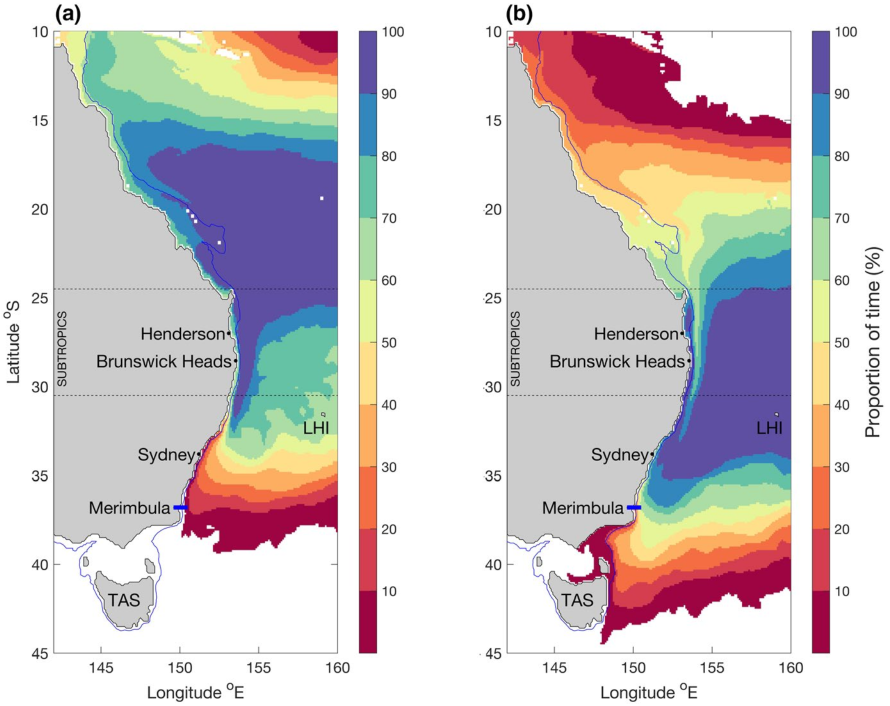


FIGURE 3 Maps showing proportion of time that temperature is suitable for spawning of *Tripneustes* in a contemporary scenario (2006–2015; a) and future RCP 8.5 scenario (2090–2100); b. Blue line indicates the 75 m isobath. The subtropical region lies between the dotted lines, north is the tropical, and south is the temperate region. White indicates 0%. Thick blue line indicates southernmost point where *Tripneustes* has been recorded to date (Williamson, 2015). RCP, Representative Concentration Pathway

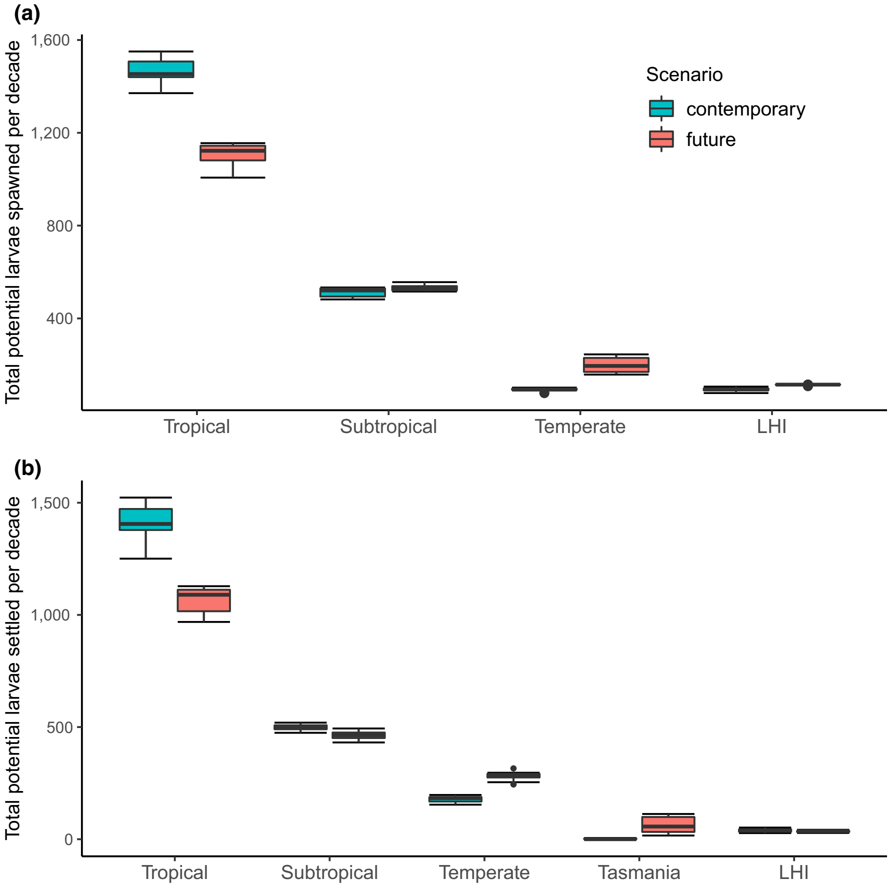


FIGURE 4 Total number of *Tripneustes* larvae spawned (a) and settled (b) in each region in both a contemporary (2006–2015; *n* = 10) and future (2090–2100; *n* = 11) RCP 8.5 scenario (square root transformed data). Boxplots indicate the distribution, median and whiskers plot 1.5× the interquartile range (IQR). LHI, Lord Howe Island; RCP, Representative Concentration Pathway

Contemporary settlement extends further south than spawning grounds reaching regions within the continental shelf between mainland Australia and Tasmania (Figure 5); however, south of 35.2°S, the southernmost spawning latitude, settlement density (i.e. within grid cells of ~10 km^2) accounts for less than 0.01% relative to total settlement. In the future scenario, settlement occurs as far south as 43.6°S along the coast off Tasmania and settlement densities larger than 0.01% extend ~400 km poleward to 39.2°S, relative to those in the contemporary scenario. Maximum settlement densities within temperate latitudes off Tasmania increase two orders of magnitude,

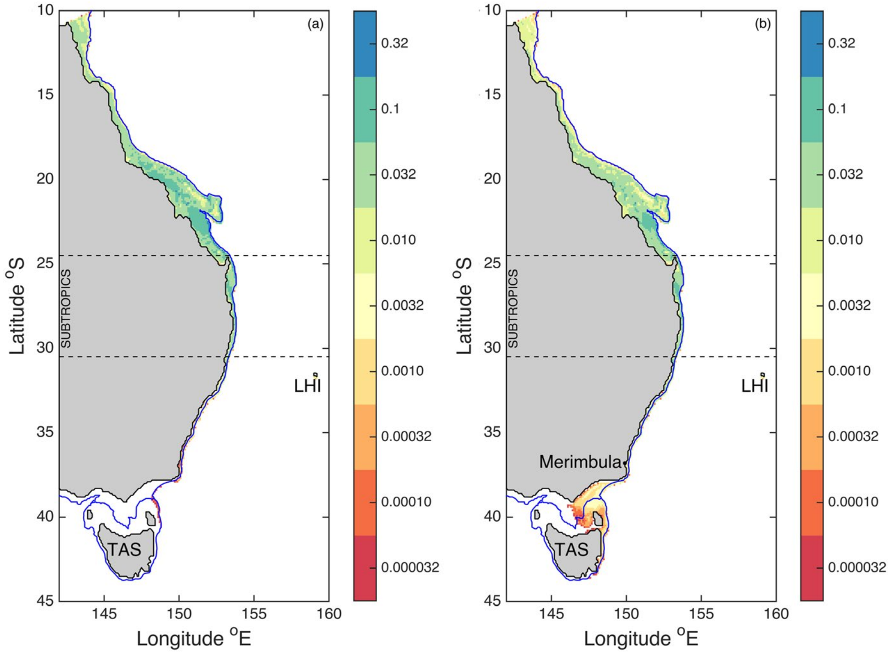


FIGURE 5 Maps showing *Tripneustes* settlement densities as percentage relative to total contemporary settlement per 10 km^2 in a contemporary scenario (2006–2015; a) and future RCP 8.5 scenario (2090–2100; b). Blue line indicates the limits of settlement polygons. The subtropical region lies between the dotted lines, north is the tropical, and south is the temperate region. White indicates 0%. RCP, Representative Concentration Pathway

from ~0.0003% in the contemporary scenario to 0.01% in the future (Figure 5). Similar to changes in spawning within the tropics, settlement densities decrease noticeably, rarely falling below 0.03% in the contemporary scenario, while often being an order of magnitude smaller ~0.003% in the future (Figure 5).

Temperate regions experienced the greatest changes to potential settlement, with a 1.5-fold increase in temperate zones (not including Tasmania) and a 677-fold increase in Tasmania, where previously settlement was close to zero (Figure 4b; Table S1). Settlement in the tropics and subtropics experienced a decrease of 43% and 13.7% with respect to contemporary settlement, respectively (Figure 4b; Table S1). However, potential settlement was still greater in the tropics and subtropics than within temperate regions. LHI experienced no significant change in settlement (Figure 4b; Table S1).

3.3 | Changes in regions of *Tripneustes* and *Ecklonia* co-occurrence

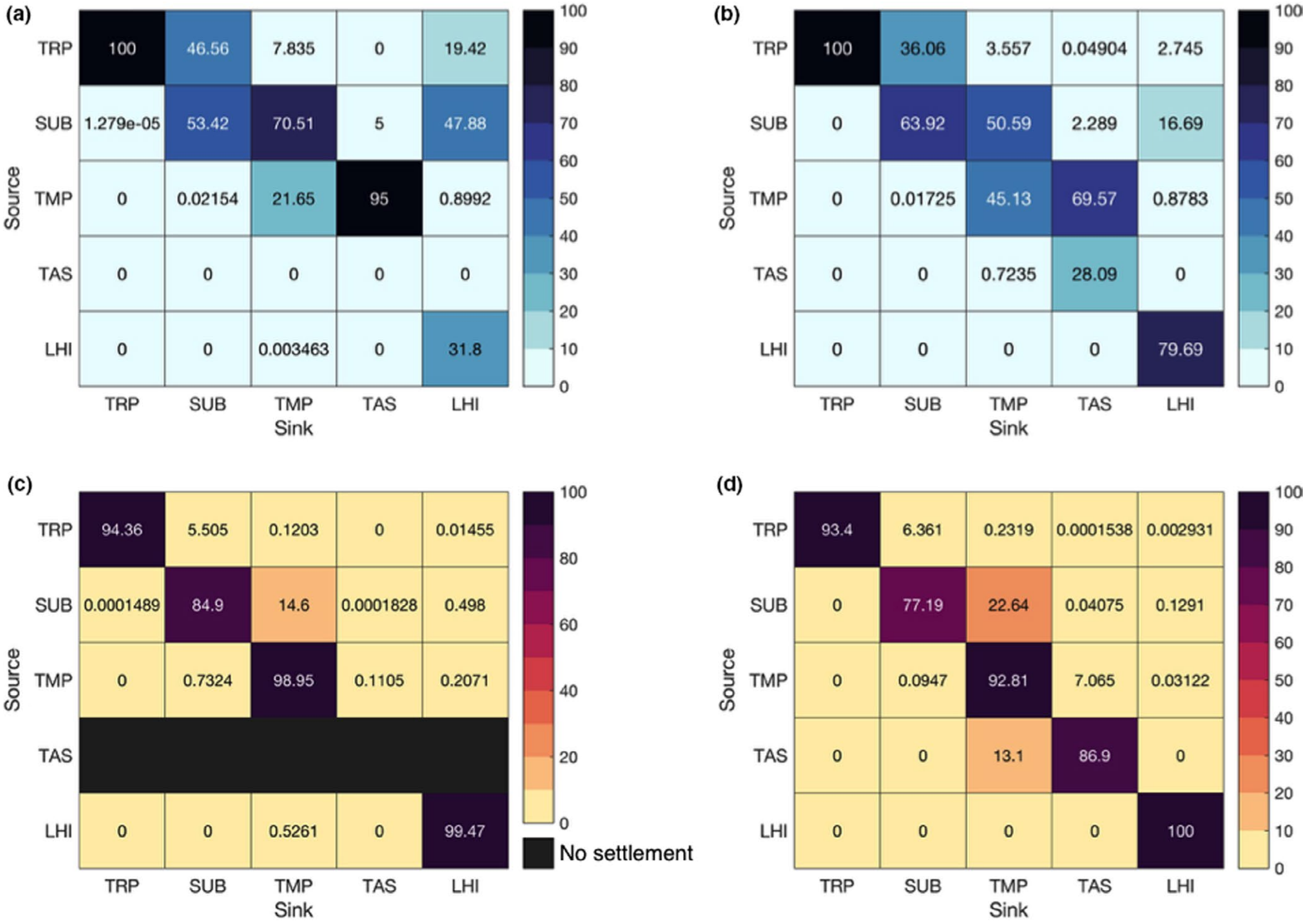
Future predictions of regions suitable for *Tripneustes* spawning and settlement show a poleward expansion of *Tripneustes* into areas where *Ecklonia* occurs, and the rise of new areas of interaction between this tropical herbivore and habitat-forming kelp in temperate regions (Figure 2, orange region). Additionally, areas where they currently co-occur, at the equatorward range edge of *Ecklonia*'s future distribution (Figure 2, blue region), temperatures will become more suitable for year-round spawning of *Tripneustes* and settlement densities are predicted to increase (Figure 3).

3.4 | Main *Tripneustes* larval sources

Climate change leads to substantial changes on the connectivity between urchin populations in different regions. Under the contemporary scenario, only 21.7% of the larvae that settle in temperate regions are sourced from within temperate latitudes, whereas in the future nearly half of the larvae (45.1%) settling in temperate reefs will be sourced from within that same region (Figure 6a,b). Additionally, the proportion of larvae released in the subtropics that are predicted to settle in temperate regions also changes, increasing from 14.6% to 22.6% (contemporary and future climate, respectively; Figure 6c,d). LHI experienced the greatest changes to larval sources. In a contemporary scenario, both the tropics and subtropics are significant sources of larvae for LHI urchin populations, with the subtropics contributing most larvae (Figure 6a). In a future scenario, self-recruitment becomes the largest source of larvae to LHI, and almost no larvae are sourced from the tropics (Figure 6b).

3.5 | Phenology changes

The most obvious changes to phenology occur in the tropics and subtropics for both potential spawning and settlement (Figures 7 and 8). In the tropics, spawning and settlement in a contemporary scenario are highest across eight months of the year from May to December (late autumn–early summer). In a future scenario, this is halved to only four months of the year and the timing shifts from July to October (mid-winter–early spring). In the subtropics contemporary scenario, spawning and settlement are constant throughout the year with a small decline in late winter–early spring. In contrast, in the future scenario, the decline occurs in late summer–early autumn. In temperate regions, no clear phenological changes can be seen, with seasonal patterns of potential spawning and settlement remaining constant across both scenarios. In Tasmania, settlement experiences an increase in autumn with little settlement throughout the rest of the year. In LHI, future spawning remains constant throughout the year, whereas in a contemporary scenario it declines in late winter–spring. No clear changes in settlement patterns can



(a)

	TRP	SUB	TMP	TAS	LHI
TRP	100	46.56	7.835	0	19.42
SUB	1.279e-05	53.42	70.51	5	47.88
TMP	0	0.02154	21.65	95	0.8992
TAS	0	0	0	0	0
LHI	0	0	0.003463	0	31.8

(b)

	TRP	SUB	TMP	TAS	LHI
TRP	100	36.06	3.557	0.04904	2.745
SUB	0	63.92	50.59	2.289	16.69
TMP	0	0.01725	45.13	69.57	0.8783
TAS	0	0	0.7235	28.09	0
LHI	0	0	0	0	79.69

(c)

	TRP	SUB	TMP	TAS	LHI
TRP	94.36	5.505	0.1203	0	0.01455
SUB	0.0001489	84.9	14.6	0.0001828	0.498
TMP	0	0.7324	98.95	0.1105	0.2071
TAS	■	■	■	■	■
LHI	0	0	0.5261	0	99.47

■ No settlement

(d)

	TRP	SUB	TMP	TAS	LHI
TRP	93.4	6.361	0.2319	0.0001538	0.002931
SUB	0	77.19	22.64	0.04075	0.1291
TMP	0	0.0947	92.81	7.065	0.03122
TAS	0	0	13.1	86.9	0
LHI	0	0	0	0	100

FIGURE 6 Connectivity matrices showing source of *Tripneustes* larvae that settle/sink in a region. Panels on the left represent a contemporary scenario (2006–2015). Panels on the right represent a future RCP 8.5 scenario (2090–2100). (a) and (b) indicate where the % of larvae that settle/sink in a region were originally sourced from, with values totalling 100% in the vertical direction. (c) and (d) indicate where the % of larvae released from a specific source/region then settle/sink, with values totalling 100% in the horizontal direction. LHI, Lord Howe Island; NaN, no spawning; SUB, subtropics; TAS, Tasmania; TMP, temperate region; TRP, tropics; RCP, Representative Concentration Pathway

be observed for LHI, although settlement appears less variable in the future.

3.6 | Larvae dispersal distance

In both, a contemporary and future scenario most larvae settled within 15 days (Figure S3a,b) and travelled <400 km (Figure S3c,d) while potential for dispersal was >3,500 km.

4 | DISCUSSION

In this study, we have used a combined mechanistic modelling approach to create a predictive map that investigates climate-driven changes in the habitat suitability of a habitat-forming kelp species (*Ecklonia*), climate-driven changes in the distribution of an ecologically important tropical herbivore (*Tripneustes*) that account for dispersal processes, and lastly potential changes in the future interaction between these two species caused by new areas of co-occurrence. Overall, we predict that *Ecklonia*'s range will contract poleward substantially due to warming; additionally, we find that climate-driven changes in the oceanic environment shift the spawning and settlement range of *Tripneustes*, causing its poleward expansion, and an increased area of interaction between this herbivore and *Ecklonia* with potential consequences on ecosystem health if kelp is overgrazed (Figures 2, 3 and 5). Our case study explores a new method to model species range shifts that incorporates all three aspects of the BAM framework including the anticipation of species interactions in new regions of co-occurrence, a concept that is often overlooked in SDMs. As climate change strengthens WBCs and creates global warming hotspots alongside the eastern coasts of many continents (Cetina-Heredia et al., 2015; Hobday & Pecl, 2014), this approach is relevant and can be applied to predict future shifts and interactions between foundation species and consumers in other temperate ecosystems globally aiding adaptive management.

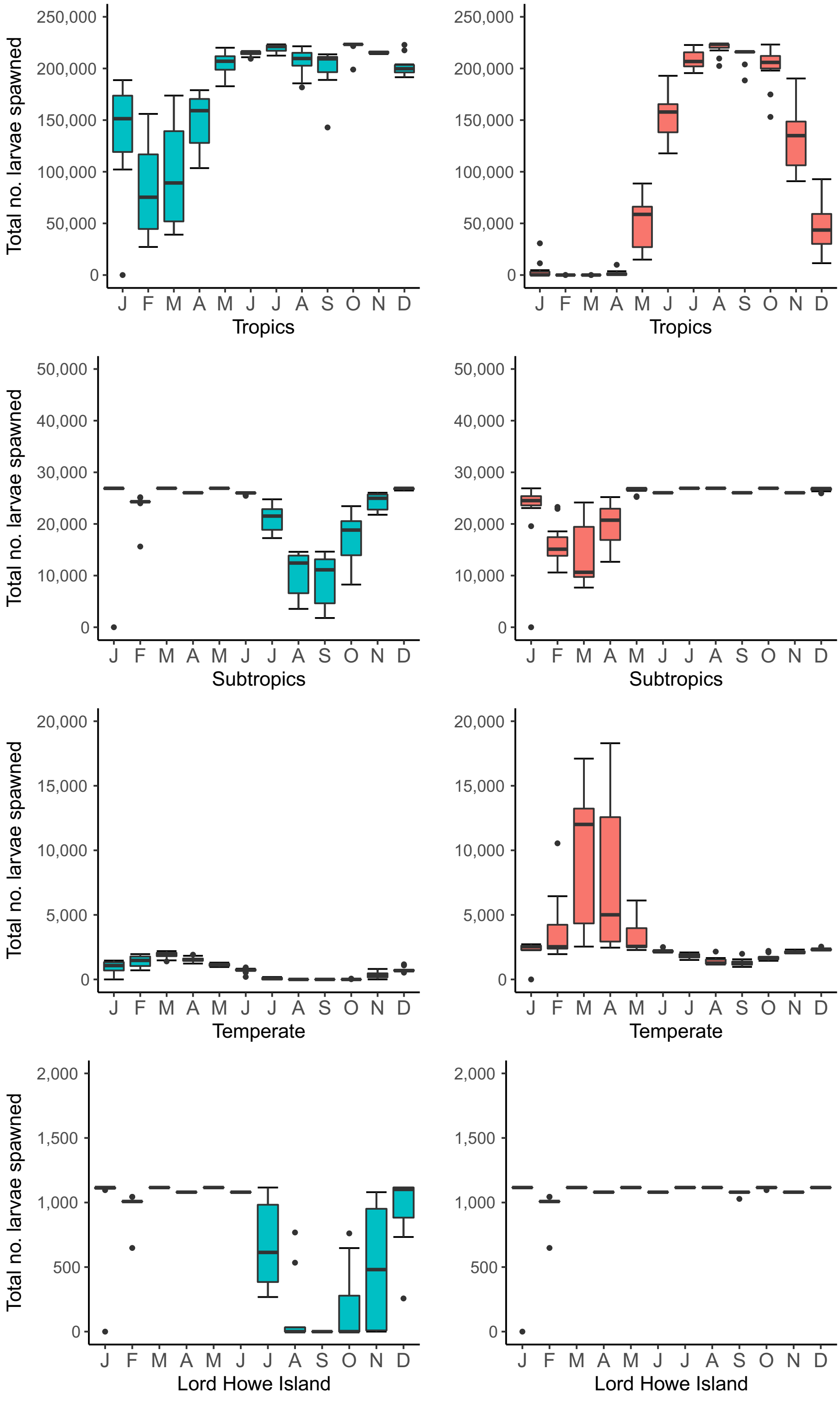


FIGURE 7 The total number of *Tripneustes* larvae spawned each month within each region of a contemporary (left panel, n = 10 monthly; 2006–2015) and future RCP 8.5 scenario (right panel, n = 11 monthly; 2090–2100). Letters on x-axis indicate months of the year. Boxplots indicate the distribution, median and whiskers plot 1.5× IQR. IQR, interquartile range; RCP, Representative Concentration Pathway

4.1 | Future loss of kelp caused by warming and a range-shifting tropical herbivore

Our findings predict a smaller range contraction for *Ecklonia* based on temperature changes alone (Figures 1 and 2) than a previous study by Martínez et al. (2018), which used an SDM approach through MAXENT to also model the future distribution of *Ecklonia*. Their investigation resulted in a more extreme range-shift estimation for kelp (~1,200 km range retraction), with *Ecklonia* restricted to only Australia's south coast (<37.7°S) under more optimistic climate

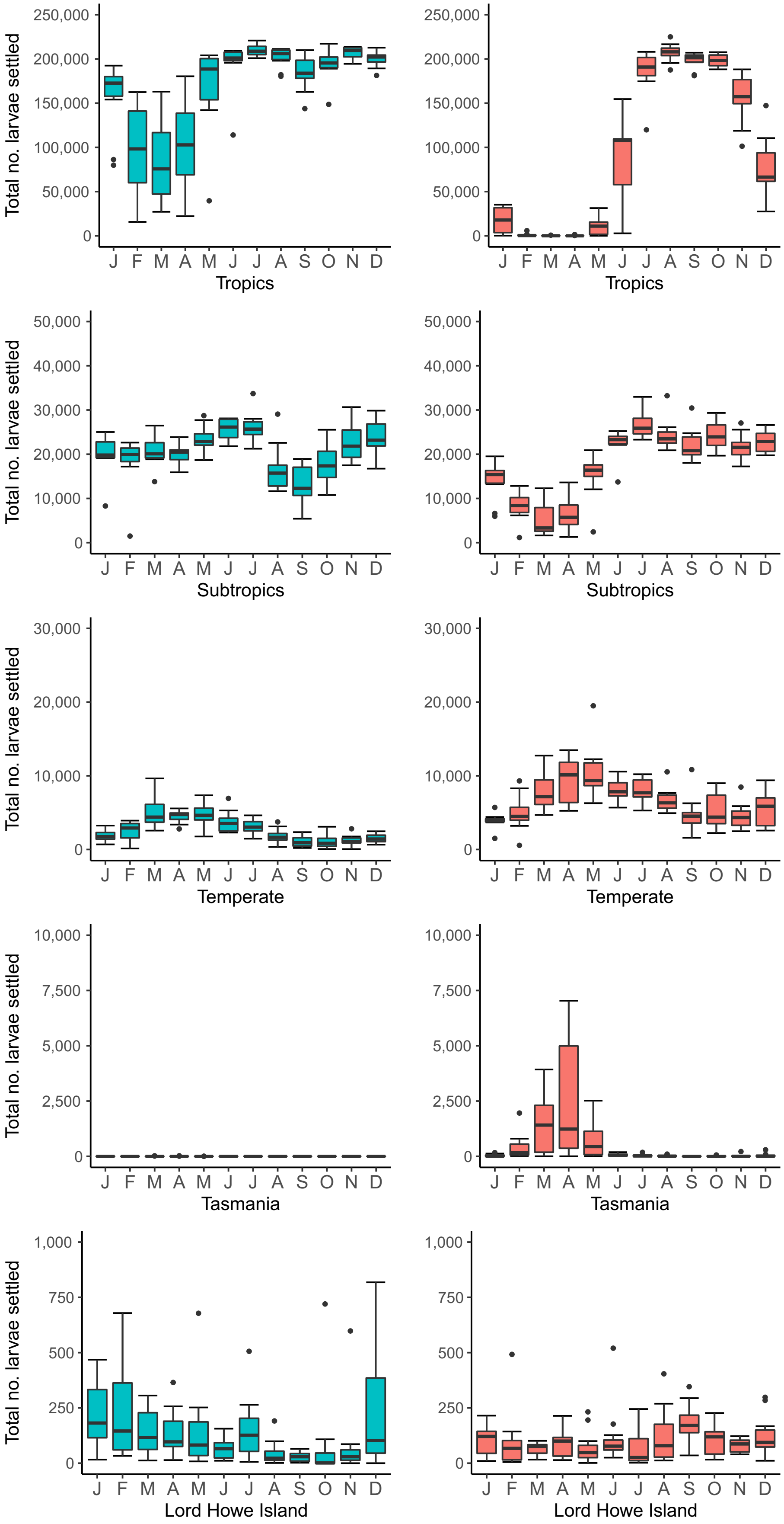


FIGURE 8 The total number of *Tripneustes* larvae settled each month within each region of a contemporary (left panel, n = 10 monthly; 2006–2015) and future RCP 8.5 scenario (right panel, n = 11 monthly; 2090–2100). Letters on x-axis indicate months of the year. Boxplots indicate the distribution, median and whiskers plot 1.5× IQR. IQR, interquartile range; RCP, Representative Concentration Pathway

change scenarios by 2100 (RCP 2.6 and 6.0). We suggest that disparities in results may be caused by the different datasets used in each study for predicting future conditions. For instance, Martínez et al. (2018) MAXENT predictions use monthly maximum and minimum mean SSTs to determine habitat range, while our approach considered daily depth-averaged (surface to 75 m) temperatures. Furthermore, future conditions used in MAXENT were obtained from Bio-ORACLE, which provides ocean data produced from averaging three CMIP5 climate models (Assis et al., 2017). In contrast, OFAM3 future projection (Zhang et al., 2016) uses an ensemble of 17 CMIP5 models as forcing. Our approach provides a more optimistic outlook for kelp distribution in the future where temperature alone may not cause the severe retraction of habitat that was estimated by Martínez et al., (2018). However, further losses to those we predicted may be expected with the increased frequency of marine heatwaves (Frolicher, Fischer, & Gruber, 2018). Our predictions of *Ecklonia*'s distribution are based on mean temperatures, possibly underestimating potential severe decimation of *Ecklonia* populations due to isolated marine heatwave events, which were not explored in this study (Wernberg, Bennett, et al., 2016).

The expansion of *Tripneustes* is likely to contribute to the tropicalization of temperate areas in the future and may cause a greater loss of kelp canopy cover through increased grazing pressure and through the creation of novel areas of interactions (Figure 2, orange region) between this tropical herbivore and kelp in temperate regions. Particularly at the equatorward range edge of *Ecklonia*'s future distribution (Figure 2, blue region), temperatures will become more suitable for year-round spawning of *Tripneustes* (Figures 3 and 7), and settlement densities are expected to increase notably (Figures 5 and 8), support larger adult populations and increase grazing of *Ecklonia*. *Tripneustes* has already been identified as a key consumer of *Ecklonia* in warming tropical–temperate transition zones where this kelp is declining (Vergés et al., 2016). Hence, an increased abundance of *Tripneustes* could facilitate a greater contraction of *Ecklonia*'s forecasted range. Further, *Tripneustes* is also able to tolerate higher temperatures (22–29°C) (Rahman et al., 2009) than *Ecklonia*. Therefore, as extreme heat events are expected to increase in frequency (Frolicher et al., 2018), *Tripneustes* may pose an even greater grazing risk to *Ecklonia* during these periods of thermal stress. Evidence for a range expansion of *Tripneustes* is already emerging in Western Australia, where increases in abundance have been observed following a marine heatwave event (Smale, Wernberg, & Vanderklift, 2017). Furthermore, phenological changes in the timing of spawning and settlement peaks for *Tripneustes* (Figures 7 and 8) may have unknown consequences for other species that interact with *Tripneustes*, such as creating a mismatch between predators and the availability of larvae as food (Durant, Hjermann, Ottersen, & Stenseth, 2007). If a mismatch occurred in favour of the larvae, this could cause *Tripneustes* outbreaks. *Tripneustes* is forecasted to spread into Tasmania where kelp forests are already being decimated by range-shifting *Centrostephanus rodgersii* (Ling, Johnson, Frusher, & Ridgway, 2009), novel interactions between kelp and *Tripneustes* in these areas where previously they did not co-occur (Figure 2, orange area) could lead to a significantly greater loss of kelp than was predicted by using optimal temperature range in our model (Figure 2, black area). Future management techniques, such as ensuring *Tripneustes* predators are not overfished (Eklöf et al., 2008; Ling et al., 2009) or potentially harvesting urchins as a new commercial fishery (Scheibling, Hennigar, & Balch, 1999) would aid in decreasing the risk of population outbreaks in the future.

4.2 | Drivers of change in *Tripneustes* settlement patterns

Within the aspects considered in the BAM framework, warming (abiotic factor) rather than changes in larval pathways (movement) appeared to be a greater driver of poleward range expansion for *Tripneustes*. This may also be the case for species with short PLD for which changes in transport by altered ocean currents is restricted to a few days, while changes in temperature affect species throughout their life span. Opening up of temperate spawning grounds in the future substantially increased the supply of larvae recruiting into temperate regions (Figures 3 and 6b). As temperatures become suitable for spawning, they are likely to allow the persistence of settlers that can develop into adult populations. For instance, currently there are no *Tripneustes* in Tasmania (Figure 3) but in the future scenario 87% of future recruits will originate from adults breeding in Tasmania (Figure 6c,d). The proportions of settlement in each region relative to total larvae sourced from the tropics remain similar across scenarios (Figure 6c,d). Thus, it is more likely that the increase of future settlement in temperate regions is driven by warming enabling greater spawning of larvae in temperate areas rather than current intensification carrying larvae from the tropics further poleward into temperate regions. Perhaps dispersal pathways from the tropics in a future scenario could have resulted in increased settlement in temperate regions had the PLD and distance travelled by larvae been greater (Figure S3). However, warming also increases the metabolism of larvae, accelerating growth and resulting in a reduced PLD up until a certain temperature threshold after which mortality increases (McLeod et al., 2015; O'Connor et al., 2007). This is likely the case for *Tripneustes* larvae, as warming of +3°C (27°C) increased growth of early-stage larvae, but a +6°C (30°C) triggered abnormal development in most larvae (Sheppard Brennand, Soars, Dworjanyn, Davis, & Byrne, 2010). The study by Sheppard Brennand et al. (2010) suggests that settlement patterns of larvae that drift the minimum time of the pelagic stage (i.e. 15 days) rather than the maximum (52 days) are more likely to represent settlement patterns of a warming scenario. This was the case in our simulations, where maximum settlement occurred in the first 15 days (Figure S3a,b). Future research may consider separating the effects of a strengthened EAC from warming, to determine precisely the dispersal mechanisms for increased poleward range shift of *Tripneustes* into temperate ecosystems.

Conversely, in the tropics potential spawning and settlement is predicted to decrease due to warming temperatures reducing suitability as a year-round spawning location (Figures 3–5 and 7). This could contribute to reduced health of tropical coral reef ecosystems in the future, as sea urchins are considered to have an important ecological role in maintaining the balance of coral–algae competition on coral reefs (Coyer, Ambrose, Engle, & Carroll, 1993). Removal of important herbivores such as sea urchins can cause overgrowth of algae and facilitate ecosystem phase shifts from coral to algae dominated reefs (Coyer et al., 1993; Hughes, Reed, & Boyle, 1987). Consequently, a reduction in *Tripneustes* urchins may have negative consequences to tropical coral reefs, particularly if other important herbivores like fish also shift their ranges poleward (Vergés, Steinberg, et al., 2014).

4.3 | Connectivity implications for LHI

The results from LHI have particular conservation relevance due to the unique status of this island as a UNESCO World Heritage site (Environment Australia, 2002) and given records of past outbreaks of *Tripneustes* in this region (Valentine & Edgar, 2010). They also highlight the importance of considering dispersal when predicting species range shifts. Even though we did find that warming increased the suitability of LHI as a year-round spawning site (Figures 3 and 4a), we found no significant difference in settlement (Figure 4b) and there appeared to be less variability in monthly settlement rates (Figure 8), suggesting no particular greater risk of outbreaks. However, we discovered a significant change in source regions supplying *Tripneustes* larvae to LHI (Figure 6a,b). In the future scenario, most larvae are self-recruited from LHI itself, the proportion of larvae exported from temperate regions remains unchanged and small, and there is a drastic reduction in supply from the subtropics and tropics (only significant sources in the contemporary scenario). These changes are most likely driven by alterations to ocean circulation; as the EAC strengthens with increased flow in a poleward direction, eastward flow towards New Zealand diminishes (Oliver & Holbrook, 2014), which may reduce larval transport from mainland Australia to South Pacific Islands such as LHI of all species with a planktonic phase. Furthermore, the EAC is projected to separate further south (Oliver & Holbrook, 2014); therefore, the EAC eastward flowing extension may also extend poleward and bypass LHI. These changes imply that LHI may become more isolated from tropical/subtropical Australia in the future, which could alter ecosystem composition and reduce population resilience through gene flow changes decreasing genetic diversity (Sgrò, Lowe, & Hoffmann, 2011), as species rely more on self-recruitment to maintain populations. The changes in connectivity patterns revealed here are likely to influence many other species and highlight the benefits of using a Lagrangian approach that considers dispersal mechanisms.

4.4 | Limitations to the dispersal model

We included the most current research on the biological properties of *Tripneustes* into our model, however, there are still knowledge gaps that limited our dispersal simulations. For example, in our model *Tripneustes* spawning was based solely on temperature determined by laboratory experiments in controlled environments (Mos et al., 2011; Rahman et al., 2009), as there is currently no certainty of spawning cues for wild populations. Furthermore, ocean acidification may have important impacts on future populations of calcifying organisms like *Tripneustes*, reducing reproductive output (Dworjanyn & Byrne, 2018) and larval success (Sheppard Brennand et al., 2010). Ocean pH was not projected with the downscaled ocean climate model; therefore, we could not incorporate these effects. Further research into these areas would improve representation of *Tripneustes* larvae and are factors to consider if using this approach for other species.

Additionally, the very recent discovery of a new species of sea urchin *Tripneustes kermadecensis*, which overlaps in range and has long been confused with *T. gratilla*, may mean that some of the biological properties used in our model may have potentially come from studies that unknowingly used *T. kermadecensis* or hybrids of the two species in their research. Bronstein et al. (2019) suggest that populations poleward of Sydney are likely to belong to *T. kermadecensis*. Given that frequency of suitable spawning temperature in our models is only high north of Sydney (Figure 3) and this coincides with the southernmost distribution of *T. gratilla* inferred from genetic analysis (Bronstein et al., 2019), we are fairly confident that *T. gratilla*'s distribution was well represented in our model. Nonetheless, findings should be interpreted with some caution until further genetic sampling is undertaken to determine with certainty the full range of the two species.

4.5 | Concluding remarks

This study provides a novel combined modelling approach that accounts for all three aspects of the BAM framework (Peterson et al., 2015) to address the limitations that other SDMs and mechanistic models encounter when modelling species distributions. The model uses output from OFAM3 to map the contemporary and future realized and fundamental thermal niches of a dominant temperate kelp species, and a Lagrangian particle-tracking framework to forecast and map range shifts of a tropical sea urchin due to climate-driven changes in dispersal. The output from these two approaches is then combined into one predictive map, which shows potential for strengthened interactions between the species in the future due to new regions of co-occurrence, possibly leading to greater kelp loss through increased grazing pressure. We were also able to inadvertently discover changes to connectivity of *Tripneustes* between source–sink locations. Our approach of niche characterization, dispersal modelling and distributional prediction is transferable to other marine ecosystems and can be used to determine range shifts and forecast changes to species interactions between other foundation species and consumers. It can assist managers worldwide to predict future ecosystem composition and important species interactions, and potentially prepare adaptive measures to better manage changing marine ecosystems.

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DATA AVAILABILITY STATEMENT

The larval trajectories generated for this study are available through Dryad https://doi.org/10.5061/dryad.n5tb2rbsh.

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BIOSKETCH

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Author contributions: L.C., P.C.-H., A.V. and M.R. conceived the idea; S.D. informed the modelling of *Tripneustes* spawning; M.C. and M.F. provided the hydrodynamic model data for dispersal simulations; L.C. and P. C.-H. conducted dispersal simulations, analysed the data and interpreted results; L.C. led the writing; L.T. contributed to the statistical analyses of the data. All authors contributed to the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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