Spatial Distributions and Co-Occurrence of New Zealand Shallow Reef Urchins

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General Abstract

Globally, ecosystems are experiencing significant disruption due to unprecedented environmental changes. These environmental changes result in many species undergoing range shifts, creating a series of novel interspecies interactions. These changes have significantly affected several ecosystems; temperate kelp forests have seen an influx of tropical and sub-tropical herbivores resulting in many being damaged by overgrazing. Here, in chapter II I examine the drivers of variability in the abundance of three such sub-tropical grazers, the shallow reef urchin species *Centrostephanus rodgersii, Heliocidaris tuberculata*, and *Tripneustes kermadecensis* at Rangitāhua. I assessed the patterns of abundance for the urchin species, using a generalized linear mixed model, investigating relationships between abundance and three variables (Depth, topographical complexity, and algal composition) and the other species' abundance. The models show the three species being most abundant in unique combinations of variables. Significant correlations were observed between *C. rodgersii* and the other species (negative at the site level for *T. kermadecensis* and positive at the transect level for *H. tuberculata*) suggesting microhabitat segregation among the species. In chapter III, I then model the present and future distribution of four urchin species present in New Zealand; the three subtropical species listed above, and the endemic kina (*Evechinus chloroticus*). I modelled the urchin's present and future distributions using four different species distribution modelling techniques, Generalized Linear Models, Maximum Entropy, Random Forests, and Support Vector Mechanics, to create an ensemble model of their distributions. I then created future models for four of the Representative Concentration Pathway (RCP) future climate scenarios for

2100, ranging from optimistic (RCP 2.6) to worst-case (RCP 8.5). The models predict poleward range shifts in all three subtropical species, under all future climate scenarios, with the range shifts' extent depending on climate change severity. Although no range shift was predicted in *E. chloroticus*, a reduction in environmental suitability was predicted. The range expansions of these urchins along north-eastern New Zealand's coast will bring them into increased contact with kina and New Zealand's kelp forests. Changes in the urchin populations could devastate New Zealand's kelp forests and better understanding is required if preemptive conservation management is to be applied.

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Chapter I: General Introduction

Species distributions and co-occurrence

A species distribution can be described as the sum of all locations the species is present. Various environmental and biotic factors shape a species' distribution (Hutchinson 1957). Should any of these factors change, the species' distribution may change in accordance (Chen et al., 2011). The environmental factors determine a species fundamental niche, a region of environmental space where fitness is greater than or equal to one in the absence of competitors or predators (Hutchinson 1957). However, a species distribution is often less than the area of the fundamental niche (Hutchinson 1957). The species' distribution instead fits the realised niche. Interactions with other species cause the difference between the realised and fundamental niches of species, be they predators, prey, or competitors, with these interactions altering the species' fitness for any given environment (Hutchinson 1957). Of particular interest are interactions between similar species, with theory predicting that the more similar two species are, the more likely they are to compete for resources (Hutchinson, 1978; Winston, 1995). Therefore, species with similar niches would not co-occur. However, there are many exceptions to this simple, intuitive prediction and well-defined explanations for the mechanisms that promote co-occurrence despite niche overlap.

Most hypotheses suggest that similar species can co-occur due to a balance between niche differentiation and fitness inequality or environmental fluctuation (Hutchinson, 1957; Anderson et al., 1981; Chesson & Warner, 1981; Adler et al., 2007; Martin, 1998; Chesson, 2000; Warning & Benedict, 2015). The impact of fitness inequality on species co-occurrence is relatively simple: the smaller the fitness differences, the more likely species are to co-occur (Chesson, 2000; Pedruski et al., 2015). Niche differentiation allows species co-occurrence by partitioning resources so that negative effects on other species' fitness are minimised (Hutchinson, 1957). This niche differentiation is typically referred to as microhabitat segregation (Anderson et al., 1981; Harris, 1986). Environmental fluctuation can obscure or modify fitness inequalities. For instance, if environmental disruptions occur frequently enough, species that typically have lower fitness in average or common conditions can recover from lower densities during periods where environmental fluctuations positively affect their fitness (Chesson & Warner, 1981). Similar species can co-occur if recruitment within the populations of both species follows the lottery model, where the environment is effectively homogenous and all species are able to settle but different levels of fitness among the species result in a dominant species (Warner & Chesson, 1985). If these increases in fitness are frequent and prolonged enough for at least one reproductive cycle to occur, then weaker species can persist in an ecosystem with a superior competitor (Chesson & Warner, 1981; Warner & Chesson, 1985). One last factor to consider when examining the ability of species to co-occur is abundance. If two species are naturally rare, then it is likely that they will be unable to monopolise all available niche space (Levins & Culver, 1971).

Two of the leading hypotheses for the co-occurrence of similar species that maintain high abundance are the lottery model (Chesson & Warner, 1981) and microhabitat segregation (Hutchinson, 1957; Anderson et al., 1981). These two hypotheses operate under quite different conditions; the lottery model is a mechanism explaining co-occurrence in an unstable ecosystem, while microhabitat segregation can explain co-occurrence in a stable ecosystem (Hutchinson, 1957; Anderson et al., 1981). The lottery model suggests that environmental variability results in semi-frequent shifts in fitness inequality, resulting in neither species remaining dominant long enough to competitively exclude the other (Hardin, 1960; Chesson & Warner, 1981). The lottery model should result in a random or uniform pattern of abundance amongst the species of interest. In the case of microhabitat segregation, there is presumed to be sufficient niche differentiation amongst the species for them to segregate into distinct realised niches. Microhabitat segregation should result in negative spatial associations among species, with these patterns being tied to unique combinations of environmental variables or microhabitat features.

Impact of a changing climate on species distributions and co-occurrence

The earth is currently undergoing unprecedented human-driven climate change occurring at a rate not seen in the recent geological past (Karl & Trenberth, 2003; Harley et al., 2006; Hoegh-Guldberg et al., 2007; Hoegh-Guldberg & Bruno, 2010; Diffenbaugh & Field, 2013; Kemp et al., 2015). The average ocean temperature has risen ~0.8°C between 1880 and 2012 (Solomon et al., 2007; UNFCCC, 2015). In areas such as the Tasman Sea, an increase of ~1.5°C has been observed in just the last sixty years (Ridgway, 2007). Even the best-case climate scenarios predict an average increase in temperature of ~2°C by 2100 (Pachauri et al., 2014). However, these estimates require significant changes in human greenhouse gas emissions, and are therefore quite optimistic (Rogelj et al., 2016). Some estimates suggest that ocean temperatures are likely to rise by up to 4 °C in some areas (Oliver et al., 2014). Almost all species will likely be affected by the earth's changing climate, either directly or indirectly. Marine species are expected to experience particularly significant changes, as not only are temperatures rising, but the ocean is becoming more acidic, and salinity is slowly decreasing as the polar ice caps melt (Munk, 2003; Hoegh-Guldberg et al., 2007; Rignot et al., 2013).

The warming ocean temperature and increasing acidity have devastating effects on marine ecosystems (Hughes et al., 2003). As a result, marine ecosystems are undergoing significant changes on a global scale. Some species are undergoing range shifts into more suitable habitat, in many cases shifting their ranges toward the poles (Perry et al., 2005; Doney et al., 2012; Poloczanska et al., 2013; Molinos et al., 2016). In some areas, the changes result in complete shifts in the ecosystem (Hughes et al., 2003; Hoegh-Guldberg et al., 2007; Ling et al., 2013). As a result of these changes, many species are at risk of becoming locally extinct (Gilman et al., 2010). For species that are unable to adapt or undergo range shifts they instead are faced with complete extinction (Gilman et al., 2010).

Species are migrating poleward on mass resulting in many historically temperate ecosystems are currently undergoing considerable changes (Molinos et al., 2016). As more tropical species arrive in these historically more temperate regions, they can cause significant disruption to the ecosystems they are entering (Perry et al., 2005; Doney et al., 2012; Poloczanska et al., 2013; Molinos et al., 2016). Some of the most noticeable impacts come from the arrival of voracious tropical grazing species that have been devastating temperate kelp forests, negatively affecting the species that rely on them (Booth et al., 2007; Ling et al., 2013; Nakamura et al., 2012; Vergés et al., 2014; Ling et al., 2015). In some cases, these tropical species are already present in temperate regions in low numbers successfully co-occurring with the temperate species. However, changes to the environment may disrupt this equilibrium by inducing an increase in relative fitness, increasing the abundance of the more tropical species within the ecosystem.

In a scenario of directional environmental change, such as climate change, the distribution of species and the mechanisms maintaining species co-occurrences can undergo drastic changes, resulting in significant species composition shifts. Species whose reproductive success is strongly tied to environmental variables such as temperature or ocean chemistry are early indicators of environmental changes, as their populations will often be the first to respond in the event of climate shifts (Colloca et al., 2014). Species that respond quickly to environmental change are also good candidates for examining co-occurrence in the presence of disruptive environmental changes (Chesson & Warner, 1981; Warner & Chesson, 1985). One group of temperature-sensitive species is urchins. This is due to urchins' reproductive success being strongly tied to temperature (Byrne et al., 2009; Delorme & Sewell, 2013; Pecorino et al., 2014).

Examining and predicting species distributions

As many species' ranges are changing, it is more important than ever to understand constraints on species' ranges to better prepare for near future conservation and management challenges. Accurately modelling a species present range requires two things: sufficient species occurrence data and an understanding of what environmental variables affect the species (Tsoar et al., 2007; Hijmans & Elith, 2011). In the case of urchins and many other marine organisms, various biotic and abiotic variables are responsible for determining if an area is suitable habitat. Abiotic variables such as sea surface temperature, salinity, turbidity and pH effect have significant impacts on the probability of reproductive success of urchins (Delorme & Sewell, 2013; Delorme & Sewell, 2014; King et al., 1994; Pecorino et al., 2013; Irlandi et al., 1997; O'Connor & Mulley, 1997; Phillips & Shima, 2006; Cowart et al., 2008; Byrne et al., 2013). Other abiotic factors such as wave energy can affect all life stages (Edwards & Ebert, 1991; Lissner, 1993; Siddon & Witman, 2003), as can biotic variables such as the distribution predator and prey species (Nelson & Vance, 1979; Ryer & Olla, 1998; Gardner et al., 2006; Rodríguez et al., 2017; Spyksma et al., 2017; Spyksma et al., 2020). Species distribution models (SDM) are a common technique used to better understand the distribution of the species of interest using species occurrence data and selected environmental variables. These SDMs can then also predict the future distribution of the species of interest by substituting one or more environmental variables with predicted future values for that variable. This makes it possible to predict how specific changes in the environment may affect species distribution, such as increases in ocean temperatures (Pachauri et al., 2014).

Modelling a species distribution requires at least some form of presence data. Traditionally, this data would come from museum collections (Ponder et al., 2001; Williams et al., 2002), as collecting occurrence data in the field requires considerable amounts of time, money and effort (Prendergast et al., 1999; Bowker, 2000; Ottaviani et al., 2004). However, the development of online repositories such as OBIS and collaborative research programs such as Reef Life Survey (2020) have resulted in presence data being more readily available (Bisby, 2000; Tsoar et al., 2007). While some of these species occurrence databases are generated through standardised survey efforts (e.g. Reef Life Survey) and record if a species is present or absent at a surveyed site, most repositories are collections of more opportunistic occurrence records compiled from various sources. The sources used by these repositories range from peerreviewed studies to records from the general public (e.g. iNaturalist, (2020); WhatsThatFishNZ, (Middleton et al. 2021)). While presence-only data have limitations, the number of presence records available from decades of previous studies and citizen scientists, combined with methods that make use of pseudo-absences, make these crowdsourced data sets invaluable to researchers (Tsoar et al., 2007; Aranda & Lobo, 2011; Gomes et al., 2018; Hao et al., 2018).

A variety of statistical models have been developed to combine species occurrence information with environmental data to predict a species' spatial distribution. SDMs have been used to investigate a variety of questions, including identifying the "true" range of a species (Franklin, 2009) or predicting environmentally driven changes in species distribution (Kearney & Phillips, 2010). Species distribution models have grown more popular over recent years as more methods are developed (Elith et al., 2010; Hao et al., 2018). Much of the rise in popularity can be attributed to the development of more advanced techniques that allow for presence-only data. Of the variety of models, the individual model's suitability varies significantly depending on the species occurrence data available. However, even when the most suitable model is used, SDMs are still prone to minor inaccuracies (Elith et al., 2006; Yackulic et al., 2013). Therefore, it is considered best practice to create an ensemble model from a selection of the best performing models (Hao et al., 2018). As more recently developed techniques tend to perform better than older techniques in most scenarios, it is preferable to use these more recent methods in the creation of the ensemble model (Elith et al., 2006; Hernandez et al., 2006; Hijmans and Graham, 2006; Tsoar et al., 2007; Kearney & Phillips, 2010; Yackulic et al., 2013).

Examining species co-occurrence

Patterns in species co-occurrence are inherently dependent on the spatial scale of interest. For example, two species may co-occur at a specific island but still occur at different locations within an island (Anderson et al., 1981; Martin, 1998, Warning & Benedict, 2015). The scale at which co-occurrence between two species is observed is an important factor to consider when assessing the interaction among species. In the case of similar species, the smallest scale that co-occurrence can be observed at can indicate the degree of niche differentiation among the species, while at a larger scale co-occurrence can indicate the shared niche requirements of the species. Negative correlations between co-occurring species in regions where their ranges overlap have different implications depending on scale. Negative correlations at the location level indicate that some locations in their shared distribution are unsuitable for one species. In contrast, negative correlations at a smaller spatial scale would suggest there is some microhabitat differentiation between the species or some biotic interaction that determines their spatial arrangement.

The scale on which co-occurrence can be examined is dependent on the scale of available environmental information. If the environmental data scale is in km2, then it is impossible to determine if species are segregating into microhabitats at a scale of m2. Additionally, the environmental variables vary significantly in scale. Some, such as salinity, might not change appreciably over hundreds of kilometres, while topographical complexity may change significantly within a m2. Therefore, measuring as many variables as possible at the smallest possible scale over the largest possible area will yield the best results. Unfortunately cost and time are often limiting factors in collection of biological data, so it is therefore important to balance the scope of the data collection with limited time and budget (Marta et al., 2019).

Urchins of Aotearoa New Zealand's shallow reef ecosystems

This study focuses on four shallow reef urchins native to Aotearoa New Zealand (*Centrostephanus rodgersii, Heliocidaris tuberculata, Tripneustes kermadecensis* and *Evechinus chloroticus*), with one, kina, being endemic (*Evechinus chloroticus).* The most abundant of the shallow reef urchins around New Zealand is *E. chloroticus,* with it being found on most shallow rocky reefs around the main two islands and some of the southern offshore islands including the Chatham Islands and the Snares Islands (Dix, 1970). However, the range of *E. chloroticus* is threatened by rising ocean temperatures, as unless greenhouse gas emissions are rapidly reduced, temperatures in the northernmost parts of their range are likely to exceed those required for successful reproduction (Delorme & Sewell, 2013). Conversely, the range of *C. rodgersii* is likely to expand in the event of rising ocean temperatures, as not only is it quite robust to changes in the environment, but it also is quick to colonise new areas once the temperature rises (Hewitt et al., 2005; Ling et al., 2009; Foo et al., 2012; Pecorino et al., 2014).

A recent poleward range extension of *C. rodgersii* is well documented in Australia (Hewitt et al., 2005; Johnson et al., 2005; Ling et al., 2009). In New Zealand, less is known about the range history of the species. Genetic analysis suggests that the New Zealand populations have originated from New South Wales in Australia relatively recently (Banks et al. 2007), although their New Zealand populations appear to be self-sustaining (Thomas et al. in review, Sweatman, in prep.). These genetic results are corroborated by analyses of the size structures and recruitment indices of New Zealand *C. rodgersii* populations, although there is no indication of a directional poleward range extension (Sweatman, in prep). This difference in population histories between Australian and New Zealand *C. rodgersii* populations may be caused by more complex current patterns around north-eastern New Zealand instead of a more unified south-flowing current in Australia (Brodie, 1960; Stanton et al., 1997). As for the other subtropical species (*H. tuberculata* and *T. kermadecensis*), while at present there are no records of range extension in either species, range expansions have been noted in a species closely related to *H. tuberculata (H. erythrogramma)* (Keesing, 2013). Changes in ocean temperature will likely impact the distributions of all four species examined in this study. One area that may experience changes in species composition is north-eastern New Zealand; while annual warming in this region has not yet been observed many surrounding regions are undergoing warming (Francis et al., 1999; Shears & Bowen, 2017; Middleton et al., 2021). As a result of complex coastal currents ocean warming around New Zealand is unlikely to be uniform (Shears & Bowen, 2017; Law et al., 2018). Non-uniform warming in New Zealand’s coastal waters will likely result in equally non-uniform changes to the ecosystems around New Zealand (Shears & Bowen, 2017). These changes could take the form of a shift in dominant urchin species in north-eastern New Zealand with a reduction in the abundance of *E. chloroticus* and an increase in the abundance of the more subtropical species.

Rangitāhua (also known as the Kermadec Islands) is a group of subtropical islands located alongside the Kermadec trench halfway between New Zealand and Tonga and is the northernmost part of New Zealand's exclusive economic zone. Rangitāhua is home to a unique mix of tropical, subtropical, and temperate species (Francis et al., 1987; Francis, 1993). Given the warmer ocean temperatures found at Rangitāhua (Sutton et al., 2012), Rangitāhua can be used as an analogue for the future marine environment of the northern New Zealand coastal area in the event of rising ocean temperatures. As ocean temperatures rise, more tropical and subtropical marine species are likely to arrive in New Zealand's coastal waters (Francis et al., 1999). By observing the interspecies dynamics between co-occurring species at Rangitāhua we can gain insight into the future of the New Zealand mainland marine environment.

Several shallow reef urchins co-occur at Rangitāhua and the surrounding islets. Previous surveys show the three species co-occurring at various sites around Rangitāhua and the surrounding islets, down to a relatively fine-scale with different species being found within a few m^2 of each other (Gardner et al., 2006; Cole et al., 1992). However, in the future, the composition of the microhabitats found at Rangitāhua and mainland New Zealand is likely to change as climate change causes significant shifts in the environment. The impact of climate change is particularly significant in cases where the co-occurrence of species relies on microhabitat segregation which can result in an increase in abundance for the competitively dominant species and a reduction in the abundance of other species (Nagelkerken et al., 2018). If this trend continues to an extreme, it could result in the less dominant species' local extinction.

Summary of thesis structure

This thesis consists of four chapters with chapters II and III written as independent manuscripts, which are planned to be published separately after submitting the thesis. Therefore, there is repetition between the two chapters, as well as the general introduction and discussion given much of the background information is relevant to both chapters.

Chapter II examines the distribution patterns of three abundant urchin species present at Rangitāhua (*Centrostephanus rodgersii, Heliocidaris tuberculata, and Tripneustes kermadecensis*). Given the biological and ecological similarities among the three species, it would be expected that the species with the highest average fitness in the environment would competitively exclude the others (Hutchinson, 1957; Hutchinson, 1978; Winston, 1995), yet all three co-occur in relatively high abundance. In this study, I model the patterns of abundance in the three urchin populations in relation to environmental variables (depth, algal composition and topographical complexity) and examine spatial associations among the abundances of species at different spatial scales. The observed patterns between abundance and the environment are unique for each species. As in the model each species has unique correlations with the different environmental variables. This provides evidence for the hypothesis that the mechanism resulting in the co-occurrence of the three abundant urchins' co-occurrence is microhabitat segregation. Assuming the urchin species co-occur due to microhabitat segregation, it is possible to predict changes within the interspecies dynamic present at Rangitāhua more accurately. There are two likely outcomes for the urchin population at Rangitāhua in the event of climate change. In the future, it would be expected to see either an increase in the abundance of all three urchin species, similar to the short-lived explosive increases in abundance seen as a response to rare oceanographic events (Valentine & Edgar, 2010). Alternately, environmental change may disrupt the equilibrium among the species and result in significant changes to the population structure of urchins at Rangitāhua, similar to the climate change response observed in some fish populations (Nagelkerken et al., 2018).

Chapter III examines the impact of climate change on the distribution of these three species (*Centrostephanus rodgersii, Heliocidaris tuberculata, and*

Tripneustes kermadecensis) and one other species with an overlapping range in mainland New Zealand (*Evechinus chloroticus*). Like many marine species, these urchins are likely to experience poleward range shifts due to their reproductive success being dependant on a limited temperature envelope (Delorme & Sewell, 2014). In this study, I model the present and future distribution of these four urchin species to understand how global climate changes will affect their distribution. I use four different species distribution modelling methods (Generalised Linear Model, Maximum Entropy, Random Forest and Support Vector Mechanics) to create an ensemble model. These models are created using environmental variables retrieved from Bio-ORACLE v2.1 (Tyberghein et a., 2012; Assis et al., 2018) and GMED (Basher et al., 2018), and species occurrence records from several online repositories (Reef Life Survey (2020), OBIS (2020), iNaturalist (2020) and Atlas of Living Australia (2020), WhatsThatFishNZ (Middleton et al. 2021)). Future models were constructed under various climate change scenarios (RCP 2.6, RCP 4.5, RCP6.0 and RCP 8.5). The models predict a poleward range expansion in all three subtropical species, and under higher greenhouse gas emission scenarios (RCP 8.5), the models also predict a range contraction in the northernmost parts of their ranges in Australia. The models predict minimal change to the range of *E. chloroticus*, with only a slight increase in the extent of suitable environment around the South Island. This is unsurprising as temperature had a minimal contribution to the models for *E. chloroticus*. The poleward range expansion of the subtropical species, particularly *C. rodgersii*, will likely impact the temperate ecosystems found around New Zealand's east coast and southern Australia, as urchin barrens could replace many kelp forests. The impact of urchin grazing can be multiplied by other environmental stressors such as rising ocean temperatures and the overfishing of key predator species such as crayfish (Ling et al., 2009; Wernberg et al., 2010; Wernberg et al., 2019).

Chapter IV discusses chapters II and III's combined findings. I do this by focusing on how novel interspecies interactions and altered interspecies dynamics in areas affected by climate change can trigger ecosystem collapse and local extinctions of many species. I also examine the likelihood and possible extent of poleward range expansion of these four urchin species, highlighting areas that are likely to be negatively affected by these urchins' arrival. Finally, I make recommendations about possible solutions to prevent or at least limit the impact of these changes brought on by changes in New Zealand's urchin populations and what we must remain aware of in the future.

Chapter II: Microhabitat segregation in abundant subtropical urchin species at Rangitāhua

Abstract

Patterns of species abundance at different spatial scales can reveal how biotic and abiotic factors impact species distributions. Through examining correlation in the occurrences of two or more species at various scales, it is possible to learn more about how these co-occurring species interact. Several hypotheses explain how species that would be expected to compete can co-occur. By examining the patterns in abundance, it is possible to identify the mechanism by which co-occurrence is mediated. Here I examine patterns of abundance in three species of urchin at Rangitāhua (*Centrostephanus rodgersii, Heliocidaris tuberculata,* and *Tripneustes kermadecensis).* All three species co-occur along the East Australian coast, Lord Howe Island, Norfolk Island, and northern New Zealand and have high abundances at Rangitāhua. Transect surveys were conducted at Rangitāhua, recording both the number of each species present within each transect and quantifying the environment within the transect using depth, topography, and algae species present. I used these surveys to examine the patterns of abundance in the three urchin species and identify the microhabitats the three urchin species occurred in. I also was able to identify any significant correlations between the species distributions. Of the three species, *C. rodgersii* had significant correlations with *T. kermadecensis* (negative at larger scales) and *H. tuberculata* (positive at small scales). No other significant correlations were observed. As all three species show unique habitat preferences, microhabitat segregation is most likely to explain the co-occurrence observed in the urchin

species present at Rangitāhua. Long term observation is still needed to understand if these urchin species patterns of distribution are stable and identify the effects of continued environmental change on the urchin assemblages of Rangitāhua.

Introduction

Classical ecological theory predicts that the more morphologically, physiologically, and behaviourally similar two species are, the less likely they are to co-occur (Hutchinson, 1957; Hardin, 1960; Hutchinson, 1978; Winston, 1995). However, there are many examples where species with similar ecological requirements do co-occur. Several mechanisms are posited to stabilise population dynamics and allow co-occurrence. For instance, co-occurrence can occur between less abundant species as no one species can occupy all the suitable habitat at once, allowing for a fluctuating patchwork of multiple species co-occurring at a site (Levins & Culver, 1971). In the case of more abundant species, mechanisms such as environmental variability combined with a lottery model of recruitment or microhabitat segregation can also stabilise population dynamics (Hutchinson, 1957; Anderson et al., 1981; Chesson & Warner, 1981; Martin, 1998; Warning & Benedict, 2015). While producing the same result, these proposed mechanisms have significant differences regarding how the co-occurrence among similar species is maintained.

In the lottery model, any given area in the environment can be settled by either species. However, for the lottery model to support co-occurrence between two or more similar species, fluctuations in the environment must occur to prevent a state of equilibrium from being reached where one species eventually excludes the other (Hardin, 1960; Hutchinson, 1957; Chesson & Warner, 1981). The lottery model's effect can also be supplemented by the storage effect (Warner & Chesson 1985). A storage effect manifests when adults can survive multiple breeding cycles, increasing the chance that there will be at least one breeding period with favourable conditions. Therefore, the storage effect allows species to subsist in an environment for long periods provided there are fluctuations in the environment allowing for sweepstakes reproductive events. Even if the environment favours one species most of the time, there are still opportunities for other species to recruit new individuals to the population during periods of favourable conditions (Warner & Chesson 1985; Edwards & Stachowicz, 2010).

The microhabitat segregation hypothesis suggests that similar species can co-occur in a stable environment if the environment contains multiple microhabitats favouring different species. In these cases, the species present can segregate at the microhabitat level while still co-occurring at a larger spatial scale (Anderson et al., 1981; Martin, 1998, Warning & Benedict, 2015). While both microhabitat segregation and the lottery model are mechanisms that facilitate the co-occurrence of similar species (Hutchinson, 1957; Chesson & Warner, 1981; Anderson et al., 1981; Martin, 1998, Warning & Benedict, 2015), the mechanisms result in distinct patterns of abundance. The lottery model's theory is that when two or more species can colonize any space in the environment, and there is sufficiently frequent environmental disruption that alters the balance of fitness between the species, they can co-occur (Warner & Chesson 1985). The environmental disruption results in co-occurrence when a species that would typically be competitively excluded can persist in the area by having higher fitness during these periods of environmental disruption. In contrast, microhabitat segregation results in species abundance fluctuations according to distinct habitats (Edwards & Stachowicz, 2010; Edwards & Stachowicz, 2011).

In marine environments, urchins are renowned for having high abundances periodically (Valentine & Edgar, 2010). Typically, high abundance is seen only in one urchin species within an ecosystem. Nonetheless, during an unusual oceanographic event when the urchin *Tripneustes kermadecensis* (formally believed to be *T. gratilla*) at Lord Howe Island underwent a rapid increase in abundance, the populations of the other urchin species also saw an increase in abundance (Valentine & Edgar, 2010). More typically, over longer timescales, shifts in the available microhabitats within a reef environment are known to disrupt species equilibrium (Nagelkerken et al., 2018) and cause species abundances to diverge, leaving one species to be dominant.

For urchin species that co-occur, several species-specific traits and different inter-species relationships can determine their patterns of coexistence. Some species are known to differ in their fundamental niches. For example, *Arbacia lixula* and *Paracentrotus lividus*, both found in the Mediterranean, are known to segregate by depth (Kempf, 1962; Neill & Larkum, 1965; Gamble, 1966; Lawrence, 1975; Régis, 1979; Chelazzi et al., 1997; Agnetta et al., 2013). Other species are known to competitively exclude each other such as *C. rodgersii* and *Heliocidaris erythrogamma* in Australia, where negative co-occurrence patterns are well documented (Johnson et al., 2005; Ling et al., 2010). Therefore, by understanding the realised niche of co-occurring species and how the interspecies interactions alter this realised niche, it becomes possible to predict the stability of species abundance patterns over time.

At Rangitāhua, three species of large shallow water urchin (*Heliocidaris tuberculata, Centrostephanus rodgersii* and *Tripneustes kermadecensis*) co-occur (Figure 1A, 1B), with all three species being relatively abundant for at least the past 30 years (Gardner et al., 2006; Cole, 1992; Schiel et al., 1986). The geologically young island chain, approximately 1000km to the north-east of the North Island of New Zealand is home to a mix of tropical, subtropical and temperature species, including several endemics (Oliver, 1911; Gardner et al., 2006; Cole et al., 1992). It is thought that the abundance of urchins at Rangitāhua is due to there being few natural predators such as sparid or balastid fishes and lobsters. These three coastal urchin species found at Rangitāhua are also found at Lord Howe Island, Norfolk Island, northeast New Zealand, and the South East Australian coast (Figure 1A, 1B). In some macro-herbivore urchin species aggressive responses to the presence of other species have been observed (Shulman, 1990; McClanahan and Muthiga 2007). As this may also be true of the urchins studied here, the mechanisms maintaining the high density and co-occurrence of these species at Rangitāhua is of great interest.

Previous studies that have examined the structure of benthic communities at Rangitāhua suggest the three urchins co-occur at various scales (Gardner et al., 2006; Cole et al., 1992). Gardner et al. (2006) noted differences in the benthic communities between sites separated by two kilometres, suggesting a wide variety of habitats present at Rangitāhua. It has also been noted that the urchin species may have different depth preferences, with previous studies finding *H. tuberculata* to be more abundant at depths of less than 9m, and *C. rodgersii* appearing to be more common at slightly greater depths (Cole, 1992; Mortensen, 1943). Of the three species, the habitat preferences of *C. rodgersii* are best understood with this species preferring areas with boulders to shelter among (Andrew, 1993) at a wide range of depths (7-58m, Perkins et al., 2015), though what drives the difference in depth range between different locations is not known. The preferred food of *C. rodgersii* is believed to be foliose algae as opposed to crustose algae (Fletcher, 1987). Therefore, they are often found in patches of crustose algae due to overgrazing all foliose algae within their home range (Dean et al., 1984; Harrold & Reed, 1985; Vadas et al., 1986; Fletcher, 1987; Andrew & Underwood, 1989; Hill et al., 2003). Less is known about the habitat preferences of *Heliocidaris tuberculata*, and particularly T. *kermadecensis,* as the species was only recently described with it formerly believed to be *T. gratilla* (Bronstein et al., 2017). However, examining the co-occurrence pattern among these three species at Rangitāhua may provide insight into their habitat preferences and how these species can co-occur and whether these populations are likely to remain stable in the future.

Here, I aimed to identify co-occurrence patterns among the three common urchin species present at Rangitāhua (Raoul Island). Specifically, I aimed to identify the microhabitats formed by depth, topography and algal composition and measure how the species were distributed among these microhabitats. I hypothesised that the urchin species would co-occur at the scale of 100's of meters (henceforth, "sites") as noted by previous studies. Over scales of < 10's of meters (transects), I predicted a negative correlation among species abundances, with species likely occupying different microhabitats. Thus, I hypothesised that these urchin species could co-occur at high densities by occupying distinct microhabitats and therefore partitioning the available resources.

Methods

Study species and location

The three urchin species selected for this study (*Centrostephanus rodgersii, Heliocidaris tuberculata*, and *Tripneustes kermadecensis)*, are endemic to the Tasman region being found in South East Australia and New Zealand, in addition to the Tasman islands (Figure, 1A). From data retrieved from Reef Life survey (2019) I found that of the three species, *C. rodgersii* has the most expansive range, being found much further south in Australia along the coast of Victoria and Tasmania, while the other two species ranges do not extend past Cape Howe In New South Wales (Figure, 1A). In surveyed sites within the region where the three species are known to co-occur, co-occurrence was observed between all three species at 14% of the sites surveyed (Figure, 1B). The three species co-occurred most frequently in the Tasman Islands (Figure 1B). Of the three species, *C. rodgersii* was present at almost all sites in the study area, with the distributions of *H. tuberculata* and *T. kermadecensis* almost entirely contained within the distribution of *C. rodgersii*.

The eight sites (Figure 1C) for this study were selected due to their accessibility, and because these were sites that had been sampled in previous studies of the benthic invertebrates at Rangitāhua (Cole et al., 1992; Gardner et al., 2006). The sites also covered much of the variation in the environment present at Rangitāhua, with varying levels of exposure, varying geological features, and covering both large islands and smaller islets to represent best the diversity of the shallow rocky reef habitats surrounding Rangitāhua.

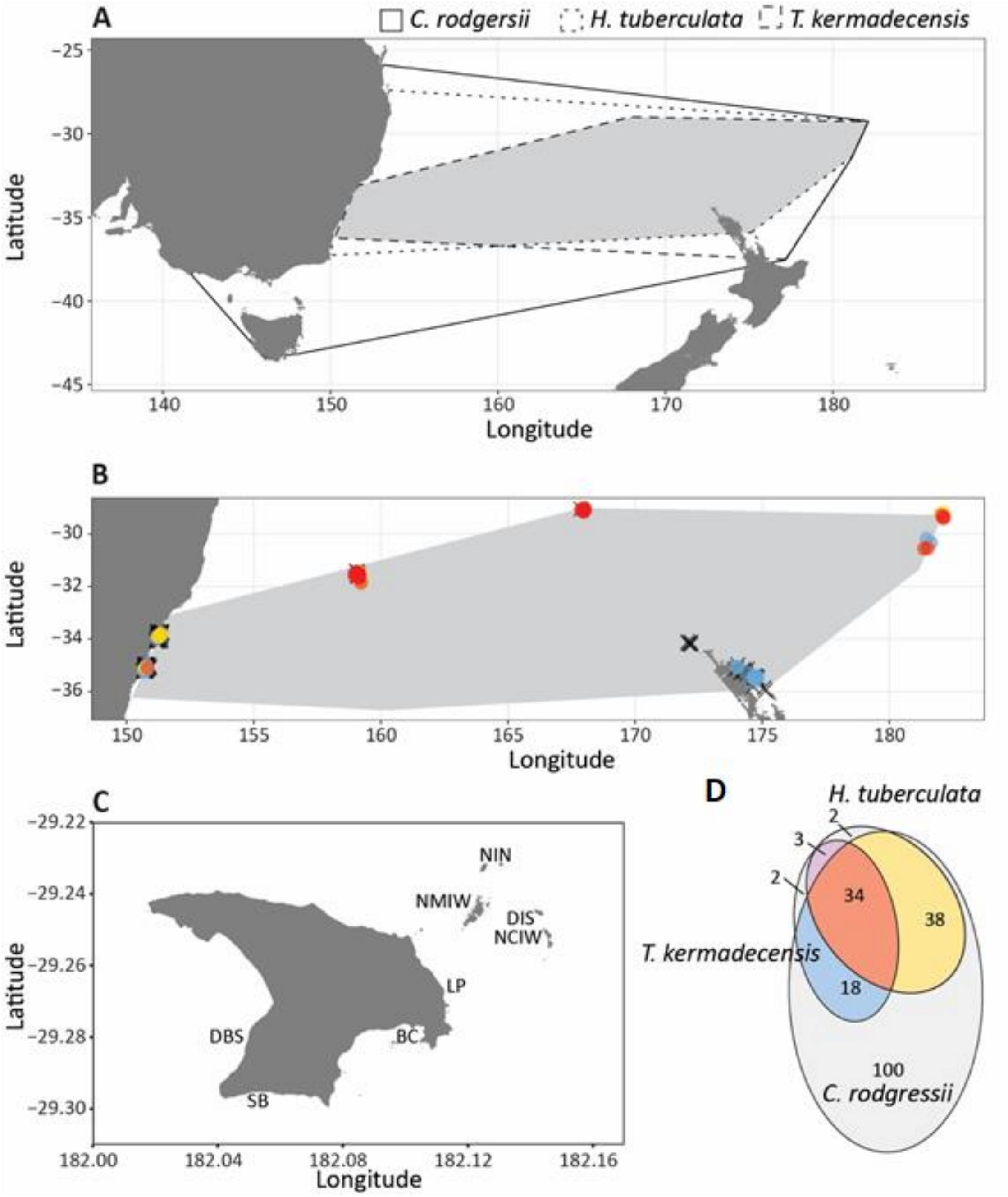

Figure 1) A) Range maps for the three focal urchin species. The region where all three species co-occur is shown in light grey. B) Frequency of co-occurrence for the three focal urchin species with their co-occurring range (light grey polygon). The colours of the circles are indicated in the Venn diagram below. Crosses indicate locations where only one focal species was sampled. Symbols are jittered slightly for display purposes. C) Map of Rangitāhua (Raoul Island) showing the location of the sampling sites. From west to east: Denham Bay South (DBS), Smiths Bluff (SB), Boat Cove (BC), Lava Point (LP), North Meyer Island West (NMIW), Nuggent Island North (NIN), Dayrell Island South (DIS) and North Chanter Island West (NCIW). D) shown is a Venn diagram showing the number of transects where each species was recorded.

Survey protocol

In October 2015, a series of belt transect surveys of mobile macroinvertebrate populations were conducted using SCUBA at Rangitāhua. Several methods have been used to survey rocky reef communities at Rangitāhua (Cole et al., 1992; Gardner et al., 2006). In this study 5 × 1m belt transects were selected as this spatial scale was large enough (compared with, for example, 0.25m^2 quadrats) to avoid zero-inflation, and small enough (compared with, for example, 50m x 1m transects) that each diver (four divers total) would be able to complete two replicate transects at each depth strata and site combination. Transect placement was done haphazardly. However, the section of the reef surveyed was parallel to the primary contour of the reef while avoiding areas of reef where topographical features (large boulders, ledges, or crevasses) extended more than 1m above or below the depth at the start of the transect. The surveys were designed to sample five contiguous depth strata at 3m intervals from 18m to 3m depth (18m-15m, 15m-12m, 12m-9m, 9m-6m, and 6m-3m). Depth was recorded to the nearest 0.1m and treated as a continuous variable in our analyses. For each transect (269 total transects), divers recorded the occurrence of the following topographical features: depth (to the nearest 0.1m); aspect (vertical, sloping or flat); basal substrate (flat bedrock (<30cm relief), undulating bedrock (relief >30cm), large boulders (>30cm diameter), boulders (10cm – 30cm diameter), cobbles (3cm – 10cm diameter), gravel (<3cm diameter or sand); mobile secondary substrate (absent, large boulders (>30cm diameter), boulders (10cm – 30cm diameter), cobbles (3cm – 10cm diameter), gravel (<3cm diameter or sand), large features (absent, crevasses (>30cm wide), overhangs and caves) and small features (absent, cracks (<30cm wide), and ledges). Also, the divers recorded the percentage algal cover in the following categories: crustose coralline algae, turfing red algae, foliose red algae, filamentous green algae, foliose green algae, and foliose brown algae. Lastly, the divers identified and counted the number of mobile macroinvertebrates within the transect. Divers would search caves, crevasses, and the interstitial spaces between boulders, but the divers did not disturb the substrate. The macroinvertebrates identified in the survey consisted of five species of urchins. The most abundant species were the three urchin species, *Centrostephanus rodgersii, Heliocidaris tuberculata,* and *Tripneustes kermadecensis.* These three were used in this study while the much rarer *Echinodermata mathaei* and *Psudoboletia Indiana* were excluded.

Statistical analysis

All analyses were implemented in R v. 3.6.1 (R Core Team, 2019). To assist with interpretation, the dimensionality of the topographical and algal community data was reduced by calculating the transect scores for the first principal axes of topographical variation and algal community composition. For the topographical features, I calculated an indicator matrix for the presence or absence of each category of each feature (21 categories in total) for each transect. I then used the package vegan v. 2.5-6 (Oksanen et al., 2019) to conduct a constrained correspondence analysis of the indicator matrix and calculated the transect scores for the first principal axis of topographical variation. The first principal axis of topographical variation described a gradient between transects dominated by vertical rock, bedrock habitats with overhangs, ledges, cracks, and no mobile substrates at one extreme, and transects dominated by flat or sloping sand and cobbles with mobile substrates and caves at the other extreme (Appendix 1). Accordingly, the first principle component of topographical complexity describes a gradient from transects sampling reef-wall habitats to transects sampling boulder habitats at the reef-sand interface. I used the package vegan v. 2.5-6 (Oksanen et al., 2019) to apply a principal components analysis to algal percentage cover data for each transect for the first principal component of algal community composition. The algal composition's first principal axis described a gradient between transects dominated by crustose coralline algae at one extreme and transects dominated by foliose and turfing red algae at the other extreme. After collapsing both the filamentous and foliose groups of green algae into one category, "green algae", neither the green algae nor the brown algae contributed strongly to variation in algal community composition among transects at Rangitāhua.

To partition variation in urchin community composition, I used the MCMCglmm package (Hadfield, 2010) to fit a generalised linear mixed model in a Bayesian framework, using Markov chain Monte Carlo methods to sample the posterior distribution of the parameters. The response variables were the counts for each urchin species within each transect, which I modelled assuming a Poisson error distribution and a log link. The model considered the following fixed effects: species as a categorical predictor with three levels, depth as a continuous predictor fit as an orthogonal polynomial of degree two, and topography along with algal community composition as linear continuous predictors. I also included all possible 2-way interactions among the fixed factors, after preliminary analyses performed on each species' data in isolation indicated that 3-way interactions between depth, topography, and algal composition were unlikely. Site was treated as a random effect with eight levels and transect was included as an observation level random effect. To estimate correlations in each species' abundance at different spatial scales, I fit random intercepts for the species term at the site and transect levels. If the 95% credible intervals for posterior distributions of the fixed effects or the correlations estimated at site and transect levels did not overlap zero, I considered this evidence that the parameter explained a significant amount of variation in the abundance of urchins at Rangitāhua. I assumed a diffuse prior for the fixed effects with a mean of zero and a variance of 1×10^{10}. I used a non-informative inverse-Wishart for the random effects prior the scale parameter equal 1×10^{-10} and four degrees of freedom. I used an inverse-Wishart prior the random effects because it is relatively uninformative for the correlations (Anderson, 1958). In addition, to confirm that my results were robust to the prior specification, I also explored the use of priors conforming to Cauchy distribution and adjusting the scale and degree of freedom parameters for the inverse Wishart distribution to unreasonably large and unreasonably small numbers. There was very little change in the posterior mean estimates in both these cases, suggesting the prior was indeed uninformative. I stored 1000 posterior samples of the distribution for each parameter by specifying a chain length of 50,300,000 iterations, with a burn-in of 300,000 iterations and a thinning interval of 5000 iterations. Lastly, I examined the model-fit by ensuring that the number of zeros' posterior predictive distribution overlapped the observed number of zeros in each species. This confirmed whether the posterior predictive distribution of the mean counts overlapped the observed mean counts for each species.

Results

Interactions between depth, topography, and algal composition are common and explained significant variation in urchin abundance at Rangitāhua (Figure 2). Interactions between algal composition and depth significantly affected the abundance of *Centrostephanus rodgersii* and *Tripneustes kermadecensis.* However, this is not the case for *Heliocidaris tuberculata* (Figure 2). As for the interactions between algal composition and topography, a significant interaction is observed for *C. rodgersii* (Figure 2). Algal composition explained most of the variation in abundance for *C. rodgersii*, with my studies finding abundance is greatest in habitats dominated by crustose coralline algae cover and little turfing and foliose red algae cover. Conversely, in *T. kermadecensis*, abundance is greatest in habitats with low crustose coralline algae cover and high turfing and foliose red algae cover (Figure 3).

The abundance of *Heliocidaris tuberculata* does not seem influenced by the algal community's composition. Instead, I found a significant interaction between topographical variation, depth, and *H. tuberculata* abundance (Figure 2). In this instance, it appears depth is the strongest predictor of abundance, with *H. tuberculata* being the most abundant urchin in shallow habitats, particularly in boulder habitats at the reef-sand interface (Figure 3). In contrast, *T. kermadecensis* is most abundant in deep, boulder habitats at the reef-sand interface (Figure 3). Lastly, for *C. rodgersii* I observed a significant interaction between topographical complexity and algal community composition indicating *C. rodgersii* is the most abundant in crustose coralline algae dominated reef wall habitats at Rangitāhua.

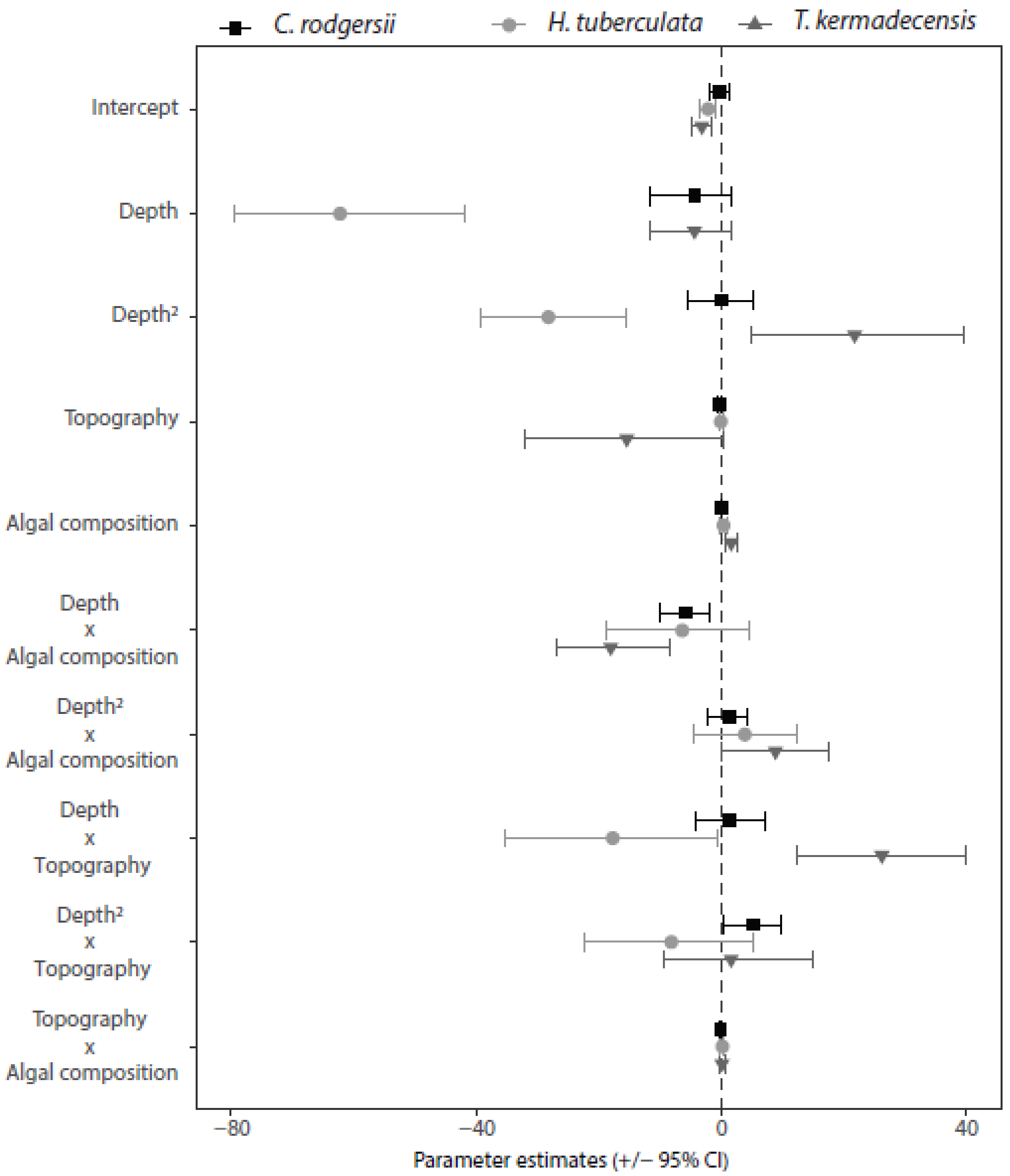

Figure 2) Parameter estimates and 95% credible intervals (CI) for the environmental drivers of variation in urchin abundance at Rangitāhua (Raoul Island). Parameters where the 95% credible interval does not overlap zero indicate parameters explaining significant variation in urchin abundance. Given that for each species there was at least one significant 2-way interaction, I did not interpret the main effects of the environmental drivers in isolation.

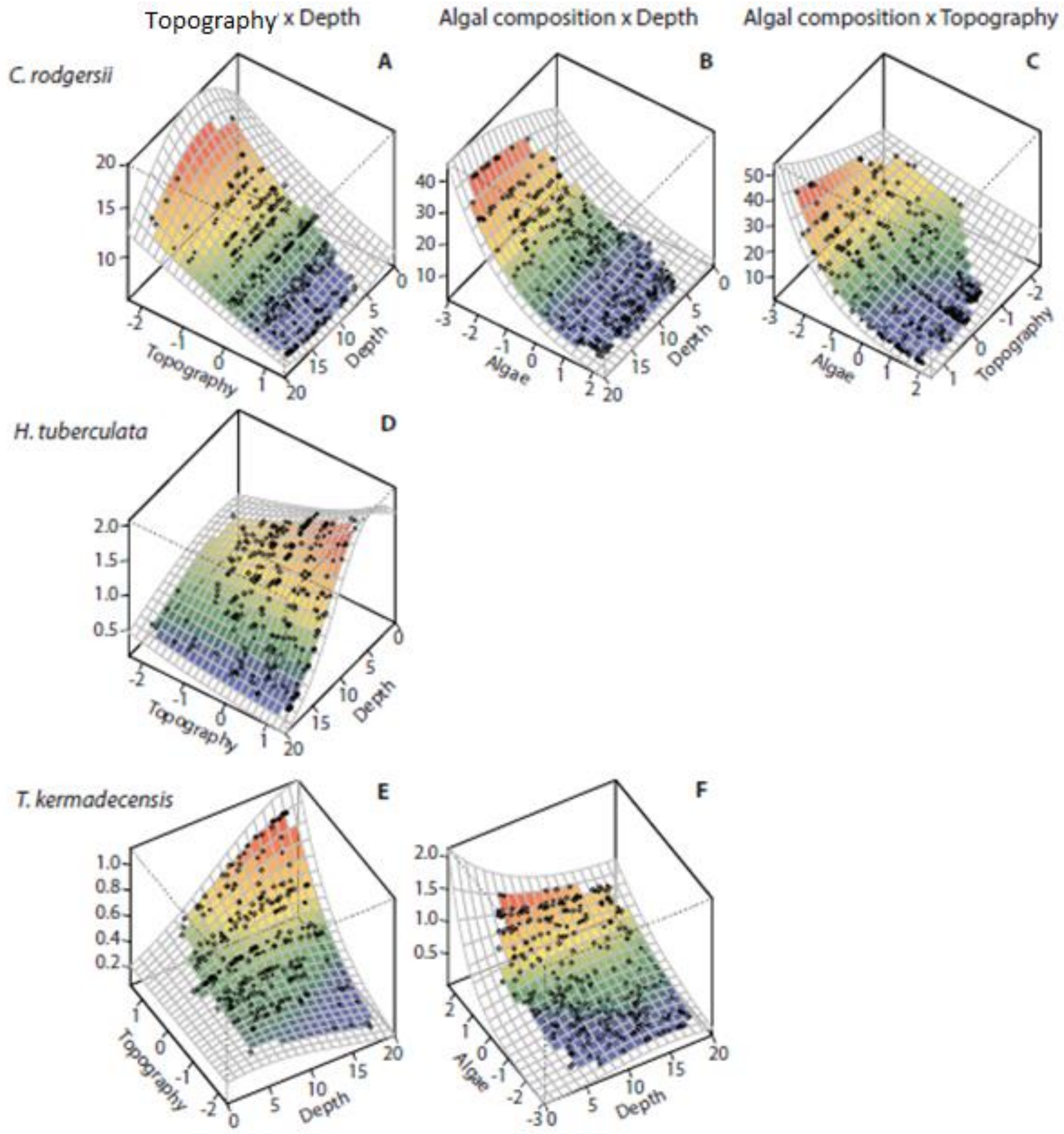

Figure 3) Posterior mean predicted values for significant 2-way interactions among environmental drivers of urchin abundance. Open circles indicate observed values that lie below the posterior mean predicted value, and closed circles indicate observed values that lie above the posterior mean predicted value. Warm and cool colours indicate parameter combinations with relatively high and relatively low predicted mean abundance, respectively. The predicted mean values capture the contributions from both the first- and second-order polynomial terms for interactions involving depth.

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After the effects of depth, topography, and algal composition were considered, spatial variation in the associations between the three species remained. At the site level, I found that sites are either favourable for *C. rodgersii* or *T. kermadecensis* (Table. 1, Figure 4). This suggests that additional, unmeasured environmental factors (for example, wave energy), operating at the site-scale, determine variability in the abundance of *C. rodgersii* and *T. kermadecensis*. *Heliocidaris tuberculata,* on the other hand, showed no significant associations with the other two dominant urchin species at the site level. Even so, at the smallest spatial scale, the transect level, there is a positive relationship between *H. tuberculata* and *C. rodgersii* abundance. The relationship between the two species means that in areas where *H. tuberculata* is abundant, *C. rodgersii* will also likely be abundant, suggesting that the two species have similar preferences for micro-environmental features not captured by depth, topography, and algal composition.

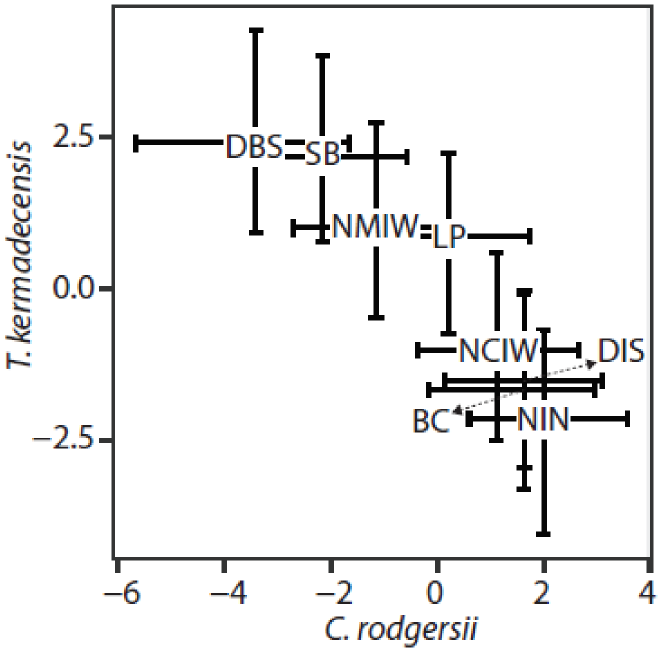

Figure 4) Posterior mean (+/- 95% credible intervals) for the site level negative correlation in Centro and Trip's abundance. Sites (refer to figure for labels and geographic location) are generally arranged west to east, where sites in the west tend to be dominated by Trip and sites in the east tend to be dominated by Centro.

Site level	*C. rodgersii*	*H. tuberculata*	*T. kermadecensis*
C. rodgersii	**4.267**	-0.035 (-0.667, 0.571)	-0.94 (-0.998, -0.824) *
H. tuberculata	-0.104	**2.748**	0.278 (-0.31, 0.851)
T. kermadecensis	-3.571	0.898	**3.682**

Transect level	*C. rodgersii*	*H. tuberculata*	*T. kermadecensis*
C. rodgersii	**0.674**	0.287 (0.007, 0.566) *	0.244 (-0.76, 0.985)
H. tuberculata	0.248	**1.107**	0.539 (-0.525, 0.994)
T. kermadecensis	0.164	0.482	**0.719**

Table 1. Posterior mean covariance matrices for the site and transect level effects. Variances are along the diagonal in bold; covariances are below the diagonal, and correlations with associated 95% credible intervals are above the diagonal. Asterisks indicate significant correlations where the posterior distribution of the correlation does not overlap zero.

Discussion

The three urchin species examined in this study each appear to segregate into distinct microhabitats, although they co-occur over scales of kilometres to tens of meters at Rangitāhua. The three species appear to segregate most strongly by depth. Each species is most abundant at different depths; *Centrostephanus rodgersii* primarily occupied the moderate depths while *Tripneustes kermadecensis* more abundant in the deeper areas surveyed, and *Heliocidaris tuberculata* primarily occupied the shallower areas. Of the three species, *C. rodgersii* is primarily found on rock wall habitats, while *T. kermadecensis* and *H. tuberculata* both preferred boulder reefs at the reef sand interface despite preferring opposite ends of the observed depth spectrum. The only species to show any correlation with algal community composition was *C. rodgersii,* which showed a significant positive correlation with crustose coralline algae. However, the cause of this correlation is likely that *C. rodgersii* heavily grazes foliose and turfing algae in its homesites leaving only crustose coralline algae (Dean et al., 1984; Harrold & Reed, 1985; Vadas et al., 1986; Fletcher, 1987; Andrew & Underwood, 1989). The last of the recorded variables, the topography, is most likely to have a direct causal relationship with the urchin's distribution, and my results for topographical preferences match with earlier observations for *C. rodgersii* which show it to prefer habitat (Andrew & Underwood, 1989; Byrne & Andrew, 2013).

There are several potential explanations for how depth and topography affect the distributions of the three urchin species. For example, the correlations between *Tripneustes kermadecensis* and depth may be explained by the species' relatively weak attachment strength (L. Liggins pers. Comm.). This weak attachment strength would mean that individuals are less likely to be damaged in deeper areas that are less exposed to waves than in shallower water. Likewise, a possible explanation for *C. rodgersii* not being as abundant in the shallow areas would be that the longer spines of *C. rodgersii* are more likely to be damaged in a high energy environment. It has been found that damage to an urchin’s spines can result in lower reproductive success (Edwards & Ebert, 1991; Haag et al., 2016). In addition to this, areas that are more affected by wave action and strong currents are also known to disrupt urchins' settlement (Lissner, 1083; Siddon & Witman, 2003). Also, previous studies of *C. rodgersii* populations' show patterns in the genetics of the species being correlated with topography, and there is evidence to suggest that the topographical complexity preferences of urchins are predominantly related to predator avoidance (Andrew & Underwood, 1989; Banks et al., 2007).

The two mechanisms most likely to result in the co-occurrence of the urchin species at Rangitāhua are the lottery model and microhabitat segregation (Hutchinson, 1957; Chesson & Warner, 1981; Anderson et al., 1981; Martin, 1998, Warning & Benedict, 2015). Identifying these mechanisms using the survey data collected is done by identifying the presence or absence of patterns in the abundance of the urchin species. If there are patterns present, they should correlate with the measured environmental variables. Given the data patterns observed with each species having the highest abundance in a unique combination of environmental variables, the most likely explanation is that the species are segregating by microhabitat (Anderson et al., 1981; Martin, 1998, Warning & Benedict, 2015). If the lottery model drove the species co-occurrence, we would expect a random distribution of all species in a homogeneous environment. Otherwise, the species should have similar correlations with the environmental variables (Hutchinson, 1957; Chesson & Warner, 1981). However, as there are significant species occurrence patterns throughout the observed environmental variables, the lottery model can almost certainly be ruled out in favour of microhabitat segregation.

The results indicate that the urchin species co-occur at Rangitāhua due to microhabitat segregation. Microhabitat segregation also likely explains co-occurrence in other parts of their range, including areas where they overlap with other urchin species, shown by their response to short term environmental change at other locations (Valentine & Edgar, 2010). Given the environmental variables observed at Rangitāhua, it appears that there is not a dominant species for every combination of the environmental variables surveyed. It could be possible that other species co-occurring outside of Rangitāhua are occupying these microhabitats. For example, the three species observed in this study all segregated over the depth gradient. However, *Centrostephanus rodgersii* is most abundant in moderate depths and associated more with habitat described as a rock wall, while the other two species are more abundant at the boulder sand interface. Therefore, there may still be available niche space in the shallow and deep rock wall habitat or the mid-depth boulder sand interface. It is also possible that urchin species will present entirely different realised niches depending on the other co-occurring urchin species. In the case of *E. chloroticus,* which is known to be most abundant in shallower water from the intertidal zone to depths of 15m (McRae, 1957; Dix, 1970; Barker, 2013), it would most likely occupy a very similar niche to that occupied by *Heliocidaris tuberculata* at Rangitāhua, possibly outcompeting it in these shallow areas. Future studies may wish to examine other areas where these three species co-occur including mainland sites in Australia and New Zealand where additional urchin species co-occur. These mainland sites also offer larger-scale environmental gradients absent from Rangitāhua that can also be observed, allowing for more insight into how the species will react to a changing environment.

We conclude from this study that the three large coastal urchin species present at Rangitāhua can co-occur in great abundance despite sharing a primary food resource, as they can segregate into separate microhabitats. This microhabitat segregation is likely a result of slight differences in fitness for the different environmental conditions present in each microhabitat. Given that Rangitāhua is part of the northernmost part of the three urchins ranges, it will likely be one of the first areas where the rising ocean temperatures affect the urchins' populations examined in this study. It is difficult to predict the effect of a changing climate on the interspecies dynamics present among the urchin species at Rangitāhua; however, should ocean temperatures at Rangitāhua rise, the interspecies dynamics will most likely be disrupted. Therefore, continued monitoring of the marine flora and fauna present at Rangitāhua is vital for identifying the effect of rising ocean temperatures on the interspecies dynamics current in subtropical marine ecosystems.

Chapter II: Acknowledgements

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Chapter III: Present and forecasted distributions of shallow reef urchins in New Zealand

Abstract

Many species are currently undergoing range shifts, driven by unprecedented environmental change. These global environmental changes include rising temperatures, where temperatures are predicted to increase by up to 4°C in some areas over the next hundred years. As a result, many species are experiencing climate tracking range shifts, and these range-shifts can result in widescale ecological disruption. For example, the arrival of subtropical grazers in temperate kelp forest ecosystems has resulted in the loss of many kelp forests. I model the present and future distributions of four grazing urchin species, three subtropical (*Centrostephanus rodgersii*, *Heliocidaris tuberculata* and *Tripneustes kermadecensis*) and New Zealand endemic (*Evechinus chloroticus*). I model the urchin's distributions using four different species distribution modelling techniques, Generalised Linear Models (GLM), Maximum Entropy (MaxEnt), Random Forests (RF), and Support Vector Mechanics (SVM), to create an ensemble model of their distributions. These methods are repeated for four Representative Concentration Pathway (RCP) future climate scenarios for 2100 ranging from optimistic (RCP 2.6) to worst-case (RCP 8.5). The models show the subtropical species' present distribution encompasses Australia's south-east coast, the north-eastern coast of New Zealand (NZ), and several Tasman Islands (Lord Howe, Norfolk and Rangitāhua). In contrast, *Evechinus chloroticus* was found around NZ's coastal rocky reefs and some offshore islands (the Snares and the Chathams) but excluding Rangitāhua. The models predict

poleward range shifts in all three subtropical species under all future climate scenarios, with the range shift's extent depending on the severity of climate change. While no range shift was predicted in *E. chloroticus,* a reduction in suitable environment was predicted in north-eastern NZ under more extreme climate scenarios. The poleward range shifts of these subtropical urchins have the potential to devastate New Zealand's subtropical kelp forests if action is not taken to minimise their impact.

Introduction

With plans to limit climate change still allowing for up to double the warming observed over the past hundred years under the UN's Paris agreement (UNFCCC, 2015), species will continue to experience some of the most rapid environmental change in recent history (Harley et al., 2006; Hoegh-Guldberg et al., 2007; Hoegh-Guldberg & Bruno, 2010). Alarmingly, these plans assume a best-case future emissions scenario (Pachauri et al., 2014). Thus, unless further measures are implemented (Rogelj et al., 2016), changes in the global climate are likely to persist if not intensify before 2100. In the marine environment, rising sea surface temperatures and ocean acidification have been occurring at a rate and magnitude equal to or greater than most times since the end of the Cretaceous period (Diffenbaugh & Field, 2013; Kemp et al., 2015). The average ocean temperature has risen an average of ~0.8 °C between 1880 and 2012 (Solomon et al., 2007; UNFCCC, 2015). In areas such as the Tasman Sea, an increase of ~1.5°C has been observed in just the last sixty years (Ridgway, 2007). It is predicted that the maximum sea surface temperature could increase by up to 4°C in some parts of the Tasman Sea over the next hundred years (Oliver et al., 2014). When such dramatic climate change occurs, species must adapt to the new environment or undergo range shifts to avoid extinction (Berg et al., 2010).

As a result of the changing climate, many species are experiencing changes to their geographic distribution, beyond the more frequent small-scale fluctuations that have occurred historically (Pecl et al., 2017). As sea surface temperatures rise, areas that have historically been too cold for many species become habitable and areas within their current range become uninhabitable (Williams et al., 2008; Bates et al., 2014). Typically, the changes in species range being observed are expansions towards the poles or higher elevations/greater depths (Perry et al., 2005; Doney et al., 2012; Poloczanska et al., 2013; Molinos et al., 2016). However, in some cases, physical barriers, such as mountain ranges or large stretches of open ocean can prevent range shifts. Consequently, ranges tend to become more restricted, and the species slowly become extinct (Gilman et al., 2010). When species move into new areas, various issues can arise as they encounter new biotic and abiotic factors that were not present in their original ranges.

As tropical species expand their ranges toward the poles, they will begin to have novel interactions with more temperate species. As these species have had minimal or no interactions in the past, ecological and evolutionary mechanisms that regulate their interactions are unlikely. For example, a predator expanding its range will likely flourish if it encounters a new prey source with no natural defences (Aronson et al., 2015). The loss of affected species, either plant or animal, can have a cascading effect on ecosystems because of the many and often complex interspecies interactions within an ecosystem (Voigt et al., 2003; Kishi et al., 2005; Gilman et al., 2010). Similarly, competition between species can significantly impact both the native and range-extending species (Winston, 1995; Kearney & Porter, 2004). With more similar species being more likely to competitively exclude each other (Winston, 1995), more established species can limit new arrivals' available resources (Pecorino et al., 2013), limiting the ability of a new arrival to establish in the area. These new or changing biotic interactions can result in significant disruption to the ecosystems. For example, as temperatures have risen, many tropical herbivorous fish species have begun expanding their ranges poleward. Among these species are high-intensity grazers, such as a variety of *Acanthuridae* species which are having a significant impact on temperate ecosystems by destroying kelp forests, converting them to barrens (Booth et al., 2007; Nakamura et al., 2012; Vergés et al., 2014). Changes on this scale do not occur every time a range shift occurs, as a wide variety of biotic and abiotic factors will affect a new species' impact on the ecosystem.

Some species have a much more significant impact when arriving in a new area than others. For species that play a large role in shaping the ecosystem in which they are found, their arrival in a new ecosystem can be incredibly disruptive and their impact can sometimes be more significant than in their original range (Shurin et al., 2020). For instance, the arrival of *Centrostephanus rodgersii* in Tasmania resulted in the loss of kelp forests along much of the eastern coast, converted to urchin barrens in the years since *C. rodgersii's* arrival (Johnson et al., 2011; Ling, 2013). Contributing to the impact of *C. rodgersii* in Tasmania were the overfishing of their natural predators (Tegner & Levin, 1983; Ling et al., 2013) and reduced resilience of the kelp populations due to increased stress from rising ocean temperatures (Wernberg et al., 2010; Krumhansl et al., 2016; Martínez et al., 2018). Previous studies suggest that the effect of multiple environmental stresses is greater than the additive effects of the stresses and that species under stress become more susceptible to additional stressors (Sala et al., 2000; Sala & Knowlton, 2006; Blake & Duffy, 2010). The same problems can now be seen worldwide as many of the key marine predator species have been overfished and combined with rising temperature leaves the kelp vulnerable to invasion by herbivores from more tropical regions or loss due to climatic shifts. Therefore, the combined stresses of rising ocean temperatures and intensive grazing have resulted in the catastrophic collapse of many kelp forest ecosystems, a trend likely to continue in the future (Ling et al., 2009; Wernberg et al., 2010; Ling, 2013; Wernberg et al., 2016; Verges et al., 2016). The loss of these kelp forests can severely affect many species that rely on the kelp forest habitat. For example, in Tasmania the loss of kelp forests has seen a reduction in population for commercially fished abalone (*Haliotis rubra*) and rock lobster (*Jasus edwardsii*).

In New Zealand, there are four species of large coastal urchin, including the most common and endemic *Evechinus chloroticus* and three species of subtropical urchin that are less common *(Centrostephanus rodgersii, Heliocidaris tuberculata* and *Tripneustes kermadecensis*). The range of *Evechinus chloroticus* extends around the entire coast of the two main islands and Stewart Island, the Chatham Islands, and the Snares Islands (Dix, 1970). In New Zealand, the subtropical species are present only in the northeast of the North Island, with the most widespread (*C. rodgersii*) being found from Cape Reinga to Hawke's Bay (Pecorino et al., 2013). The other two subtropical urchin species primarily occur north of Auckland, with a few exceptions. All four species recorded ranges overlap on the east coast of Northland, though this overlap is likely to expand in future under current climate trends.

The changing marine environment and the corresponding effect this will likely have on their abundance may affect the interspecies dynamics for the urchin species present in New Zealand, (Valentine & Edgar, 2010; Sherman, 2015). The rising ocean temperatures and changing currents could increase the abundance of the subtropical species around northern New Zealand and a southwards expansion of the subtropical species range in New Zealand. The effect of rising ocean temperatures on the endemic kina (*Evechinus chloroticus*) could include a loss of suitable habitat in Northern New Zealand based on climate change projections (Intergovernmental Panel on Climate Change, 2014; Intergovernmental Panel on Climate Change, 2018). Studies suggest that the upper thermal limit for the successful reproduction of *E. chloroticus* could be reached or exceeded within the next hundred years (Delorme & Sewell, 2013; Delorme & Sewell, 2014). It is also possible that along with the increase in ocean temperature, there would be an increase in abundance for the subtropical urchin species resulting in increased competition for resources such as food and space. The increased interactions of the subtropical species with the endemic *E. chloroticus* will likely result in increased grazing pressure around much of the north-eastern North Island. This combined with changes in the environmental pressures has the potential to cause significant changes to New Zealand's ecosystems.

For this study, I use species distribution models (SDMs) to determine the current range extent of the four large urchin species: *Centrostephanus rodgersii, Heliocidaris tuberculata, Tripneustes kermadecensis* and *Evechinus chloroticus*, and examine the predicted present range-overlap between the endemic *Evechinus chloroticus* and the three subtropical urchins. Furthermore, I examine the predicted future range overlap under different IPCC climate scenarios to predict how future interaction may be affected. Using this information, I can identify some of the likely conservation challenges that may occur over the next hundred years regarding the four urchin species used in this study and the potential ecosystem and Socioeconomic consequences of changes in species' ranges.

Methods

Study area

The study area encompassed the entire known range of the four focal urchin species (*Centrostephanus rodgersii, Heliocidaris tuberculata, Tripneustes kermadecensis* and *Evechinus chloroticus*), from the subtropics to sub-Antarctic (25° to 56° South) and from Central South Australia to Rangitāhua (137° East to 176° West). The coastal areas included south-east Australia from southern Queensland to the Spencer Gulf, including Tasmania, the entire coastal region surrounding New Zealand's North Island, South Island and Stewart Island, and offshore islands within Australia's Exclusive Economic Zone (EEZ; Norfolk Island and Lord Howe Island), and New Zealand's EEZ (Rangitāhua, Chatham Islands, and New Zealand's sub-Antarctic Islands).

Environmental data

In species distribution modelling, it is essential to select variables relevant to the study species' ecology to produce meaningful results (Tsoar et al., 2007; Hijmans & Elith, 2011). For this study, nine predictor variables were selected to model the range of my four urchin species: dissolved oxygen, diffuse attenuation, primary productivity, current velocity, wave height, depth, sea surface temperature, salinity and pH. The mean, maximum, and minimum values were used for current velocity, sea surface temperature, and salinity. Only the mean was used for all other variables, resulting in fifteen environmental variables (Figure 1). These environmental variables were selected as they are all known to impact the four selected urchin species' phenology, behaviour, and life-history. For example, all four species of urchin's reproductive cycle and success are determined by temperature (Delorme & Sewell, 2013; Delorme & Sewell, 2014; King et al., 1994; Pecorino et al., 2013; O'Connor & Mulley, 1997). Other environmental factors that affect the early development of the species of interest are pH (Byrne et al., 2013), suspended sediment/turbidity (Phillips & Shima, 2006) and salinity (Irlandi et al., 1997; Cowart et al., 2008). Factors that impact the health of the adult population include the availability of food (Harrold & Reed, 1985; Edbert, 1968) and the strength of currents/waves, which can result in damage to the spines or the disruption of settlement and foraging behaviour (Edwards & Ebert, 1991; Lissner, 1993; Siddon & Witman, 2003). Some environmental factors of interest are indirectly represented as variables, such as how primary productivity, diffuse attenuation and dissolved oxygen are proxies for macroalgae abundance (Brodie et al., 2007; Fabricius & De’ath, 2010; De’ath & Fabricius, 2010). Diffuse attenuation is also strongly correlated with turbidity. The predicted 2100 environmental variables consist of current velocity, sea surface temperature and salinity (mean, maximum and minimum). The other variables in the model were treated as static between the present and 2100, primarily due to data availability. The environmental layers were retrieved from Bio-ORACLE v2.1 (Tyberghein et a., 2012; Assis et al., 2018) except for depth and wave height which were retrieved from GMED (Basher et al., 2018). The raster layers were then loaded into R v. 4.0.3 (R core team, 2020) using the raster package (Hijmans & Jacob, 2016). The data was then cropped to only include areas between 0m and 500m depth within the study areas to limit the range of depth compared to the other variables while still providing a suitable buffer around the known depth range of the species of interest.

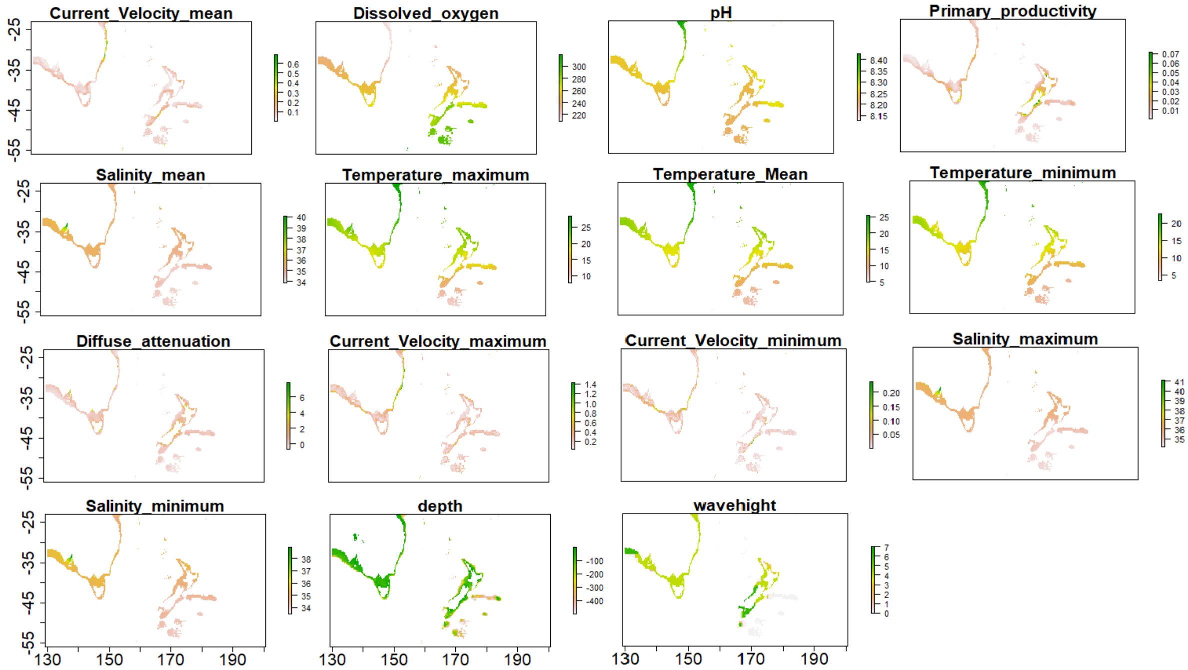


Figure 1 The environmental variables selected to model the geographic range of the study species.

The colour gradients showing Green as high values to Orange as low values, with white being zero or n/a values. From top left: Current Velocity mean, Dissolved oxygen, pH, Primary productivity, Salinity mean, Temperature Maximum, Temperature Mean, Temperature Minimum, Diffuse attenuation, Current Velocity Maximum, Current Velocity Minimum, Salinity Maximum, Salinity Minimum, depth, and wave height.

Species occurrence data

Occurrence data for the species of interest was compiled from various sources, including What's That Fish NZ (Middleton et al. 2021), C. Duffy's dive log, L. Liggins records, as well as open access sources (Reef Life Survey (2020), OBIS (2020), iNaturalist (2020) and Atlas of Living Australia (2020)). *Tripneustes kermadecensis* is a recently described cryptic-species previously thought to be *T. gratilla* (Bronstein et al., 2017). To disentangle the occurrence data of *T. kermadecensis* from *T. gratilla*, occurrences were cross-referenced with genetic data verifying the species identities at several locations (according to Bronstein et al., 2017; Bronstein et al., 2019; and genetic data for New Zealand wide populations, L. Liggins unpublished data). As a result, all *T. gratilla* presence points from New Zealand, Rangitāhua, Lord Howe Island, Norfolk Island and any records south of -32.5° on the Australian coast were treated as *T. kermadecensis.* The data was then cleaned, with any records that lacked coordinates removed in addition to any erroneous records; for instance, points on land or in the deep sea were removed. While presence-absence data is more informative (Aarts et al., 2012; González-Irusta et al., 2015), recent advanced modelling methods can function well if random background points that serve as 'pseudo-absences' are included. For this study, to simulate absences, I generated background points roughly equal to the number of presence points for each species, within my research area (Barbet-Massin et al., 2012). Any species occurrence records that fell outside of the crop by a small margin (often the result of minor rounding errors in the latitude/longitude) were moved to the nearest location within the cropped raster.

Statistical modelling approach

A variety of statistical models can predict a species' distribution based on occurrence records and environmental factors. These models are commonly referred to as species distribution models (SDMs). When selecting a method to model the distribution of a species, it is crucial to consider the strengths and weaknesses of different approaches, and the type of data i.e. presence-absence or presence-only data. For this reason, the use of ensemble models is regarded as the best practice (Araujo & New, 2006), with weighted means being the most widely used method for creating these ensemble models (Hao et al., 2018). There are three types of model that are typically used for presence-only data:

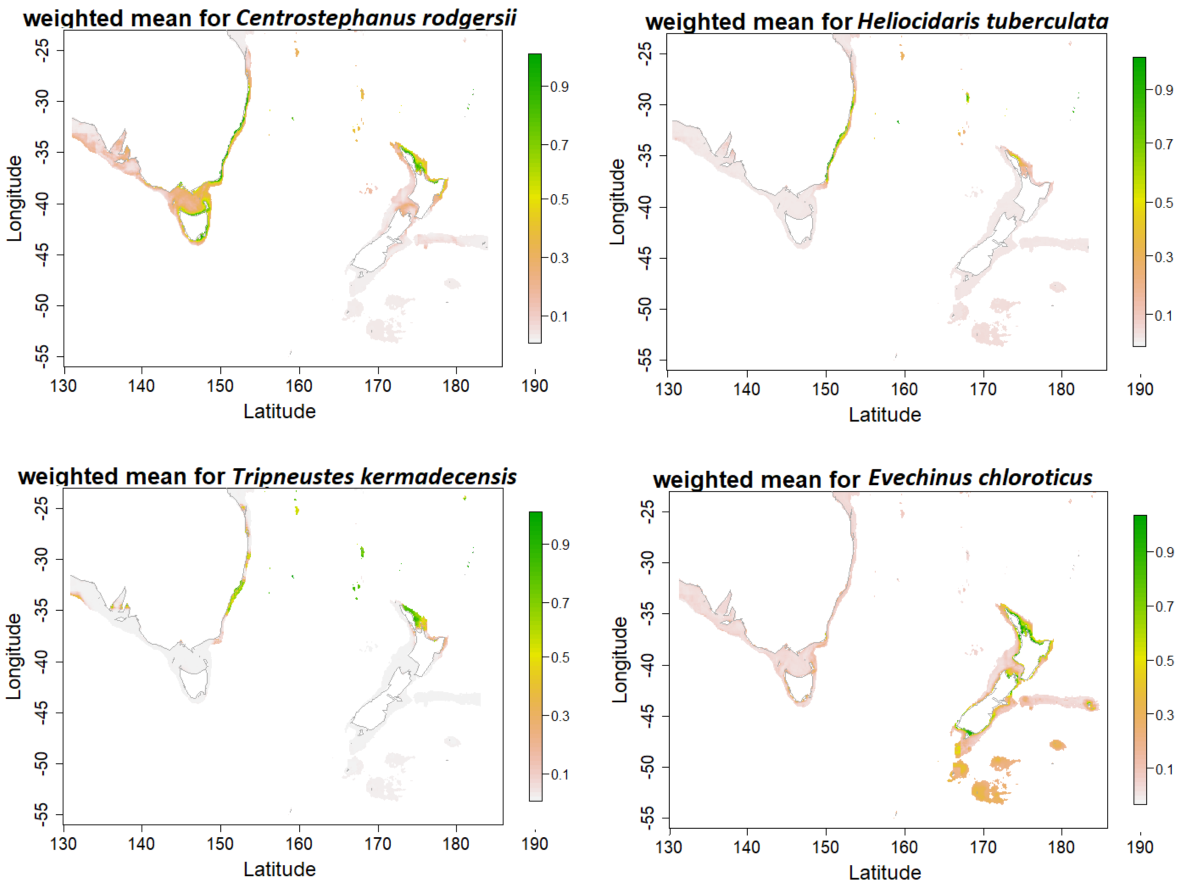
‘Profile’, which only uses presence data and does not include any background points; ‘Regression’ models such as generalised linear or generalised additive models; and ‘Machine Learning’ methods which use background points to better inform the model about the range of environments present in the study area (Hijmans & Elith, 2013). In my study, I created a weighted means ensemble model using a Generalised Linear Model and three machine learning methods: MaxEnt (Philips et al., 2004), Random Forest (Breiman, 2001) and Support Vector Mechanics, all of which are supported by the R package dismo version 1.1-4 a (Hijmans et al., 2017).

Creation of Models

To predict the distribution of my four species of interest, the present environmental data was loaded as raster layers into R v4.0.3 (R core team, 2013). The data was then modelled using the four different techniques described above to predict the range of the species of interest. Testing of the models showed incredibly high area under the curve (AUC) scores (>0.9). However, this is an indicator of spatial sorting bias in the models. Therefore, the AUC scores were adjusted for spatial sorting bias (Hijmans, 2012). The corrected AUC scores were then used to weight the four models and create the ensemble models. For predicting the 2100 distribution of my four species of interest, the modelled relationship with the environmental variables was then used to forecast the species distributions according to a new environmental dataset. This dataset contained the future predicted sea surface temperature, salinity, and current velocity (mean, minimum and maximum), and the present-day values for all other variables (dissolved oxygen, diffuse attenuation, primary productivity, pH, wave height and depth). This process was repeated for four RCP scenarios: RCP 2.6, a scenario where greenhouse gas emissions begin to decline by 2020 reaching zero by 2100; RCP 4.5 and RCP 6.0 which predict greenhouse gas emissions to rise until 2040 and 2080 respectively and then begin to decline; and RCP 8.5, a scenario where greenhouse gas emissions continue to rise throughout the 21st century. The AUC scores were once again corrected for spatial sorting bias and the future weighted mean ensemble models constructed. From the AUC weighted ensembles, I visualised the overlap between each subtropical species and *Evechinus chloroticus*.

Results

The recorded presence points (Appendix 3) were consistent with all four species' known geographic range extent, although there were some outliers, for example, a record of *Centrostephanus rodgersii* from the Spencer Gulf and a *Tripneustes kermadecensis* specimen from Tasmania. While these points appear to be outliers, there is no evidence that they are erroneous and therefore have been retained. *Centrostephanus rodgersii* was the most widespread of the three subtropical urchin species, with its range in New Zealand extending from 28°S to 32°S (Rangitāhua in the north to Hawke's Bay in the south), and 28°S to 32°S in Australia (from southern Queensland to the Spencer Gulf, as well as Tasmania). *Heliocidaris tuberculata* has a similar range to *C. rodgersii*. However, it appears much less frequently south of 37.5°S and is absent from Tasmania; In New Zealand *H. tuberculata*, it was not recorded south of 36.5°S. *Tripneustes kermadecensis* shares a similar distribution with the other two subtropical species, with all three subtropical species being found at the Australian east coast, Rangitāhua, the Tasman Islands and the northeast North Island of New Zealand; however, it does differ from the others in its Australian distribution with it only occurring between 33.5°S (Sydney harbour) and 37.5°S (Cape Howe) (Bronstein et al., 2019). *Evechinus chloroticus* was distributed between 34°S and 48°S around both the North and South Islands of New Zealand and some of the smaller islands (Stewart Island, Snares Island and the Chatham Islands). The models also predict some suitable areas around Tasmania where *E. chloroticus* could settle if introduced.



weighted mean for *Centrostephanus rodgersii*

weighted mean for *Heliocidaris tuberculata*

weighted mean for *Tripneustes kermadecensis*

weighted mean for *Evechinus chloroticus*

Figure 2: Maps showing the predicted present distributions of the four urchins' species. High probability of occurrence is shown as green and low probability of occurrence is shown as orange.

The AUC weighted mean models (Figure 2) show the four species predicted present distribution. For the three subtropical species (*C. rodgersii, H. tuberculata* & *T. kermadecensis*) predicted distributions cover the Australian coast, Lord Howe Island, Norfolk Island, Rangitāhua and the northeast North Island.

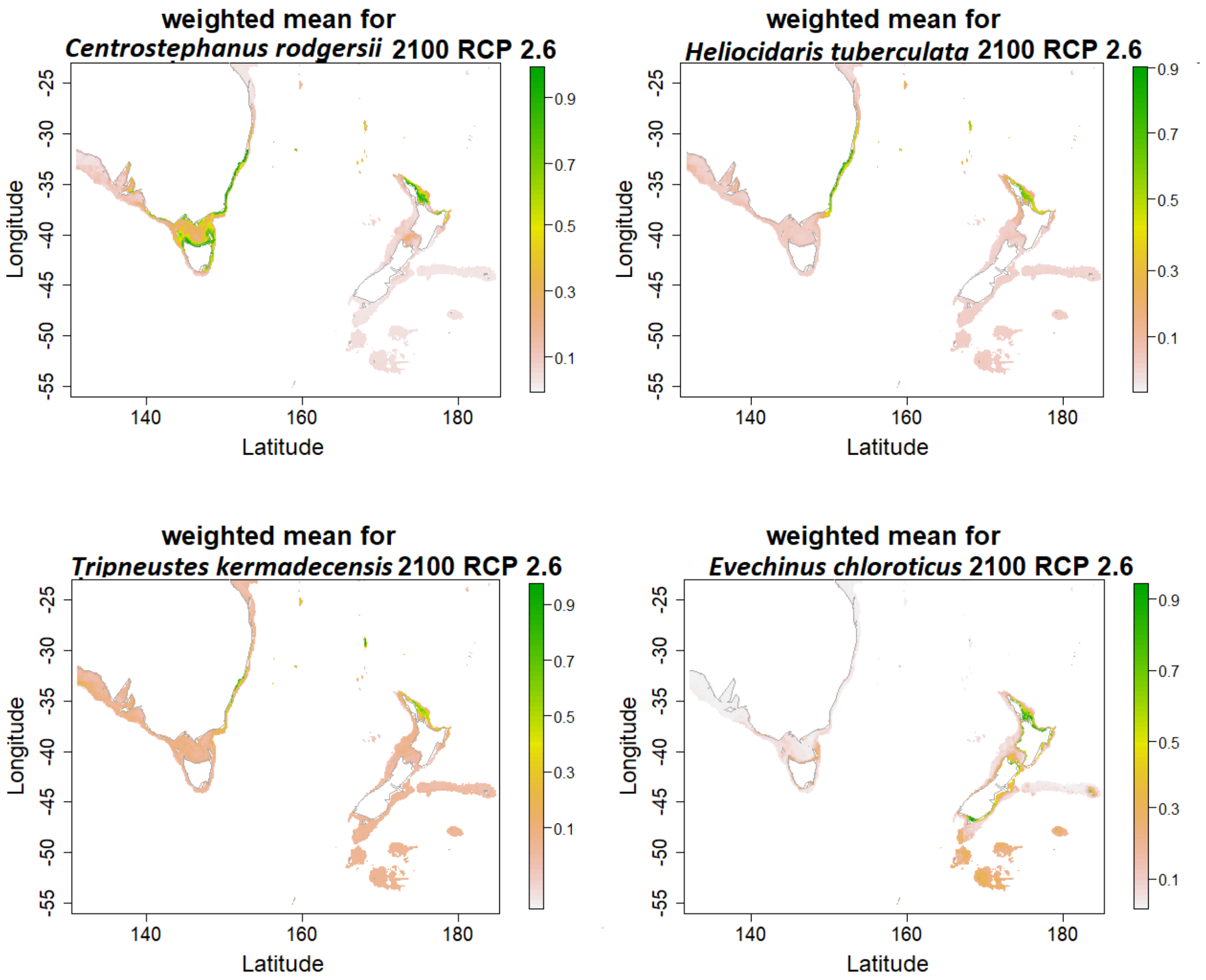


Figure 3: Maps showing the predicted future distribution under the most optimistic climate change scenario (RCP 2.6) distributions of the four urchins' species. High probability of occurrence is shown as green and low probability of occurrence is shown as orange.

For *E. chloroticus,* its predicted range covered both the main islands of New Zealand and some of the smaller islands listed earlier. The predicted distribution is slightly 'patchy' in places, likely due to a lack of data for some regions rather than a result of true absence. The future weighted mean models for the four RCP scenarios (Figure 3-4) predictably show a greater impact on the four species' distribution for climate scenarios that predict more significant environmental change.

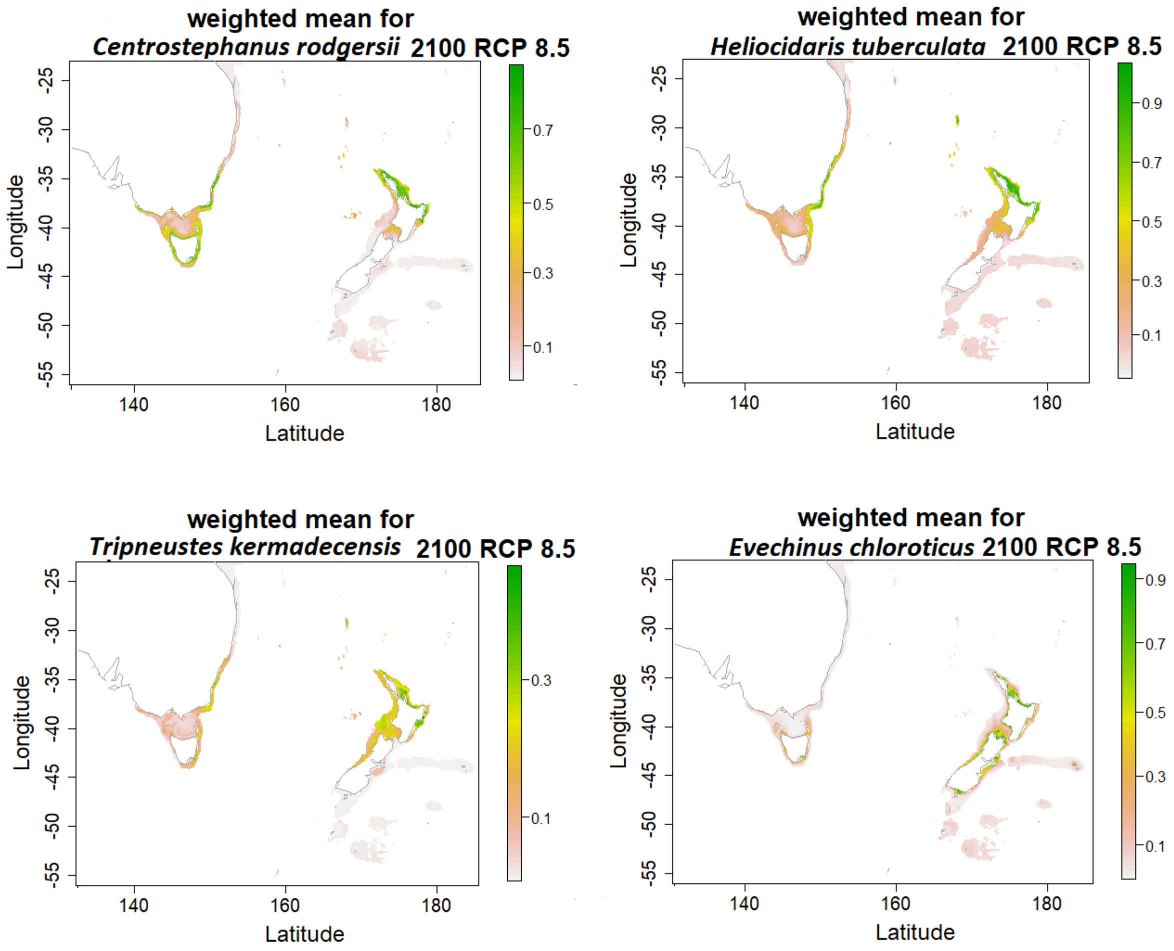


Figure 4: Maps showing the predicted future distributions under the worst-case climate scenario (RCP 8.5) of the four urchins' species. High probability of occurrence is shown as green and low probability of occurrence is shown as orange.

For *C. rodgersii,* as the severity of the climate change increases, various changes can be observed, such as a reduction of its range along the east coast of Australia and an increase in the distribution around Tasmania. Observations show it spreading from primarily the north and east coast of Tasmania to the south and west, eventually predicting presence around the entire island of Tasmania. In New Zealand, my models predict that the Bay of Plenty and around Hawke's Bay will become considerably more favourable for *C. rodgersii* by the year 2100. *Centrostephanus rodgersii* could spread to the Manawatu region between Wellington and New Plymouth on the west coast in the most extreme scenario. In the case of *H. tuberculata* in Australia, the model predicts a slight southern range extension reaching into the Bass Strait. In New Zealand, the model predicts that the northeast North Island will be more suited to *H. tuberculata* by the year 2100, and it will be able to expand its range south to Hawke's Bay. *Tripneustes kermadecensis* shows a minimal change in its Australian distribution under all but the most extreme of predicted scenarios where my model predicts a possible range expansion onto the Tasmanian east coast. For New Zealand, its predicted future distribution follows much the same pattern as *H. tuberculata.* Surprisingly, the distribution of *E. chloroticus* is not predicted to significantly change under any future climate scenarios, with its distribution predicted to continue covering most of the New Zealand coastline, albeit with minor losses in north-eastern New Zealand.

For each model, except for support vector mechanics, it is possible to show each variable's contribution to the model. As there is some variance between the models regarding the order of variable importance, I used the mean ranking (between 1st and 15th) of variable importance to assess the contributions of the variables to the distribution of my study species (Table.1). There is also considerable variation in the rankings of variables among species, with the most significant difference between two subtropical species, *H. tuberculata* and *T. kermadecensis,* and the temperate *E. chloroticus*. In the models the relationship between predicted abundance and each environmental variable as shown in the response plots could be broadly categorised as one of four relationships: a positive linear relationship, negative linear relationship, suitable bracket, or required threshold (Appendix 10-13). The maximum temperature had a very high average rank for the three subtropical species (highest ranked for *H. tuberculata* and *T. kermadecensis*). Mean and minimum temperature contributed considerably less to the model, with an average ranking greater than sixth for all species. The minimum salinity consistently had the highest average rank for salinity, particularly for *C. rodgersii,* where it had the highest average rank. The mean and maximum values of salinity showed considerably greater variance between species but, mean and maximum salinity tended to fall in the lower half of the average rankings for all species except *E. chloroticus*. However, for *E. chloroticus* maximum salinity had the third-highest average rank. The contribution of current velocity ranked very low for *C. rodgersii*, but for the other subtropical species maximum current velocity ranked moderately high with the fourth and fifth-highest average rank for *H. tuberculata* and *T. kermadecensis* respectively. For *E. chloroticus*, the mean and maximum values for current velocity fell in the middle of the average rankings, while the minimum value ranked considerably lower at the thirteenth for average contribution ranking. Diffuse attenuation was the highest average ranking variable for *E. chloroticus,* and for *C. rodgersii,* diffuse attenuation had the third-highest average rank, whereas for *H. tuberculata* and *T. kermadecensis* diffuse attenuation ranked in the lower half. The average rank for primary productivity fell roughly in the middle of the rankings, with it being slightly higher for *E. chloroticus* and *C. rodgersii* (fourth and fifth-highest average rank respectively). Dissolved oxygen ranked highly for *H. tuberculata* and *T. kermadecensis,* with it having the second-highest average rank for both species. For *E. chloroticus* and *C. rodgersii,* dissolved oxygen ranked relatively low. A low average rank was observed in pH for all species except *H. tuberculata*, where it had the third-highest average rank. Wave height fell somewhere in the middle in terms of average rank for all species between the seventh and twelfth-highest average rank.

Centrostephanus rodgersii

Variable	Maxent	Random Forest	GLM	Mean ranking
Salinity Minimum	15%	29.5%	6.5%	3.3
Temperature Maximum	3.4%	6.5%	16.3%	4.6
Diffuse attenuation	25.6%	4.6%	3.6%	6.3
Salinity Maximum	11.7%	10.5%	1.3%	6.6
Primary productivity	10.9%	2.0%	8.5%	6.6
Salinity mean	9.3%	16.4%	3.0%	6.6
Temperature Mean	0.5%	5.7%	13.7%	7.3
Dissolved oxygen	2.2%	3.5%	10.7%	7.6
pH	1.7%	4.2%	6.4%	9.3
Wave height	5%	1.8%	6.3%	9.6
Current Velocity Maximum	6.8%	2.8%	0.9%	10.6
Temperature Minimum	0.1%	6.5%	7.0%	8.6
depth	3.1%	3.0%	4.4%	10
Current Velocity Minimum	1.1%	1.4%	8.0%	11
Current Velocity mean	3.5%	1.7%	3.3%	11.3

Heliocidaris tuberculata

Variable	Maxent	Random Forest	GLM	Mean ranking
Temperature Maximum	49.9%	30.7%	13.2%	1
Dissolved oxygen	2.4%	13.5%	12.0%	3.3
pH	8.6%	8.5%	7.3%	5.3
Current Velocity Maximum	25.1%	4.4%	5.4%	6.6
Wave height	2.2%	1.0%	11.2%	7
Temperature Mean	0.4%	19.1%	7.8%	7.3
Salinity Minimum	0.4%	4.5%	9.2%	7.6
Diffuse attenuation	4.5%	1.9%	0.8%	8.3
Primary productivity	1.6%	1.7%	6.7%	8.6
Current Velocity mean	0.6%	0.6%	8.4%	10.6
depth	1.9%	0.9%	9.2%	11
Temperature Minimum	0%	9.7%	0.6%	11
Salinity mean	0%	1.5%	5.6%	11.6
Current Velocity Minimum	1.6%	0.8%	2.3%	11.6
Salinity Maximum	0.8%	1.2%	0.3%	12

Table 1: Chart showing the percentage of variable contribution to the model for the Maxent, Random Forest and GLM models, for *Centrostephanus rodgersii* and *Heliocidaris tuberculata.* The rank variable importance was then averaged for the final column giving a value of between 1 and 15, 1 being the variable with the highest contribution for each individual model and 15 being the variable with the lowest contribution for each individual model.

Tripneustes kermadecensis

Variable	Maxent	Random Forest	GLM	Mean ranking
Temperature Maximum	45.7%	28.6%	12.3%	1
Dissolved oxygen	25.8%	18.9%	11.6%	2.3
Salinity Minimum	1.4%	5.0%	9.2%	6.3
Temperature Mean	0%	13.8%	11.8%	6.6
Current Velocity Maximum	12.5%	5.8%	4.7%	6.6
Wave height	6.9%	4.7%	5.6%	7.3
Salinity Maximum	2%	1.0%	8.0%	8
Salinity mean	0.1%	2.2%	8.8%	8.6
Primary productivity	1.7%	1.6%	6.4%	9
pH	0%	5.9%	7.7%	9
Diffuse attenuation	1.5%	1.9%	0.8%	10.3
Temperature Minimum	0%	7.3%	3.6%	10.3
Current Velocity mean	0.4%	1.7%	7.2%	11
depth	1.3%	0.8%	2.0%	12
Current Velocity Minimum	0.6%	0.8%	0.5%	13.3

Evechinus chloroticus

Variable	Maxent	Random Forest	GLM	Mean ranking
Diffuse attenuation	61.3%	17.4%	13.0%	2
Salinity Minimum	1.3%	10.0%	13.3%	5
Salinity Maximum	2.7%	4.9%	20.2%	5.3
Primary productivity	9.3%	7.3%	4.4%	5.3
Salinity mean	11.1%	6.1%	6.1%	5.3
Current Velocity Maximum	1.7%	14.2%	2.5%	6.6
Wave height	3.7%	4.3%	5.3%	7.3
Current Velocity mean	3.7%	4.1%	4.8%	8
Temperature Maximum	0.2%	4.2%	15.1%	8.6
depth	1%	6.6%	2.2%	9
Dissolved oxygen	0.5%	2.5%	9.4%	10.3
pH	0.2%	7.0%	1.2%	10.3
Current Velocity Minimum	2.6%	3.0%	0.7%	11.3
Temperature Mean	0.1%	6.3%	1.1%	11.6
Temperature Minimum	0.6%	2.3%	0.6%	13.6

Table 2: Chart showing the percentage of variable contribution to the model for the Maxent, Random Forest and GLM models, for *Tripneustes kermadecensis* and *Evechinus chloroticus.* The rank variable importance was then averaged for the final column giving a value of between 1 and 15, 1 being the variable with the highest contribution for each individual model and 15 being the variable with the lowest contribution for each individual model.

Finally, depth had a low average rank for all species, never exceeding the tenth-highest average rank. Based on my models, the subtropical species with the greatest present overlap with *E. chloroticus* is *C. rodgersii,* with areas of substantial overlap occurring from the top of the North Island of New Zealand down much of the east coast into the Bay of Plenty (Figure 5). For *T. kermadecensis,* the areas of significant overlap with *E. chloroticus* are along the east coast between the North Cape and the Hauraki Gulf. *Heliocidaris tuberculata* has the most limited predicted to overlap with *E. chloroticus* occurring in only some of the east coast of Northland.

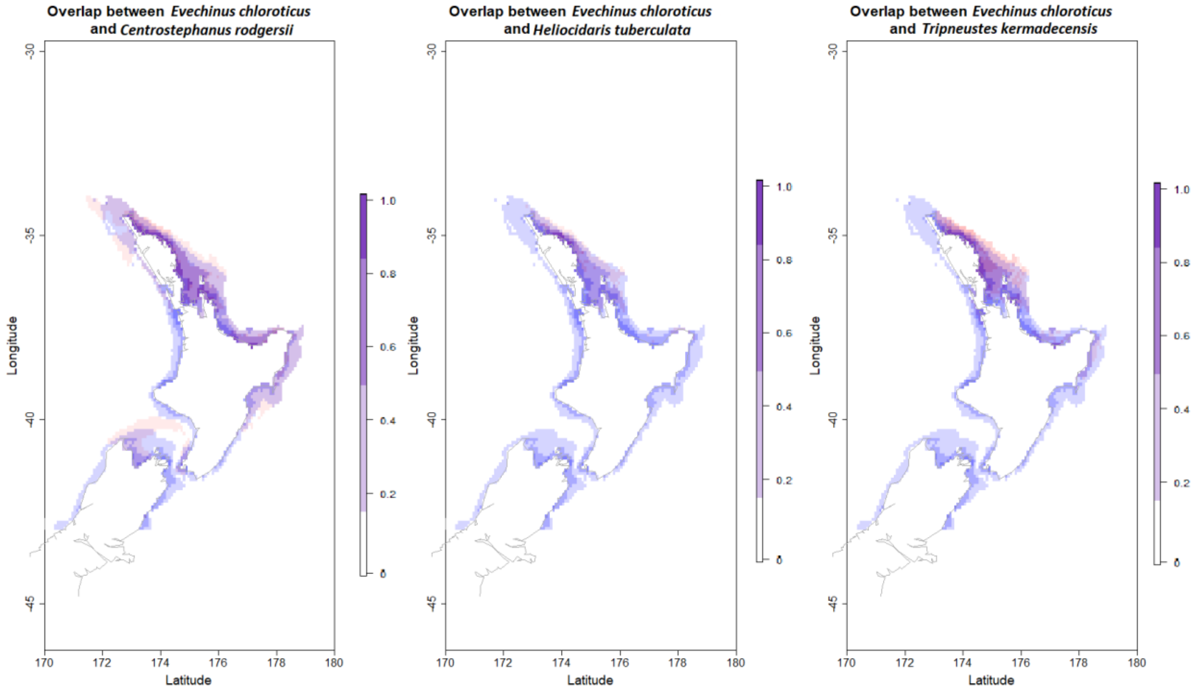
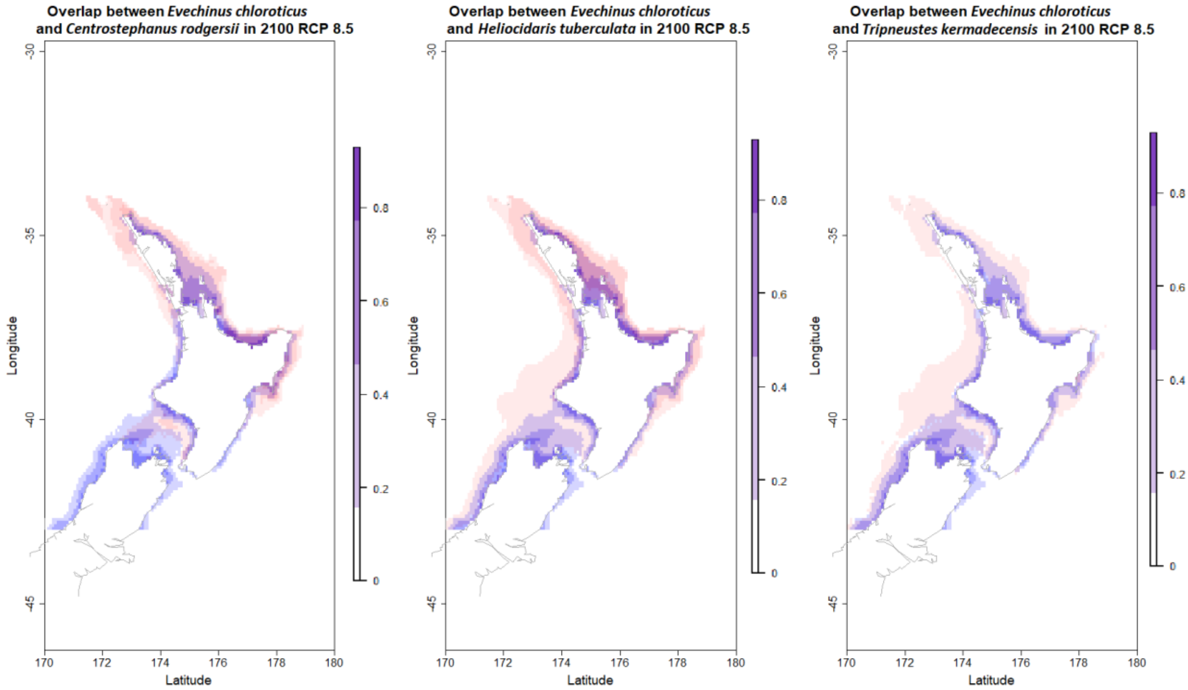


Figure 5: Map showing the present overlap between the three subtropical species and *Evechinus chloroticus.*

Evechinus chloroticus has been plotted in blue at 50% opacity while the subtropical species have been plotted in red at 50% opacity. Areas of overlap are shown as purple, with darker purple indicating where the two species are more likely to overlap, while red and blue areas show where only one species is present.


Overlap between *Evechinus chloroticus* and *Centrostephanus rodgersii* in 2100 RCP 8.5

Overlap between *Evechinus chloroticus* and *Heliocidaris tuberculata* in 2100 RCP 8.5

Overlap between *Evechinus chloroticus* and *Tripneustes kermadecensis* in 2100 RCP 8.5

Figure 6: Map showing the future overlap under the worst-case climate scenario (RCP 8.5) between the three subtropical species and *Evechinus chloroticus*.

Evechinus chloroticus has been plotted in blue at 50% opacity while the subtropical species have been plotted in red at 50% opacity. Areas of overlap are shown as purple, with darker purple indicating where the two species are more likely to overlap, while red and blue areas show where only one species is present.

Throughout most of their overlapping ranges, the environment appears to favour *E. chloroticus* based on the predicted overlap. Under the most extreme climate scenario RCP 8.5 scenario (Figure 6), all three subtropical species have more extensive areas of predicted overlap with *Evechinus chloroticus* extending into the Bay of Plenty.

Discussion

I found that the subtropical species' current predicted distribution covers the Australian east coast, Tasman Islands, Rangitāhua and north-eastern New Zealand (Figure 2). However, *Centrostephanus rodgersii* extends further south than *Heliocidaris tuberculata* and *Tripneustes kermadecensis* into Tasmania in Australia and Hawke's Bay in New Zealand (Figure 2). The New Zealand endemic *Evechinus chloroticus* is predicted to cover most of the coast of both main islands and the Chatham Islands and the Snares Islands (Figure 2), with the distribution closely aligning with the known areas of rocky reef habitat (Appendix 9). In the predicted future distributions, the three subtropical species are expected to expand their ranges down the east coast of the North Island and under more extreme climate scenarios onto parts of the west coast. In Australia, I predicted a contraction of the northernmost parts of the range for *H. tuberculata* and *T. kermadecensis* and a predicted poleward expansion of their ranges into Tasmania. These results are consistent with studies that used SDMs to model the future distribution of urchin populations, with both these studies and my results predicting a poleward range expansion in these subtropical urchin populations (Castro et al., 2020). When examining the predicted present overlap between *E. chloroticus* and the three subtropical species in New Zealand, it becomes apparent that the species with the most substantial overlap being between *E. chloroticus* is *C. rodgersii* (Figure 5). While there is some overlap between *E. chloroticus* and the other subtropical species, it is not as common (Figure 5).

From the average variable ranking, I can determine each variable's overall importance in affecting the species' distribution. By combining this with what is known about the relationships among the four species and the environmental variables, I can imply how variables are responsible for shaping their distribution. In *C. rodgersii*, the variables with the five highest average ranks in descending order were: minimum salinity, maximum temperature, diffuse attenuation, maximum salinity, and primary productivity. The high average values of salinity indicate that *C. rodgersii* likely has low reproductive success outside of a certain salinity bracket, in addition to increased adult mortality in areas where salinity frequently drops such as near river mouths (Greenwood & Bennett, 1981; Irlandi et al., 1991; Cowart et al., 2009; Foo et al., 2012; Delorme & Sewell, 2014). The effect of maximum temperature would be due to the required bracket of thermal tolerance for successful reproduction in *C. rodgersii* of 17.2°C–24.5°C. Therefore, if temperatures range outside this bracket during the breeding season, *C. rodgersii* may not be able to reproduce in these areas (Pecorino et al., 2013). From the rankings of diffuse attenuation and primary productivity, we can see that food availability also plays a significant role in the distribution of *C. rodgersii,* which is unsurprising as it is known to be a voracious grazer (Andrew et al., 1993; Hill et al., 2003; Ling et al., 2010).

In *H. tuberculata*, the variables with the five highest average ranks were maximum temperature, dissolved oxygen, pH, maximum current velocity, and wave height. There was also a significant gap in the average rankings for *H. tuberculata* between second and third place, with the first two variables having noticeably higher average scores, indicating that maximum temperature and dissolved oxygen have particularly strong associations with the distribution of *H. tuberculata*. An optimal temperature bracket likely causes the strong effect of maximum temperature in the models for *H. tuberculata* (O'Connor & Mulley, 1977; Byrne et al., 2009). The high ranking of pH in the models is somewhat surprising as despite it having an impact on reproductive success, many urchin species are shown to be quite robust to pH, including *H. tuberculata*. Therefore, it is possible that pH may be affecting a different stage of *H. tuberculata*'s life cycle or pH is correlated with other unmeasured variables (Byrne et al., 2009; Stumpp et al., 2012; Byrne et al., 2013; Harianto, 2018). The high importance of maximum current velocity and wave height indicates that *H. tuberculata* is quite robust to exposure. As in the previous chapter, I found *H. tuberculata* preferred comparatively shallow water at the boulder sand interface.

For *T. kermadecensis,* the variables with the five highest average ranks were: maximum temperature, dissolved oxygen, minimum salinity, mean temperature and maximum current velocity. The effects of maximum temperature and oxygen likely share the same explanations as was the case with *H. tuberculata*. However, the inclusion of mean temperature indicates that *T. kermadecensis* may have a strong affinity for a specific temperature bracket, possibly making it more susceptible to fluctuations in temperature than the other three species (Rahman et al., 2009; Brennand et al., 2010). The effect of minimum salinity likely indicates that *T. kermadecensis* avoids lower salinity areas as reproductive success is lower in these areas (Parvez et al., 2018). The high ranking of current velocity is likely the result of *T. kermadecensis* having a comparatively weak grip strength (personal observation) and therefore experiencing a higher risk of being dislodged and damaged in more exposed areas.

The five highest-ranking variables for *E. chloroticus* were: diffuse attenuation, minimum salinity, maximum salinity, primary productivity and mean salinity. The fact that all used salinity measures had high ranks within the models is strong evidence that the effect of salinity on reproductive success plays a significant role in shaping the distribution of *E. chloroticus* (Delorme & Sewell, 2014; Glockner-Fagetti et al., 2019). The lack of temperature in the top five highest average rankings is unique among the species studied here, with *E.*

chloroticus having a maximum temperature at the 7th highest average rank. This indicates that the full range of temperatures found at present within *E. chloroticus*'s range are suitable. However, the lesser effect of temperature in the model may result in it performing worse when predicting the effect of changing ocean temperatures for *E. chloroticus*. Both diffuse attenuation and primary productivity ranked within the top five in terms of average ranked importance within the models. This indicates that food availability plays a key role in determining suitable habitat for *E. chloroticus*. However, there is a noticeable gap between the rankings for diffuse attenuation and primary productivity; this is likely caused by the other factor within diffuse attenuation, turbidity. As waterborne sediment is known to affect the settlement ability of *E. chloroticus* and juvenile mortality, this result is unsurprising (Phillips & Shima, 2006; Glockner-Fagetti et al., 2019). While the relationships between the species distribution and the environmental variables used in this study appear reasonable based on the available knowledge about the four species' life-history traits, a few other potentially significant variables are not included in this study. Some of the possibly significant variables not used in this study include rock/substrate type and topographic complexity (McClanahan, 1988). this environmental information is not currently available for the current study area.

The predicted 'true' distribution produced by the ensemble models aligned quite closely with the presence points used to generate the models. Several issues can arise from the data collection when using presence points and pseudo-absences to model a species' distribution (Liu et al., 2018). One possible issue is an uneven distribution of sampling effort (Kramer-Schadt et al., 2013; Lahoz-Monfort & Guillera-Arroita, 2014; Stolar & Nielsen, 2015). At first glance, there may appear to be gaps in the sampling effort of *E. chloroticus* along the west coast of New Zealand and around Canterbury. However, this is likely not a result of a lack of sampling effort and a lack of suitable urchin habitat, as the areas from which *E. chloroticus* is absent closely align with areas lacking in rocky reef habitat (Appendix 9). As there does not appear to be significant gaps in sampling effort, the use of an AUC weighed mean model after spatial sorting bias correction should correct for any small gaps in the data (Hijmans, 2012; Kramer-Schadt et al., 2013; Stolar & Nielsen, 2014). In the future, a model that can make use of true absences may give a more accurate model and remove any concerns about possible bias in the sampling effort. However, there is currently insufficient data available in the form of presence-absence surveys across the study area.

When examining the modelled present overlap between *E. chloroticus* and the three subtropical species in New Zealand, it becomes apparent that the species with the most substantial overlap with *E. chloroticus* is *C. rodgersii*. Areas of substantial overlap reach from the far north of New Zealand to the Bay of Plenty and more moderate regions of overlap extend around East Cape and into Hawke's Bay. From the variable contributions to the model, we see that *E. chloroticus* and *C. rodgersii* share four of the variables with the five highest average rankings while neither share more than one of the top five with the other subtropical species. The variables shared are salinity minimum and maximum, diffuse attenuation and primary productivity. The effect of salinity on *E. chloroticus* is likely due to a bracket in salinity values where reproductive success would be highest (Greenwood & Bennett, 1981; Cowart et al., 2009; Delorme & Sewell, 2014). The high average rankings of diffuse attenuation and primary productivity indicate that food availability plays a significant role in the distribution of these two species. However, as diffuse attenuation ranks higher for both species, it suggests that the other component within diffuse attenuation, turbidity, also influences the two species' distribution.

The distribution overlap between *E. chloroticus* and *H. tuberculata* and *T. kermadecensis* is considerably more limited, with their overlapping ranges being restricted to the northeast coast of the North Island. While the environmental variable rankings for *H. tuberculata* and *T. kermadecensis* had little in common with either *E. chloroticus* or *C. rodgersii,* the two species share three of the five highest-ranking variables. Most importantly, they share the top two highest-ranking variables in the same order: maximum temperature in first and dissolved oxygen in second. Both maximum temperature and dissolved oxygen have considerably higher average ranks than the variables in third place. This trend suggests that the maximum temperature is strongly associated with the ranges of *H. tuberculata* and *T. kermadecensis*. Likely reproductive success is drastically lowered for the two species if temperatures exceed a certain threshold or if the temperature is too low.

Given all four urchin species overlap in north-eastern New Zealand, there is likely an underlying mechanism resulting in their co-occurrence as all four species have similar life-history traits (Winston, 1995). At present, there is no evidence of negative interactions between the species, and in the previous chapter, the evidence points to urchin species being able to co-occur as a result of microhabitat segregation (Anderson et al., 1981; Martin, 1998; Tuya et al., 2007; Valentine & Edgar, 2010; Warning & Benedict, 2015). Microhabitat segregation is yet to be confirmed for these species on mainland New Zealand. The relationships between the four species could undergo widespread changes in the future due to environmental changes, making New Zealand's environment more favourable for subtropical species. As the ocean around New Zealand is likely to continue warming leading up to 2100 (Sutton & Brown, 2019), there will likely be an increase in the subtropical urchin species' abundance. Combined with a possible loss of environmentally tolerable areas for *E. chloroticus*, an increase in the subtropical species' abundance could significantly negatively affect *E. chloroticus*' abundance. Also, an increase in abundance of the subtropical species is of some concern as there is clear evidence of the destructive effects of *C. rodgersii* increasing in abundance (Ling, 2013). Therefore, it is necessary to monitor the abundance of *C. rodgersii* so that measures can be implemented early to limit the impact of this species grazing (Tracey et al., 2014).

While my models can assess possible range shifts in the four species and the suitability of New Zealand's coastal habitat for urchins up to the year 2100, they cannot predict any trends regarding patterns in abundance. However, we can infer from what we know of the species studied here, as well as what we know of other urchin species, that with a rising ocean temperature along with changes in ocean salinity and coastal currents, New Zealand's northeast coastline will likely become much more suitable for the three subtropical urchin species examined here. It is reasonable to assume an increase in habitat suitability will result in an increase in abundance and that this will lead to increased grazing pressure on kelp forests (Castro et al., 2020). Potentially, the most severe impact could be an increase in the abundance of *C. rodgersii* as was the case in Tasmania (Ling, 2013). The expansion of subtropical species could pose a significant threat to New Zealand's commercial and recreational fisheries. For example, Paua (*Haliotis iris*) harvesting in Hawke's Bay could be at risk should the subtropical urchins increase in abundance there. Therefore, we must remain vigilant in our contributions to climate change and the ecological shifts that occur as a result and be prepared to deal with the ecological shifts that warming ocean temperatures will bring.

Chapter III: Acknowledgements

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Chapter IV: General Discussion

This thesis aims to provide insight into how a changing climate can affect species distributions and interspecies relationships and discuss these changes' possible impacts. I chose urchins as the focus group as they are known to respond to climate change and have a significant effect on their ecosystem (Ling et al., 2009; Valentine & Edgar, 2010; Ling, 2013). By predicting their future range extent and understanding how they respond to environmental changes it is possible to predict the future conservation issues that may arise in New Zealand's marine ecosystem due to climate change. I do this by first modelling the patterns of abundance of three subtropical grazing urchins at Rangitāhua (*Centrostephanus rodgersii*, *Tripneustes kermadecensis* and *Heliocidaris tuberculata*). I also modelled the present and future distributions of these three species in addition to one temperate urchin species (*Evechinus chloroticus*). From the patterns in abundance I found that the three urchin species observed at Rangitāhua each appear to be most abundant in unique microhabitats defined primarily by depth and topographical complexity, showing that the co-occurrence of these urchin species is likely the result of microhabitat segregation (Anderson et al., 1981; Martin, 1998). In modelling the four species' present distributions, I found all four species overlap along the east coast of New Zealand between 34°S and 37°S. In the future models this overlap expands south to 40°S under the worst-case climate change scenario RCP 8.5 with predicted future distributions of *C. rodgersii* reaching as far south as 41.5°S compared with its present 39°S.

The patterns in abundance modelled in chapter II provide insight into how these three species with seemingly similar requirements can co-occur. Species with similar biology are less likely to co-occur; this is likely the result of strongly overlapping niches resulting in competition (Hutchinson, 1957; Hutchinson, 1961; Hutchinson, 1978; Winston, 1995). Therefore, it is surprising to see three similar species occur in relative abundance at Rangitāhua. Several explanations have been proposed explaining the co-occurrence of similar abundant species. This study aims to use patterns of abundance to identify which explanation best fits the observed patterns of abundance in the three urchin species studied at Rangitāhua. By examining the patterns of abundance in these three urchin species, I found that each species had different correlations with the different environmental variables measured. The three species each occurred at the highest abundance in a different depth range and in the species with neighbouring depth ranges. There was also variation in their abundance between different levels of topographical complexity. *Heliocidaris tuberculata* was the most abundant in shallow bolder-sand habitat, whereas *C. rodgersii* was most abundant in mid-depth rock wall habitat and *T. kermadecensis* was most abundant in deeper bolder-sand habitat. Only one of the three species showed a significant correlation with algal composition, the prolific gazer *C. rodgersii,* which positively correlated with areas of coralline algae. However, this is likely the result of *C. rodgersii* eliminating all foliose algae near its homesites (Dean et al., 1984; Harrold & Reed, 1985; Vadas et al., 1986; Fletcher, 1987; Andrew & Underwood, 1989).

From the patterns in abundance observed in this study, microhabitat segregation seems the most likely explanation for these three urchin species' co-occurrence at high densities. Species that co-occur due to microhabitat segregation tend to maintain stable interspecies interactions. However, environmental change can disrupt this equilibrium (Nagelkerken et al., 2018). We lack the historical data to see how ocean temperature changes have affected the interspecies dynamics at Rangitāhua. As changes in our ocean climate are likely to become more extreme in the next hundred years, there may be a significant shift in these urchins' interspecies dynamics at Rangitāhua.

When species co-occur, there is a possibility that there is a difference between their realized and fundamental niches due to biotic interactions (Hutchinson, 1957; Hutchinson, 1978; Kearney & Porter, 2004). These negative interspecies interactions can result in a species being excluded from some microhabitats within their fundamental niche. To determine if there is a difference between the fundamental and realized niches, the experimental removal of the suspected competitors can be used to see if a species will expand its realized niche when the other species is not present (Robberecht et al., 1983; Hewitt et al., 2005). However, experimental removal is not the only way to examine changes to a species' realized niches. A changing environment can also disrupt a species distribution by altering the microhabitats available at a site. Importantly, and in contrast to other mechanisms facilitating the co-occurrence among similar species, species that co-occur via segregation by microhabitat tend to remain segregated, resulting in a pattern of distribution more robust to minor shifts in the environment (Lacroix et al., 1995).

The marine environment is undergoing monumental changes, and with these changes likely to continue over the next hundred years many species are responding by shifting their ranges (Karl & Trenberth, 2003; Harley et al., 2006; Hoegh-Guldberg et al., 2007; Hoegh-Guldberg & Bruno, 2010; Diffenbaugh & Field, 2013; Kemp et al., 2015; Molinos et al., 2016). To understand how climate change can affect species distribution, it is first necessary to understand the present and historical range of the species of interest. To explore the effects of changes in the marine environment on four shallow-reef urchin species present in New Zealand (*Centrostephanus rodgersii*, *Tripneustes kermadecensis,* *Heliocidaris tuberculata* and *Evechinus chloroticus*), I modelled their present ranges using four different species distribution modelling methods and created an ensemble model. To examine the effects of a changing environment on the distributions of these four species I substituted the environmental variables: sea surface temperature, salinity, and current velocity from their present values to four future Representative Concentration Pathway (RCP) climate scenarios, where changes in the environment are predicted based on future greenhouse gas concentration. The results predict that of the four species, the three more subtropical species (*C. rodgersii*, *T. kermadecensis* and *H. tuberculata*) will undergo poleward range shifts over the next hundred years.

In contrast, the models predicted no changes in the distribution of the more temperate *E. chloroticus*. Although previous studies have shown that rising temperatures could likely affect the northernmost *E. chloroticus* populations (Delorme & Sewell, 2013; Delorme & Sewell, 2014), the lack of a predicted poleward shift in the distribution of *E. chloroticus* is likely the result of the lesser contribution of temperature to the present-day distribution of *E. chloroticus* identified in our models. Of the four species observed, only *C. rodgersii* has undergone a poleward range shift from New South Wales into Tasmania over the past 60 years (Johnson et al., 2011; Ling, 2013). While the other species' exact response to climate change is not currently known, their ranges will almost certainly be affected if the climate continues to change at the current rate.

This thesis also examines the present and future distribution overlaps between *E. chloroticus* and each of the subtropical species. All three species overlap with *E. chloroticus* along the north-eastern coast of the North Island between the North Cape and the Hauraki Gulf. *Centrostephanus rodgersii* had the greatest extent of overlap with *E. chloroticus,* while *H. tuberculata* had the least overlap. At present, the models indicate that the environment is more suitable for *E. chloroticus*. The models show in the future that not only will there be an increased extent in the overlap between *E. chloroticus* and each of the subtropical species, but the environment around north-eastern New Zealand will become more suitable for the subtropical species whilst becoming less suitable for *E. chloroticus.* The models indicate that by 2100 there may be a shift in the dominant urchin species in north-eastern New Zealand. The predicted degree of this change depends on the RCP scenario, ranging from minimal change under RCP 2.6 to a more extreme shift under RCP 8.5.

The impact of the subtropical species shifting their ranges on New Zealand's non-urchin marine fauna and flora could be equally significant. Kelp forests are already vulnerable due to rising ocean temperatures and the overfishing of key predator species makes these systems particularly susceptible to overgrazing (Tegner & Levin, 1983; Wernberg et al., 2010; Ling et al., 2013). This has been the case in Tasmania, where large amounts of kelp forest have been lost as a result of *C. rodgersii*'s intense grazing and the already vulnerable state of the kelp forests (Ling et al., 2009; Wernberg et al., 2010; Ling, 2013; Wernberg et al., 2016; Verges et al., 2016). The loss of kelp forests has a knock-on effect for the species that feed on and live amongst the kelp, such as abalone and crayfish (Johnson et al., 2005).

Preparing for future conservation challenges poses many difficulties. For example, the range shifts of these subtropical urchins are likely to disrupt the shallow reef ecosystems of north-eastern New Zealand significantly. Climate-driven range shifts are not a novel occurrence; climate tracking range shifts are a naturally occurring process even if the climate change is manmade (Davis & Ruth, 2002; Veloz et al., 2012). Therefore, it is important not to treat climate tracking species as invasive and instead develop conservation methods that conserve both the range shifting species and the ecosystem's original inhabitants (Urban, 2020). Instead, it would be better to limit the environmental stressors in the environment they will be arriving in so the ecosystem will be more robust (Sala et al., 2000; Sala & Knowlton, 2006; Blake & Duffy, 2010; Wernberg et al., 2010). To improve the robustness of these changing ecosystems, pre-emptive conservation measures must be taken such as limiting the fishing of key predator species and reducing global greenhouse gas emissions. This way, all species including these range shifting urchins can be protected as part of the effort to maintain global biodiversity.

While this thesis provides novel insight into the relationship among abundant urchin species present in New Zealand, some aspects of their relationships are still not covered in this thesis. While their biology may seem similar, there are many possible differences that could lead to varying degrees of fitness within an ecosystem. For example, the three species present at Rangitāhua appear to have different activity patterns throughout the day and night (L. Liggins pers. Comm.). The patterns of distribution are only observed among the three shallow reef urchins present at Rangitāhua, though many other urchin species overlap in other parts of their ranges. Nonetheless, it is reasonable to assume that these mechanisms of co-occurrence are also relevant where these species overlap with other urchin species, such as *Heliocidaris erythrogramma, Amblypneustes elevatus* or *Diadema palmeri.* However, this study provides a foundation for the ongoing observation of the urchin populations at Rangitāhua, as any subsequent study of the populations can be compared to this study's findings allowing for the identification of any changes in population structure or abundance. There are many other ways in which the research here can be built upon, such as experimental manipulation of urchin species population density to explore how the species interactions affect the realised niche of the species. Experimental removal experiments could prove if the interspecies relationships among these urchin species contribute to their distribution or, conversely, if the species have extreme habitat preferences (Fowler, 1981). If there is a significant increase in abundance among the subtropical species in New Zealand, future studies could investigate the potential for commercial harvesting of the species as a cost-efficient means of reducing the abundance of these species and therefore possibly limiting their impact (King et al., 1994; Scheibling et al., 1999; Blount & Worthington, 2002; Phillips et al., 2010; Johnson et al., 2013; Cresswell et al., 2019).

Despite the presence-only methods for species distribution modelling applied in this study being widely used, future models could utilise other methods once more species occurrence data becomes available (Hao et al., 2018). Methods that make use of true absences as opposed to pseudo-absences have been shown as having greater predictive power, in addition to being able to identify unsampled areas rather than treating them as areas the species is absent from (Elith et al., 2006; VanDerWal et al., 2009; Barbet-Massin et al., 2012). In the case of the four urchin species used in this study, the use of presence-only data and pseudo-absences is preferable. At present presence-only data provides considerably greater coverage. As more presence-absence data becomes available, the improved predictive power it offers would make it the superior choice. In addition to improving the present species distribution data, several environmental variables could not be included in chapter III's SDMs due to such data sets being unavailable or their creation being beyond the scope of this thesis. Environmental variables such as rock type, topographical complexity, or measures quantifying the ecosystem type were not included in the SDMs. These variables have been used in past studies as they are available for some areas and are known to affect the distribution of benthic marine invertebrates (Wiltshire et al., 2018). The datasets were not available even though some of these variables were shown to impact the species occurrence in chapter II. Should these variables become available, they should be included in future studies to improve the predictive power of the SDMs.

As the earth's climate continues to change, we will be presented with many novel conservation challenges, including balancing the conservation of range shifting species with the maintenance of global biodiversity (Bonebrake et al., 2017; Pecl et al., 2017; Urban, 2020). By identifying how these species react to the changing climate, we can gain more time to prepare and plan for these challenges. Of the four urchin species observed in this study, one is already undergoing changes in its range (Ling et al., 2009). The other three species' ranges are also likely to be affected unless rapid changes are made to reduce climate change. Preparation for range shifts of these urchin species is essential given their ability to alter their environment, so taking measures in New Zealand to mitigate the loss of key ecosystems. Measures that can be taken to protect New Zealand's shallow reef ecosystems include limiting greenhouse gas emissions, creating additional marine protected areas and placing strict quotas on the fishing of key predator species such as crayfish to ensure they are sufficiently abundant to regulate the urchin populations (Kelly et al., 2000; Eklöf et al., 2008; Ling et al., 2009).

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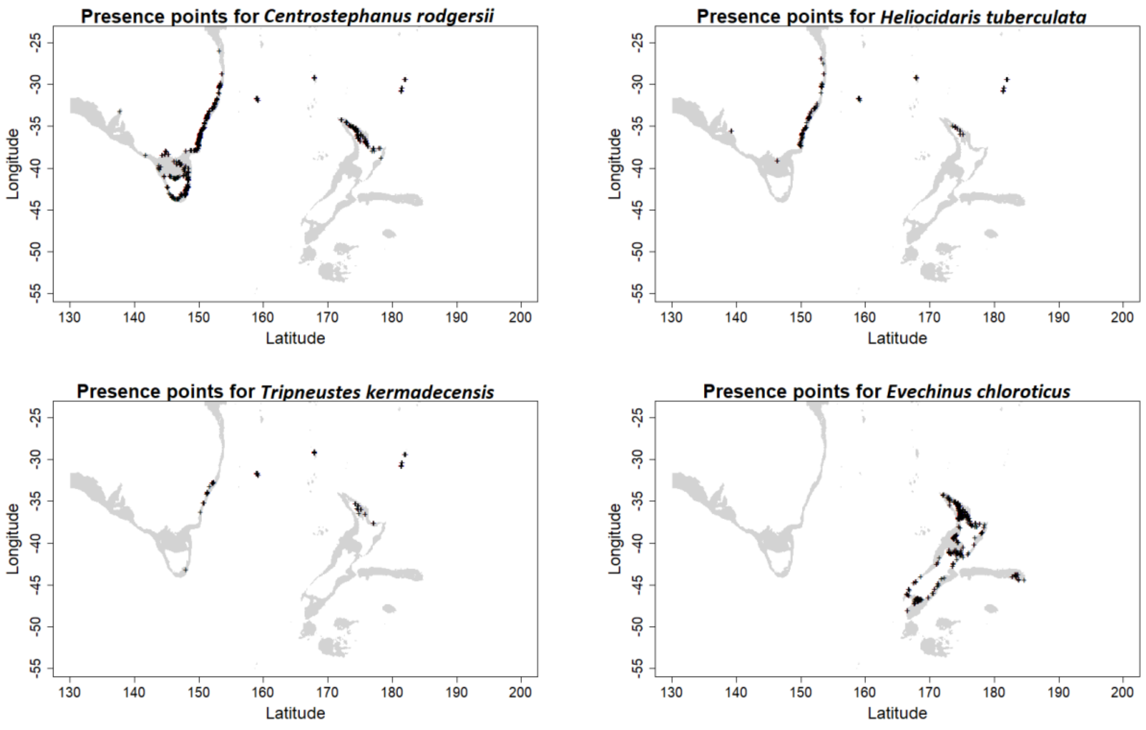
Appendices

	1st principal axis	
Eigenvalue (% contribution to inertia)	0.451 (14.08 %)	
Large features - Overhangs	-0.477	"Reef wall habitats."
Small features - Ledges	-0.313	
Aspect - Vertical	-0.308	
Small Features - Crevices	-0.171	
Basal substrate - Flat bedrock	-0.156	
Mobile secondary substrate - Absent	-0.109	
Basal substrate - Undulating bedrock	-0.099	
Large features – Crevasses	0.003	
Large features – Absent	0.007	
Aspect - Sloping	0.043	
Aspect - Flat	0.077	
Large features – Caves	0.101	
Small Features - Absent	0.102	
Basal substrate - Boulders	0.135	"Boulder reefs at the reef-sand interface."
Mobile secondary substrate - Cobbles	0.158	
Basal substrate - Large boulders	0.203	
Mobile secondary substrate - Sand	0.24	
Mobile secondary substrate - Boulders	0.253	
Mobile secondary substrate - Large boulders	0.255	
Basal substrate - Sand	0.32	
Basal substrate - Cobbles	0.321	

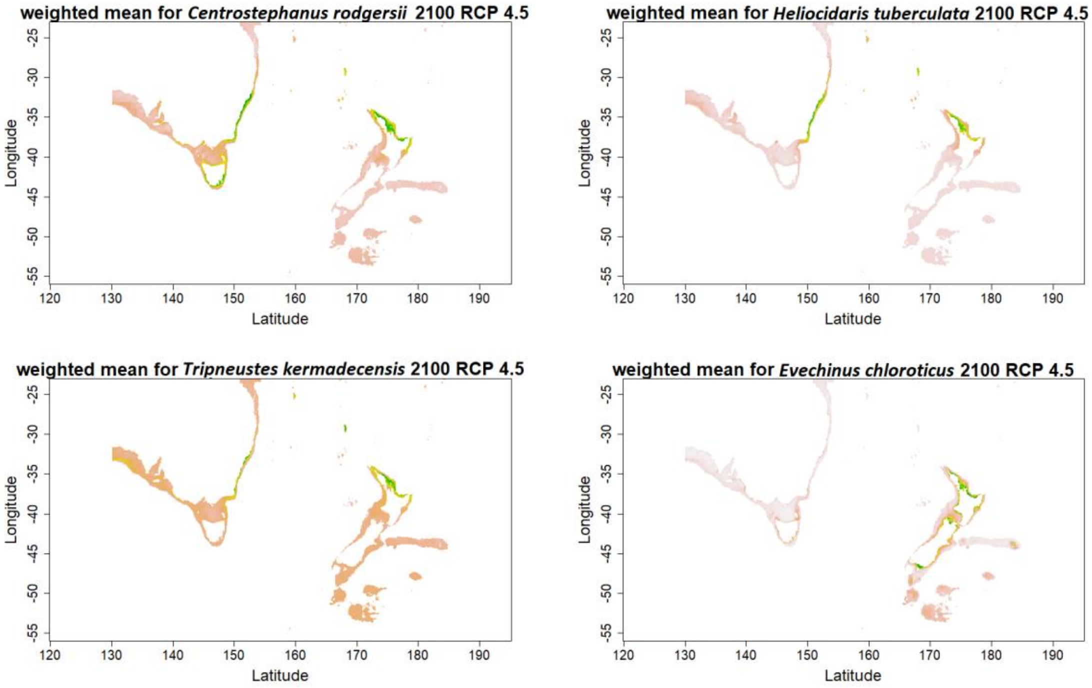
Appendix 1. First principal axis of the canonical correspondence analysis of the indicator matrix for topographical variation among transects. Features indicative of the two extreme habitat types – reef-wall and boulder reefs at the reef-sand interface – are shaded, and the habitat types are noted. Leading axes explaining relatively small proportions of the variation is a common result of canonical correspondence analysis compared with other ordination methods.

	1st principal axis
Eigenvalue (% contribution to inertia)	1442.622 (57.44 %)
Crustose coralline algae	-0.915
Green algae	0.066
Brown algae	0.086
Red foliose algae	0.26
Red turfing algae	0.289

Appendix 2. First principal axis of the principal component analysis of variation in algal community composition among transects. For the algal community composition, the interpretation of the first principal axis was more straightforward. At one extreme are habitats dominated by crustose coralline algae and, at the other extreme, habitats dominated by turfing and foliose red algae.



Appendix 3. Map showing the locations of presence points (black '+') within the area modelled.



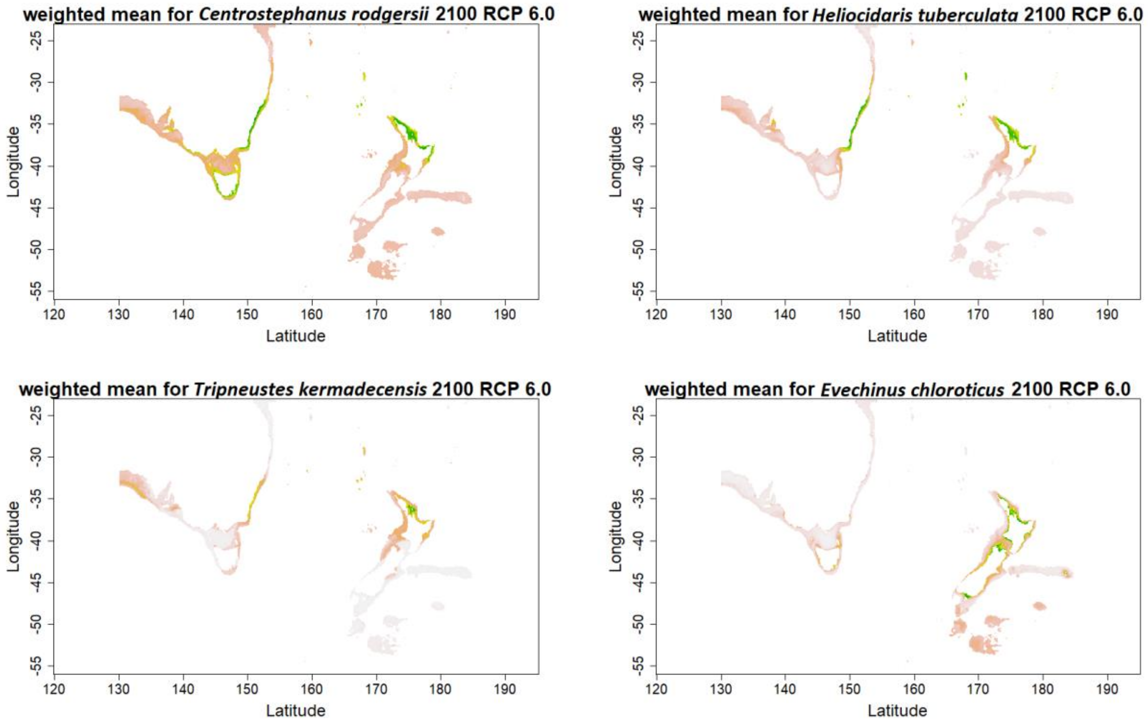
weighted mean for *Centrostephanus rodgersii* 2100 RCP 4.5

weighted mean for *Heliocidaris tuberculata* 2100 RCP 4.5

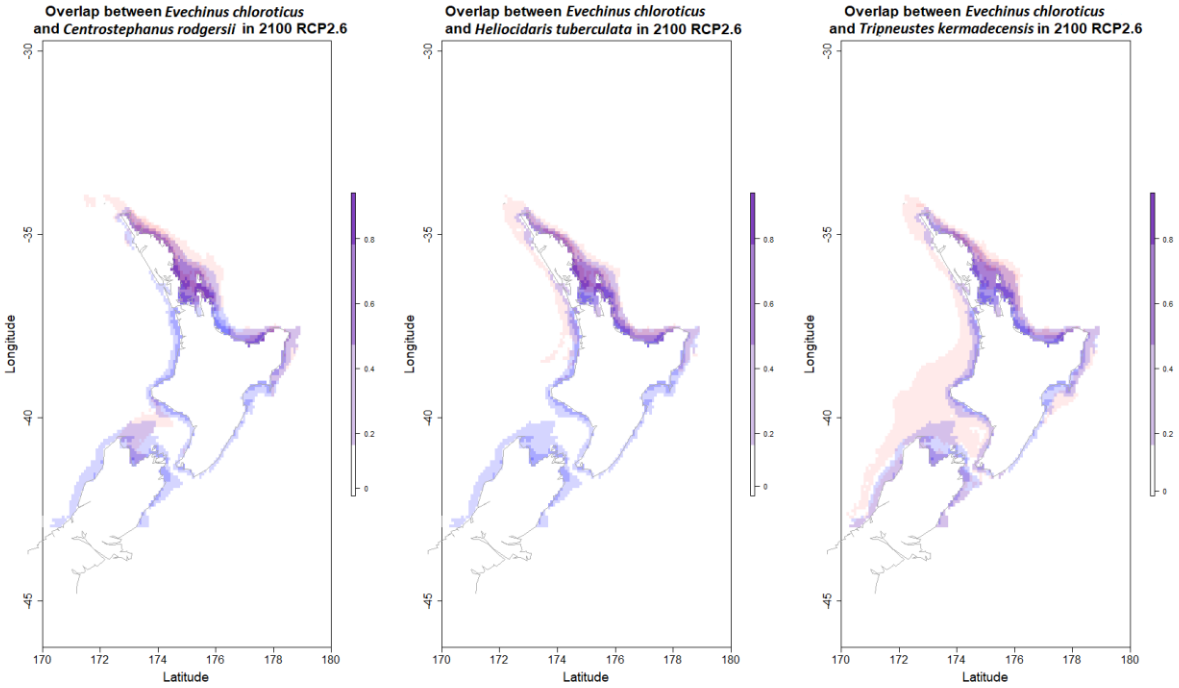
weighted mean for *Tripneustes kermadecensis* 2100 RCP 4.5

weighted mean for *Evechinus chloroticus* 2100 RCP 4.5

Appendix 4. Maps showing the predicted future distributions under the worst-case climate scenario (RCP 4.5) of the four urchins' species, high probability of occurrence is shown as green and low probability of occurrence is shown as orange.

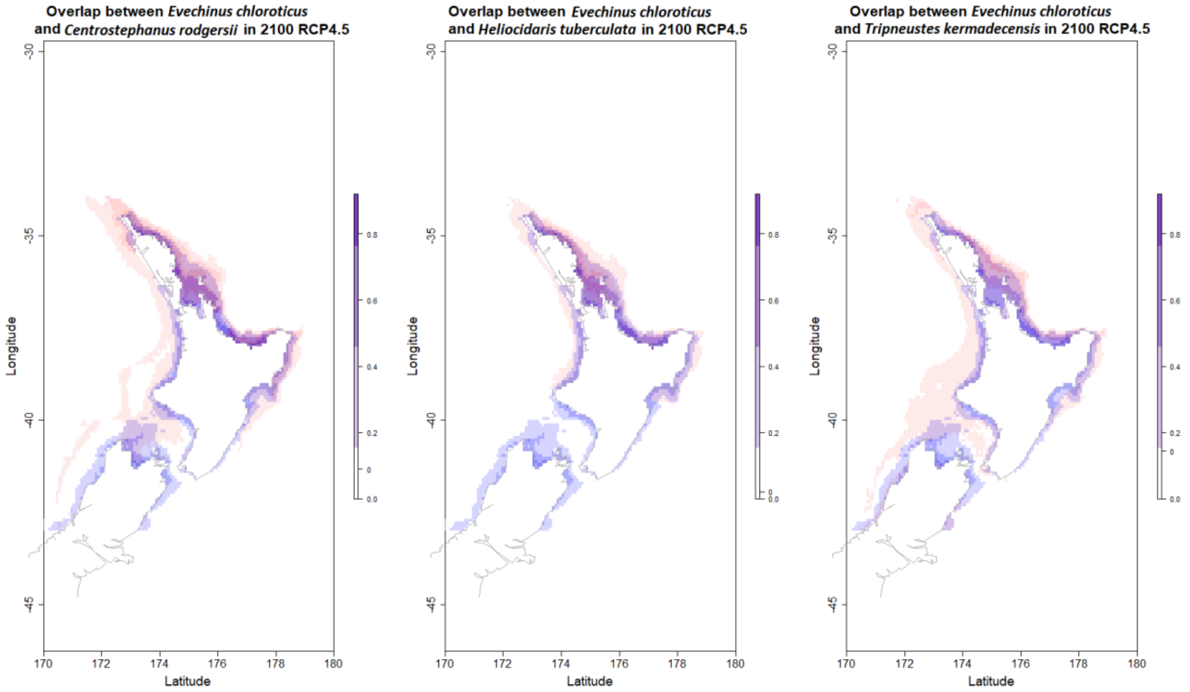


Appendix 5. Maps showing the predicted future distributions under the worst-case climate scenario (RCP 6.0) of the four urchins' species, high probability of occurrence is shown as green and low probability of occurrence is shown as orange.



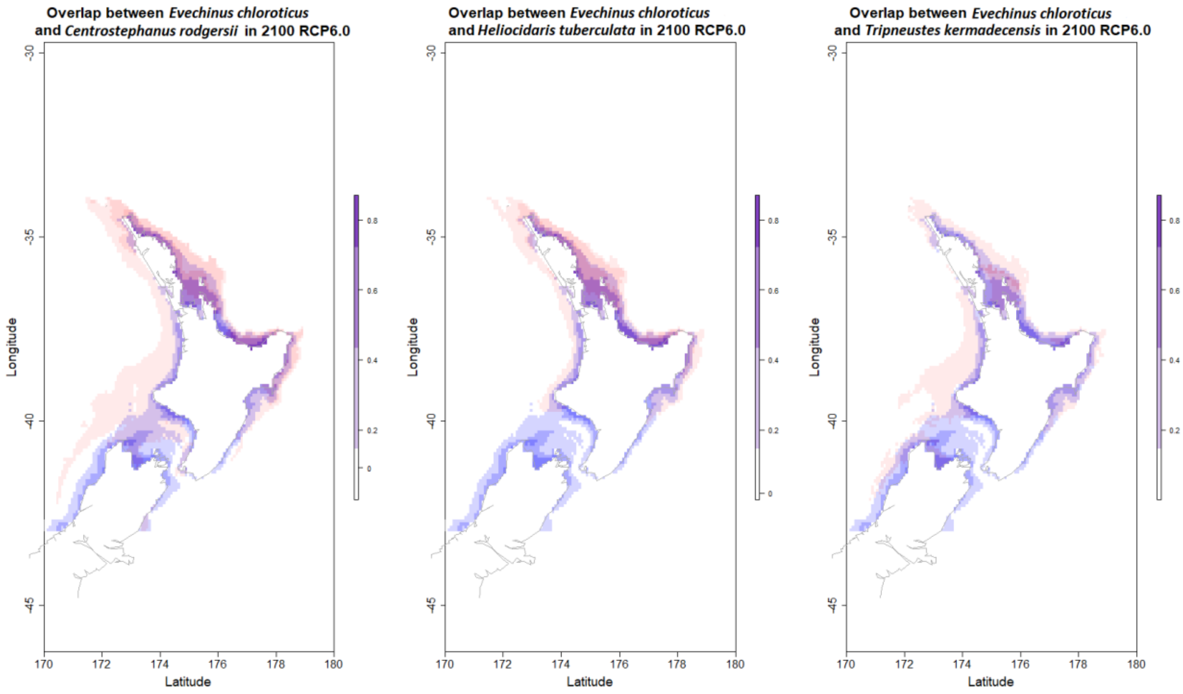
Appendix 6. Map showing the future overlap under RCP 2.6 between the three subtropical species and Evechinus chloroticus.

Evechinus chloroticus has been plotted in blue at 50% opacity while the subtropical species have been plotted in red at 50% opacity; areas of overlap are shown as purple, darker purple indicates where the two species are more likely to overlap, while red and blue areas show where only one species is present.



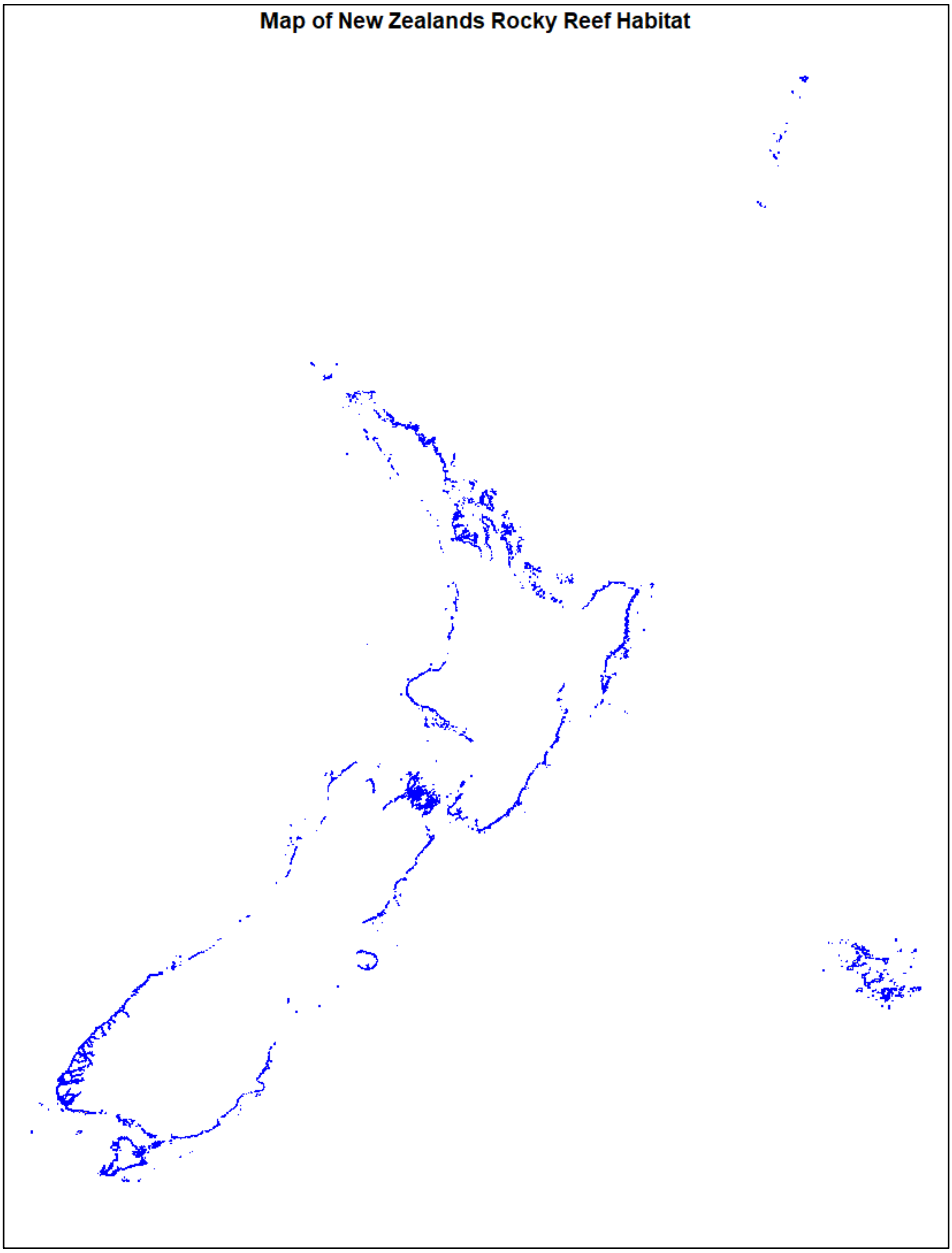
Appendix 7. Map showing the future overlap under RCP 4.5 between the three subtropical species and Evechinus chloroticus.

Evechinus chloroticus has been plotted in blue at 50% opacity while the subtropical species have been plotted in red at 50% opacity; areas of overlap are shown as purple, darker purple indicates where the two species are more likely to overlap, while red and blue areas show where only one species is present.

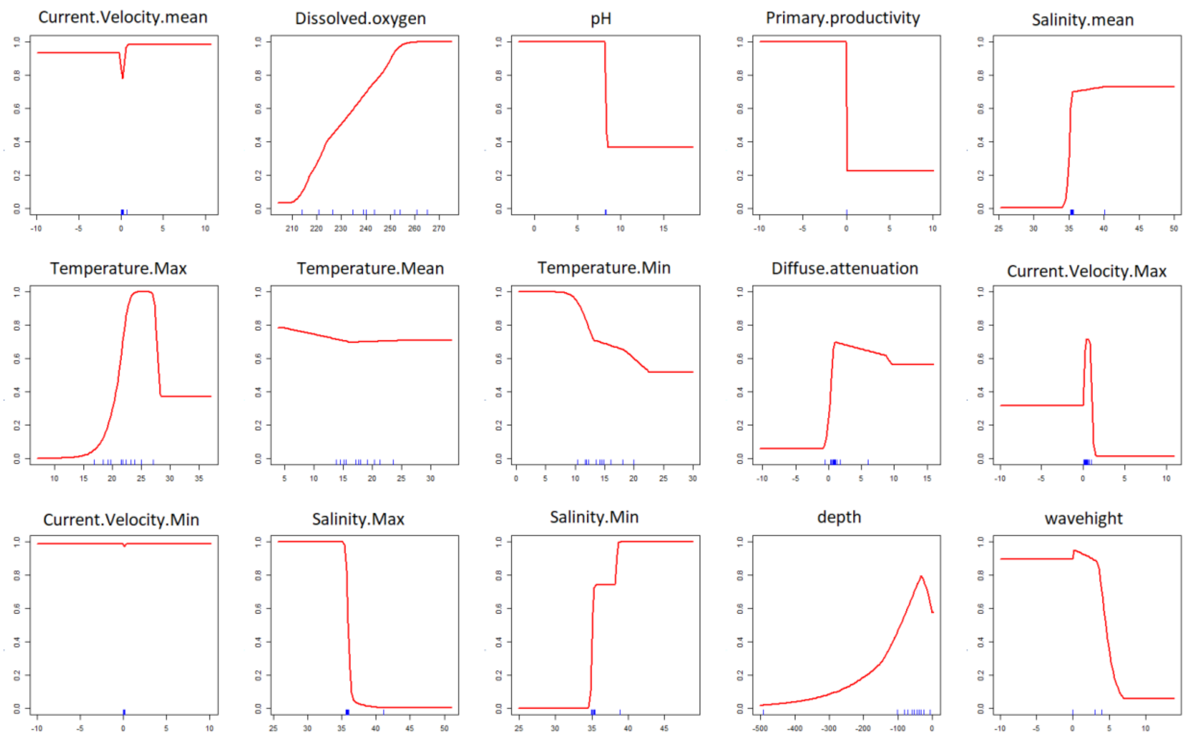


Appendix 8. Map showing the future overlap under RCP 6.0 between the three subtropical species and Evechinus chloroticus.

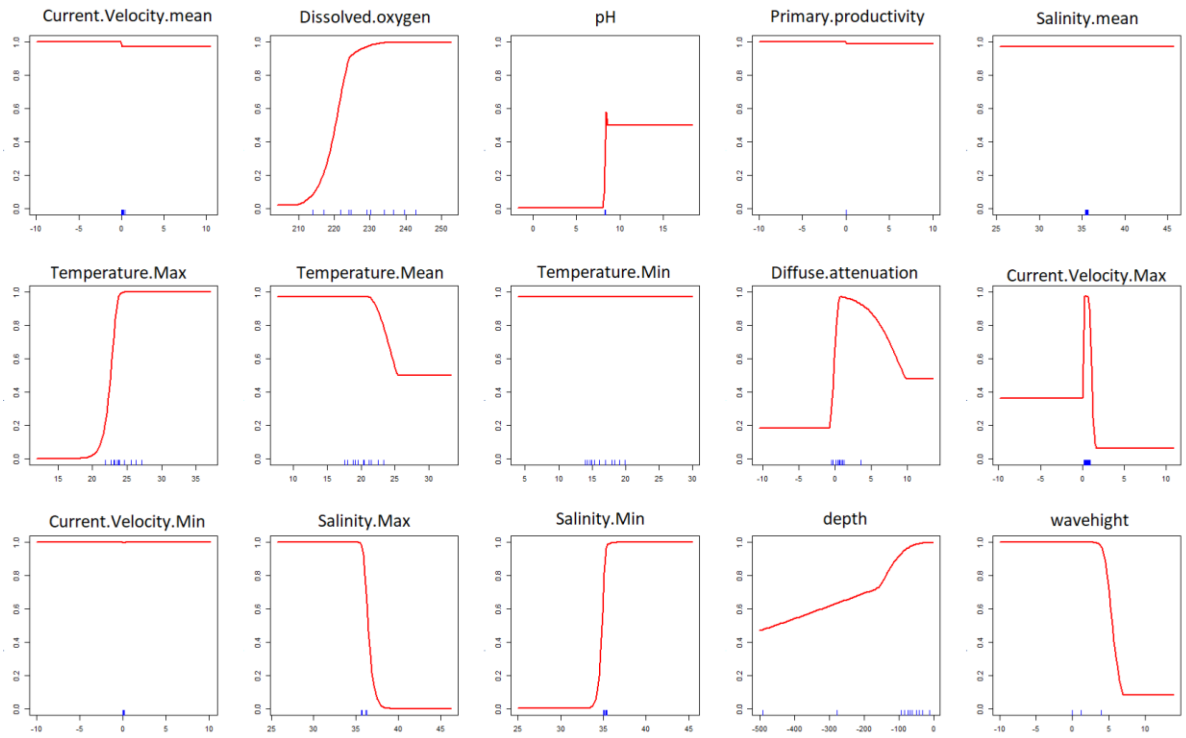
Evechinus chloroticus has been plotted in blue at 50% opacity while the subtropical species have been plotted in red at 50% opacity; areas of overlap are shown as purple, darker purple indicates where the two species are more likely to overlap, while red and blue areas show where only one species is present.



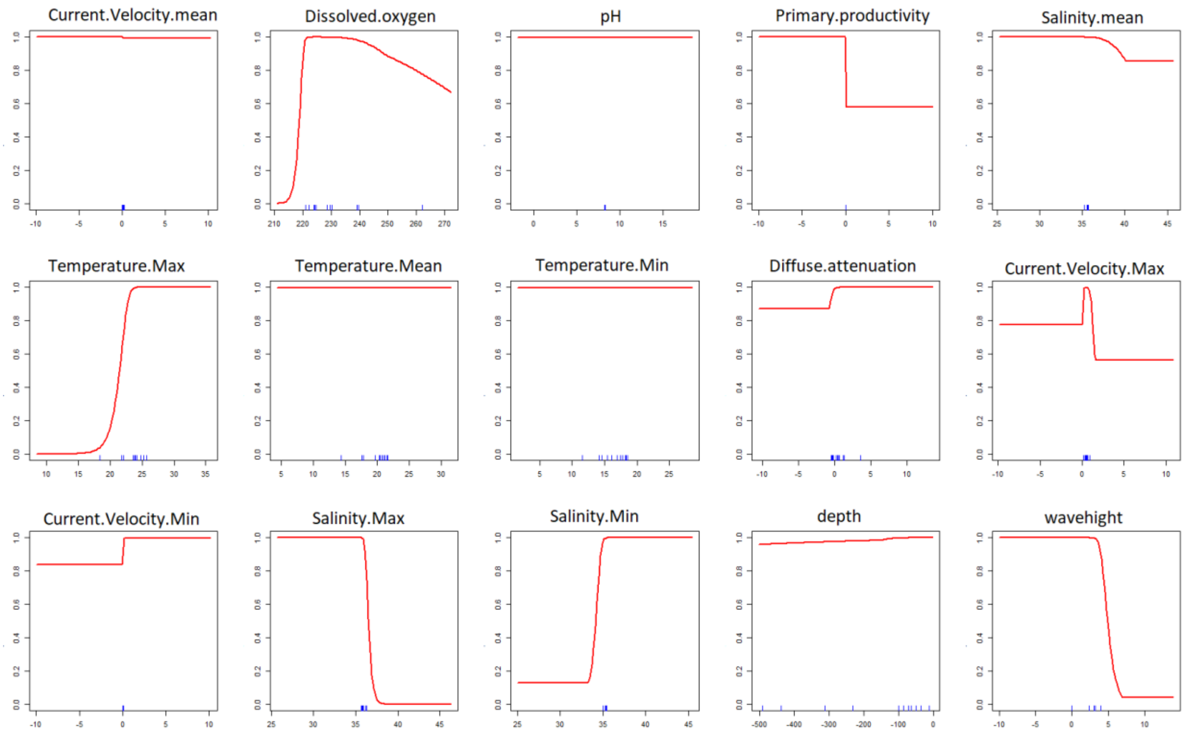
Appendix 9. Map showing the distribution of shallow rocky reefs around mainland New Zealand, Rangitāhua and the Chatham Islands



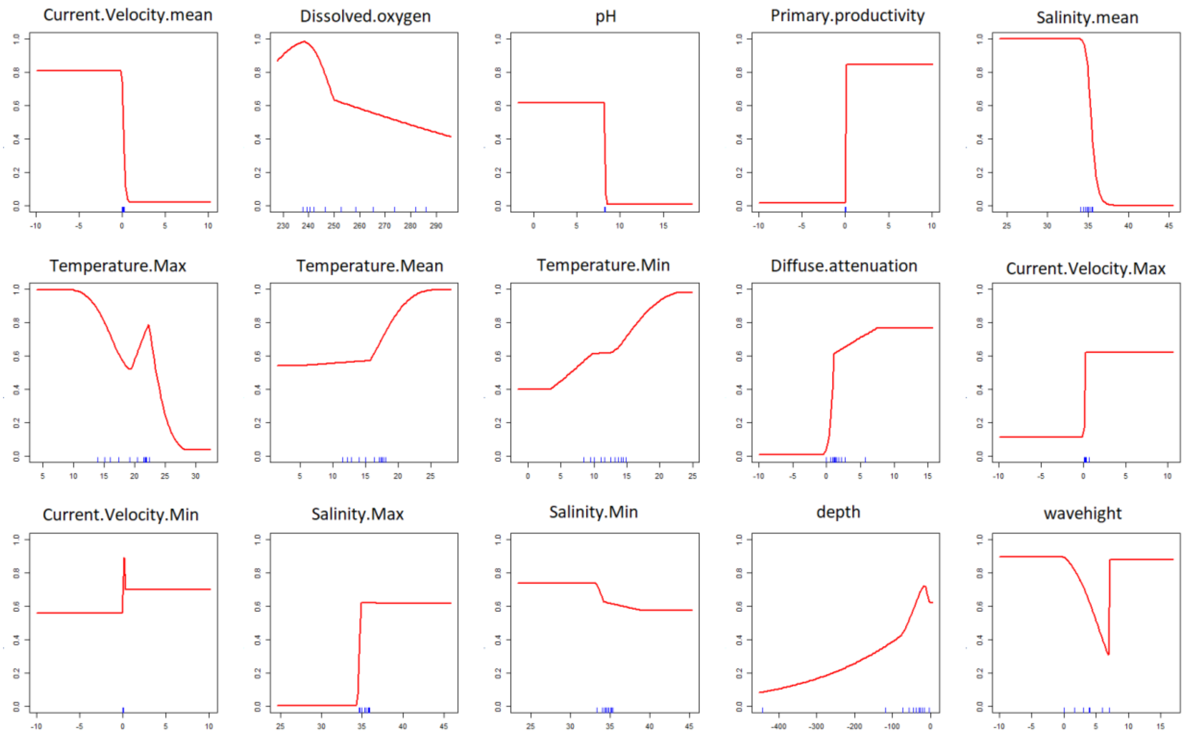
Appendix 10. Response curves for the environmental variables in the MaxEnt model for *Centrostephanus rodgersii.*



Appendix 11. Response curves for the environmental variables in the MaxEnt model for *Heliocidaris tuberculata.*



Appendix 12. Response curves for the environmental variables in the MaxEnt model for *Tripneustes kermadecensis.*



Appendix 13. Response curves for the environmental variables in the MaxEnt model for *Evechinus chloroticus.*