

PUSHING BOUNDARIES OF
RANGE AND RESILIENCE:
A REVIEW OF RANGE-EXTENSION BY A
BARRENS-FORMING SEA URCHIN

SCOTT D. LING

CLIMATE CHANGE PERSPECTIVES FROM THE ATLANTIC:
PAST, PRESENT AND FUTURE

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ABSTRACT

The barrens-forming sea urchin *Centrostephanus rodgersii* (Diadematidae) has undergone recent poleward range-extension to the Tasmanian coastline (SE Australia). By compiling field observations (including SST spanning >60yrs), broad-scale surveys and manipulative experiments conducted during the past decade, this review details knowledge on the response of this key sea urchin species to climate change and dually explores multiple processes influencing the ultimate ecological consequence of catastrophic-shift from productive kelp beds to urchin barrens, as now observed within the range-extension region. As a result of changing regional climate, eastern Tasmania has become increasingly suitable for *Centrostephanus* larval development with the timing of the sea urchins' arrival, age-structure and spatial distribution across the extension-region consistent with patterns in warming sea temperatures and current-driven dispersal potential. Furthermore, consistency in temperature dependency of larval development plus lack of genetic differentiation of the species across its entire range, confirm the critical role of changing climate in driving the range-extension.

Continued warming predicted for this region will favour increased larval survival, promoting ongoing population expansion and ultimately increased likelihood of populations reaching sufficient density to affect widespread overgrazing. As such, knowledge of patterns and mechanisms promoting overgrazing are also reviewed for the purpose of identifying kelp beds at greatest risk given climate trends, reef substratum types and predator abundance (chiefly spiny lobsters) as influenced by intense fishing pressure. Finally, this review shows how management of non-climatic local scale stressors can be used to increase resilience of kelp beds against overgrazing given large-scale climate-driven increases in key sea urchin populations.

KEYWORDS: Climate change, *Centrostephanus rodgersii*, kelp beds, sea urchin barrens, marine reserves, resilience.

INTRODUCTION

Global climate change is a mechanism that has already resulted in, and is predicted to further lead to widespread re-distribution of marine species ranges (e.g., Harley *et al.*, 2006; Poloczanska *et al.*, 2007). Consistent with the expectations of climate warming and effects on terrestrial systems, the general tide of change among marine species also involves pole-ward shifts in species distributions (reviewed by Przeslawski *et al.*, 2012). However, different to terrestrial sys-

tems, distributional patterns of marine organisms appear strongly coupled with ocean current systems that not only transport the species themselves, but also their respective thermal envelope (Sunday *et al.*, 2012). Thus shifts in the natural ranges of marine species appear heavily bound by dispersive capacity governed by ocean currents (Ling *et al.*, 2009a).

While there is a growing list of species documented to be on the move as a result of changing environmental conditions attributable to anthropogenic climate, an important feature of species re-distributions is that many documented range-shifters (e.g. Last *et al.*, 2010; Johnson *et al.*, 2011) seemingly either remain in a cryptic existence or never reach high abundance; either appearing as vagrants or establishing a presence in a novel area but being of negligible or inconspicuous consequence to overall ecosystem dynamics. Other species however, can be far more conspicuous in their arrival, not only because of their conspicuous size, shape or colour but because of their ecological function. Of profound consequence are shifts among species capable of directly or indirectly modifying habitats causing fundamental change within recipient ecosystems by impacting important species interactions and having flow-on effects to broader ecosystem dynamics (Ling, 2008).

In the southern hemisphere, the south eastern coast of Australia has been identified as a climate change hotspot (Poloczanska *et al.*, 2007; Ridgway, 2007). Here the East Australian Current (EAC) has strengthened resulting in greater poleward penetration of warm water over the past 60 years and an approximate quadrupling of ocean warming rates compared to the global ocean average (Ridgway, 2007). This pronounced change in the physical oceanography of the region, an approximate 350 km southward shift of a major current system, corroborates with a series of recent poleward range extensions (reviewed by Poloczanska *et al.*, 2007; Last *et al.*, 2010; Johnson *et al.*, 2011); with changes in both advective patterns and increased water temperature suggested as direct drivers of range extension in the world's oceans (e.g., Harley *et al.*, 2006). The physical and biological expression of changes in the dynamics of the EAC is clearly evident on the east coast of Tasmania where oceanographic data reveal rising water temperature and salinity due to this feature (Ridgway, 2007; Johnson *et al.*, 2011) and where species typical of warmer northern waters now occur (e.g., Edgar, 1997; Poloczanska *et al.*, 2007; Last *et al.*, 2010; Johnson *et al.*, 2011). Indeed the response of marine biota attributable to the changing climate of the region is striking with a documented 45 coastal fish species, (30%) of fishes in the region, considered to have shifted distribution southwards relative to historical records (Last *et al.*, 2010; reviewed by Johnson *et al.*, 2011). Here intertidal species have also been documented to have undergone similar rates of range-extension at southern margins (Pitt *et al.*, 2010).

Of all the species recently documented to have undergone range extension to eastern Tasmania, the sea urchin *Centrostephanus rodgersii* (Agassiz) is arguably the most conspicuous and ecologically important due to its ability to overgraze kelp beds and maintain an alternative and stable barrens habitat (Andrew and

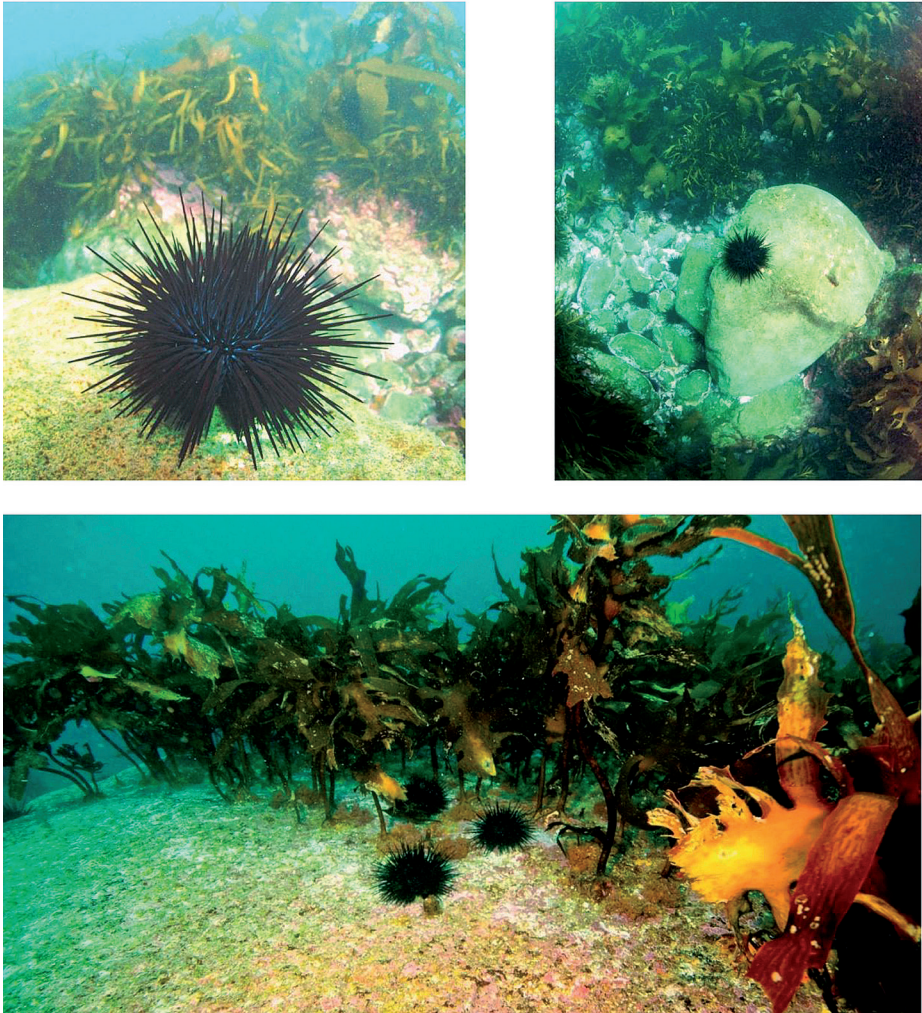


Figure 1. Patterns of overgrazing by the sea urchin *Centrostephanus rodgersii* in eastern Tasmania. Top left image is a close-up of *C. rodgersii* (test diam. of 100 mm) at a depth of 6 m at North Bay, south east Tasmania. Top right image is a planar view of a small incipient barrens patch (after Johnson *et al.*, 2005) grazed within an otherwise healthy kelp bed (dominated by *Ecklonia radiata*), North Bay. Lower image shows *C. rodgersii* grazing among kelp beds (*E. radiata*) at the edge of an extensive barrens ground (10^5 m² in size) ranging from 40 to 10 m depth at Sloop Rock, north east Tasmania, February 2011. Here, kelp beds have been documented to retreat (as a result of sea urchin overgrazing) by an average of ~1.25 metres over the period 2008 to 2011. Photography credits to the author.

Byrne, 2001; Hill *et al.*, 2003; Ling, 2008). Indeed within temperate Australia, no other benthic herbivore has as large an effect on shallow reef communities as *C. rodgersii* (Fletcher, 1987; Andrew, 1991; Andrew and Underwood, 1992; Ling, 2008). Thus its arrival to Tasmania is considered the single biggest threat to the structure and function of rocky reefs in Tasmania (Johnson *et al.*, 2005, 2011). In central and southern New South Wales (NSW) this species maintains barrens habitat over ~50% of shallow reef (Andrew and O'Neill, 2000) and observations from within Tasmania show that such levels of impact are now observable at some sites within the extended eastern Tasmanian range. Indeed, such is the impact of *C. rodgersii* on reef biodiversity that overgrazing by this single species results in localised losses of ~150 taxa that associate with Tasmanian kelp beds (Ling, 2008; see also Fig. 1). Thus population expansion and continued overgrazing by *C. rodgersii* within the range-extension region poses a major threat to rocky reef biodiversity generally (Ling, 2008) - particularly for those endemic species with very limited scope for migration given a lack of contiguous poleward landmass - but also specifically threatens lucrative commercial species dependent on kelp bed habitat including black-lip abalone and southern rock lobster (Andrew and Underwood, 1992; Andrew *et al.*, 1998; Worthington *et al.*, 1998; Johnson *et al.*, 2005; Strain and Johnson, 2009; reviewed by Johnson *et al.*, 2011).

Here I review the environmental, physiological and spatial context of the sea urchins' range extension to eastern Tasmania. Following the theme, "impacts of key sea urchin populations from larvae to ecosystems" this chapter first explores key features of the sea urchins early life history stages and moves toward the dynamics of kelp bed overgrazing and formation of extensive barrens ground. Finally, this review details how management of non-climatic stressors on rocky reefs can increase resilience of kelp beds against overgrazing given large-scale climate-driven increases in this key sea urchin population.

FEATURES OF A MARINE RANGE-EXTENDER

Belonging to a tropical sea urchin family the Diadematidae, the presence of *Centrostephanus rodgersii* in the cool temperate waters of Tasmania - where it is found grazing beneath *Macrocystis pyrifera* beds and adjacent to cold water bull 'kelp' *Durvillea potatorum* (Fucales) - may be considered anomalous. However, like its well-known tropical Diadematid relatives, the role of *C. rodgersii* as a key herbivore capable of effecting change at the scale of entire reef-scapes is by no means anomalous. Globally the distribution of *C. rodgersii* is constrained to the southwest Pacific where this large sea urchin (growing up to 133 mm TD and over 600 grams in wet weight) is conspicuously found on sub-tidal rocky reefs in south eastern Australia, Lord Howe Island, Norfolk Island, the Kermadec Islands (Schiel *et al.*, 1986) and in northern New Zealand (reviewed by Andrew and Byrne, 2007). Indeed this biogeographical distribution in itself hints to an important role of

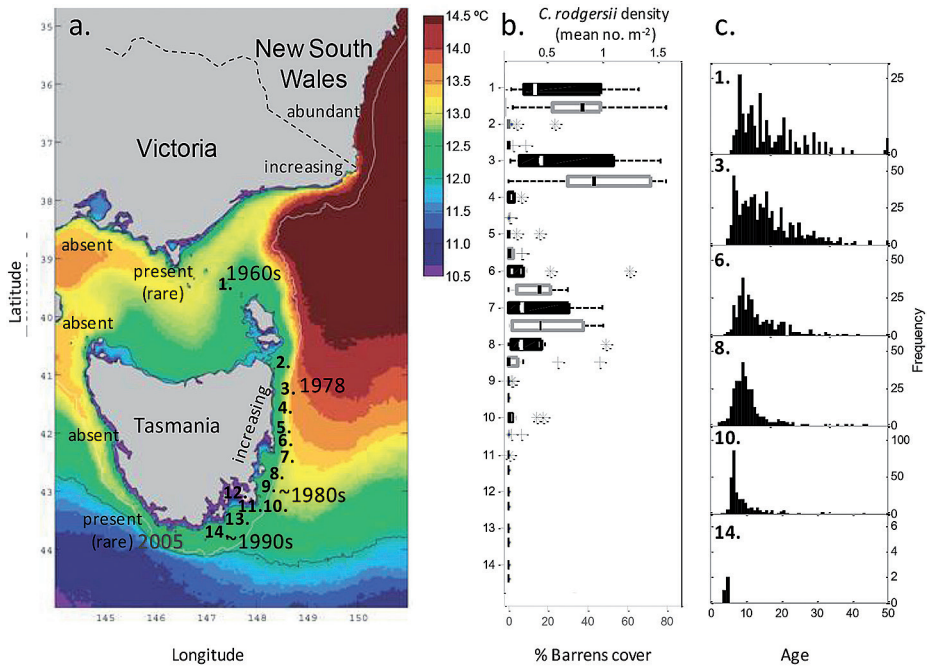


Figure 2. (a.) Map of south eastern Australia showing the dominant influence of the warm East Australian Current in eastern Tasmania during Austral winter (June–August averaged for the period 1993–2007) plus year of first discovery of *Centrostephanus rodgersii* along the coast is displayed as well as numbers showing sites (ordered north to south) where (b.) *C. rodgersii* density (black boxes) and barrens cover (grey open boxes) and (c.) age structure was assessed (survey of density and barrens conducted in 2000–2002 by Johnson *et al.*, 2005 and age assessment in 2005 by Ling *et al.*, 2009a). Both (b.) and (c.) reflect initial colonization in the north east and support the notion of recent range expansion mediated by increasing southward advection of larvae and heat.

the western boundary current, the East Australian Current (EAC), in defining the sea urchins range. Essentially the presence of *C. rodgersii* in south eastern Australia (Fig. 2a) and the south west pacific in general intuitively maps to where the various eddies of the EAC flow proximal to landmasses (Banks *et al.*, 2007).

Within Australia, the distribution of *C. rodgersii* is centred on the coast of NSW but the sea urchin is also found in high abundance in far eastern Victoria, on some of the eastern Bass Strait islands (i.e. Kent Group of Islands) and as is specifically reviewed here, the sea urchin has become progressively more abundant along the east coast of Tasmania (Johnson *et al.*, 2005). Notably, reports from abalone fishers also suggest a similar increase in *C. rodgersii* abundance in

eastern Victoria and the population in northern New Zealand is also referred to as newly established (Pecorino, 2012; Pecorino *et al.*, 2013).

TIME-LINE OF DISCOVERY

Undergoing a poleward range extension from NSW, *C. rodgersii* was first recorded in the Kent Grp. in the late 1960s; north east mainland Tasmania in 1978; south eastern Tasmania in mid-1980s; and south western Tasmania in 2005 (Fig. 2). Since first detected in Tasmania (Dartnall, 1980), the sea urchins' abundance has increased and expansive barren areas now occur in some locations (Johnson *et al.*, 2005, 2011). Long-term observations in the Kent Grp. (Site 1, Fig. 2a) indicate initial establishment in the 1960s followed by a progressive spread to 2 of 7 survey sites in 1974; 3 of 9 sites in 1981 when urchin barrens were first recorded at a single site; to ultimately extensive urchin barren grounds being recorded at 7 of 7 sites surveyed in 2000 (Johnson *et al.*, 2005, 2011). A baseline survey in 2001/2002 confirmed the presence of *C. rodgersii* throughout eastern Tasmania revealing a patchy distribution but clear overall trend of decreasing abundance from north to south along this coastline (Johnson *et al.*, 2005; see Fig. 2a). But moreover the ecological effects of this sea urchin had become manifestly obvious with extensive barren grounds being found in the north east at St. Helens (site 3, Fig. 2a), the location where the sea urchin was first documented on mainland Tasmanian reefs 1978 (Edgar, 1997).

Across this extended range, the mean population age of *Centrostephanus rodgersii* becomes progressively younger towards the poleward range limit (Fig. 2). Such an age dynamic is consistent with the historical time-course of sequential poleward discoveries and expansion of *C. rodgersii* populations across eastern Tasmania, which has occurred at a rate of ~ 160 km decade⁻¹ over the past 40 years (Ling *et al.*, 2009a, see Figure 2a-c). The sequential poleward discovery of the sea urchin, a pattern of declining age and a general poleward reduction in abundance along the eastern Tasmanian coastline is consistent with a model of range-extension driven by recent change to patterns of larval dispersal driven by change in the EAC. At the ecosystem level, the effects of grazing, as indicated by the percentage cover of sea urchin barrens, approximates the pattern in abundance of *C. rodgersii* along the eastern Tasmanian coast (Fig. 2b). Notably the described grazing impact is clearly due to grazing of the range-extending sea urchin *C. rodgersii* (Johnson *et al.*, 2005; Ling and Jacques, 2009) and not the native sea urchin *Heliocidaris erythrogramma* (Echinometridae) - which forms barrens on sheltered inshore reefs (Ling *et al.*, 2010) but constitutes negligible overall grazing impacts on fully exposed reefs in eastern Tasmania where *C. rodgersii* and its grazing impacts predominantly occur (Fig. 2b).

MECHANISMS OF RANGE-EXTENSION

While migration of benthic adult phases among sea urchins is generally very limited (*C. rodgersii* remain highly localised on rocky reefs whereby they undergo defined nocturnal homing movement [Andrew and Byrne, 2001; Williams *et al.*, 2009; Flukes *et al.*, 2012]), the key life-history stage facilitating long-distance dispersal of sea urchins is the larval phase. For the dioecious free-spawning *C. rodgersii*, adults spawn gametes into the water column where fertilisation occurs (King, 1992; Huggett *et al.*, 2005). Fertilised eggs then rapidly develop into a long-lived two-armed planktotrophic larval stage that exists in the water column for ~100 days before settling to reef substratum (Huggett *et al.*, 2005; reviewed by Byrne and Andrew, in press). This feature of the *C. rodgersii* life-cycle (indeed the common planktonic strategy among echinoids) facilitates long distance dispersal in oceanographic currents. Thus, logically it is likely that the southward incursion of *C. rodgersii* in eastern Tasmania has occurred due to increased larval dispersal driven by changes to patterns of the EAC (as originally raised by Dartnall, 1980).

Within the NSW range, *C. rodgersii* displays a seasonal cycle in gamete production with the major spawning activity occurring in winter (King *et al.*, 1994; Byrne *et al.*, 1998). Given the cooler water temperatures in eastern Tasmania (winter min. ~11 °C) relative to NSW (winter min. ~14°C), the ability of *C. rodgersii* to develop functional gonads, viable gametes and undergo normal larval development was thought to be compromised in the cooler Tasmanian environment. Indeed, Dartnall (1980) interpreted the discovery of *C. rodgersii* in north eastern Tasmania as perhaps a temporary range-extension at the southern distributional limit, clearly articulating that “We await evidence that this population is reproductively self-maintaining...”. Thus a situation whereby *C. rodgersii* undergoes annual reproduction in eastern Tasmanian waters will likely facilitate a much more rapid population expansion and opportunity for secondary spread than if Tasmanian populations are only maintained by vagrant pulses of larvae brought south via the EAC (see Fig. 2). Hence initial research on the biology of *C. rodgersii* within the range extension region involved examining evidence for reproductive capability by sampling for the existence of a reproductive cycle, an ability to produce functional gametes and to undergo successful larval development.

REPRODUCTION ON THE EDGE

Demonstrating a clear annual reproductive cycle for *Centrostephanus rodgersii*, sampling of gonad somatic indices (GI) at 4 eastern Tasmanian locations over an 18 month period (Oct 2003 to March 2005, at a 2 month sampling interval) revealed a consistent and defined rise and fall in gonad condition (Fig. 3). As evidenced by a defined drop in GI and maximal response of populations to artificial spawn induction, spawning was isolated to occur during winter with major

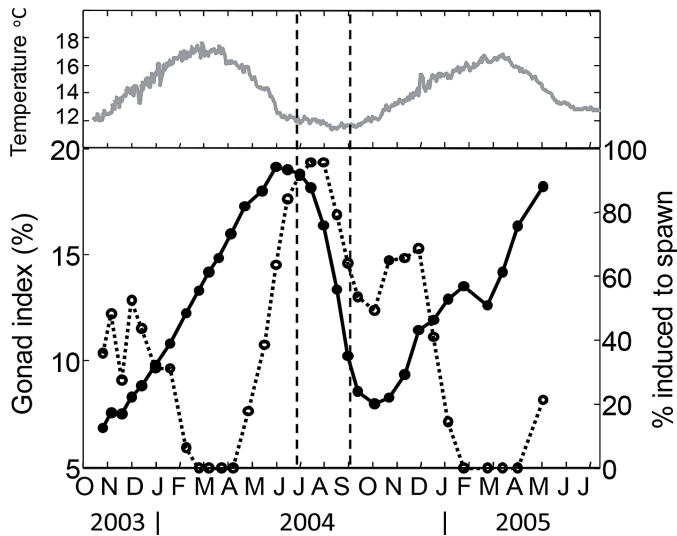


Figure 3. Reproductive cycle of *Centrostephanus rodgersii* as revealed by gonad index and the propensity of population to spawn (following artificial induction) in eastern Tasmania, Oct 2003 - Jun 2005. Smoothed cycles of gonad index (solid line) and % induced to spawn (dotted line) represent a 4 sample running mean calculated across 4 sites spanning the Tasmanian east coast (after Ling *et al.*, 2008). Gonad index was calculated from 30 individuals per sample, while propensity to spawn was calculated for each sample as the percentage of 10 individuals responding to spawn induction. Area within the dotted vertical lines indicates the major period of spawning. Top panel shows water temperature on the benthos throughout the sampling period (pooled across for 4 monitoring sites - St. Helens, Bicheno, Maria Is. and Tasman Peninsula; note temperature data prior to 23-Nov-2004 is daily mean for NE Tasmania only).

spawn-out occurring in the month of August (Fig. 3). In addition, the distribution of *C. rodgersii* sexes at each site and for eastern Tasmania as a whole did not deviate significantly from a 1:1 sex ratio (Ling *et al.*, 2008).

Given uncertainty surrounding viability of *Centrostephanus rodgersii* gametes spawned during the coldest month of the year at the cold range limit, fertilization trials were run to test gamete viability. Experiments revealed gametes to be viable, with eggs readily fertilised during the peak winter spawning period, with only a relatively subtle effect of temperature across the cooling gradient from 20 to 8°C (Fig. 4a). Embryonic and larval development for fertilized Tasmanian eggs was normal and the 2-arm pluteus stage was readily reached. While there was a small increase in fertilisation rate with increasing temperature (with 95-99 % fertilized), variation around this trend was large and thus temperature was

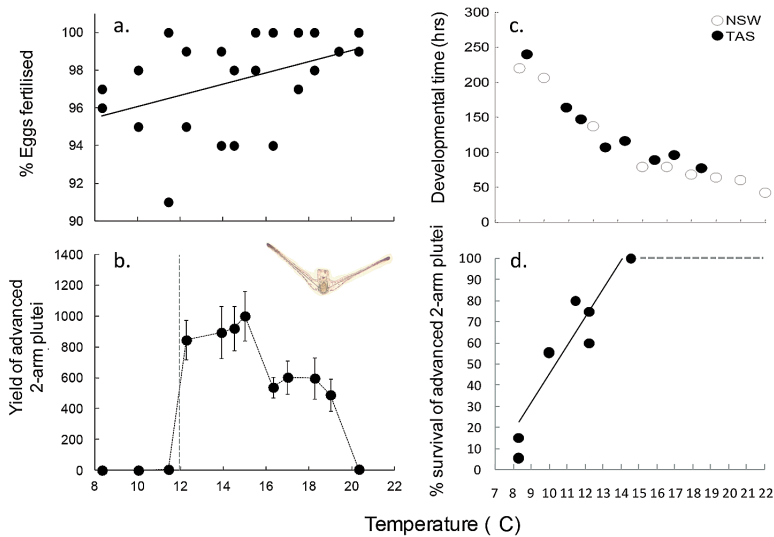


Figure 4. (a.) Temperature dependent fertilisation rates of Tasmanian *Centrostephanus rodgersii*. Data are means for 100 randomly selected eggs from 2 replicate trials, \pm SE. While linear regression revealed a significant positive trend (treatment: $F_{1,10}=18.29$, $P=0.0016$), the fit was relatively poor ($R^2=0.65$) and the size of the effect small ($y = 0.297x + 93.10$; $F_{1,22} = 5.26$, $P<0.05$; $y = 0.30x + 93.10$; $R^2 = 0.19$). (b.) Temperature dependent yield of advanced 2-arm plutei of Tasmanian *Centrostephanus rodgersii*. Data are relative yields of advanced 2-arm plutei generated at each temperature treatment expressed as a percentage of the total number of advanced 2-arm plutei produced per trial (means \pm SE of $n=3$ trials); image is of a 2-arm pluteus larva at 21 days post fertilisation (scale bar = 200µm). (c.) Development time to early 2-arm plutei versus water temperature for Tasmanian and NSW reared *Centrostephanus rodgersii* (after Ling *et al.*, 2008). (d.) Survival of 25 day old 2-arm pluteus larvae reared at 14.5°C and placed into a temperature gradient from 14.5 to 8.3°C; $n= 2$ replicate vials with 20 individual larvae per temperature, survival assessed at 17 days post assignment to temperature treatments (larval rearing as per Ling *et al.*, 2008); solid line is linear fit, $y = 13.52x - 90.36$, $R^2=0.85$; $F_{1,8}=46.93$, $P<0.001$; dashed horizontal line extrapolates high survival across temperature range of 14 to 19°C, note that due to evidence of heat shock for the 20°C treatment (b.), this treatment was excluded from (c.) and hence 100% survival was not extrapolated beyond 19°C in (d.).

considered to have relatively small biological effect on fertilization success over the 8-20 °C range examined (Fig. 4a) – although could magnify greatly in absolute terms given the total number of eggs released into the water column per individual female during spawning; which is likely in the order of 10-100 million eggs as reported for other echinoids (e.g., McShane *et al.*, 1996). But much more striking was a clear threshold type response for the effect of water temperature

on development, with essential no successful development to 2-arm plutei occurring in cultures below 12 °C (Fig. 4b).

The observation that Tasmanian *C. rodgersii* undertook spawning in water temperature below 12 °C in 2004 (Fig. 3) was intriguing given that gametes were released into a temperature environment unsuitable for successful larval development. Such a seemingly counter-productive strategy strongly suggested that *C. rodgersii* reproductive phenology had not undergone adaptive shift but was rather controlled by factors other than temperature. Such a notion was supported by research within the NSW range where consistencies in the timing of spawning of *C. rodgersii* occurred across 9 degrees in latitude even though large temperature gradients were present over this range (Byrne *et al.*, 1998). Photoperiod coinciding with the winter solstice appears as a likely proximate factor cuing the onset of spawning across this broad geographic range (Byrne *et al.*, 1998 and references therein), as has been found in other closely related echinoid species (e.g., Kennedy and Pearse, 1975; Coppard and Campbell, 2005). Not only indicating a lack of shift in phenology, a lack of acclimation for *C. rodgersii* within the extended range was also clearly indicated upon examination of the temperature dependency of larval development rate for Tasmanian and NSW larvae. That is, larvae from both NSW and eastern Tasmania showed no difference in developmental rates across temperature (Fig. 4c).

Simulating larvae spawned under normal winter conditions towards the southern margins of the NSW range, i.e. 14°C, advanced plutei larvae showed a pattern of reduced survival when transferred to cooler temperatures as anticipated to occur when larvae are advected south by the EAC to interact with cooler eastern Tasmanian coastal waters (Fig. 4d). That is, while larvae did not develop to advanced stages at temperatures < 12°C, larval survival of advanced plutei was also slightly compromised when larvae grown under warmer conditions, were exposed to cooler temperatures. Furthermore, while larvae were observed to develop to the advanced 2-arm stage above 12°C, survival of larvae grown at 14°C was indeed reduced (by ~20%) when these larvae, typical of NSW waters, were transferred to lower temperature (Fig. 4d). But note that given a 3 month planktonic developmental time, larvae spawned in conditions of 14°C during winter off NSW would likely interact with slightly warmer water (~13°C) relative to winter minima when arriving in eastern Tasmania by ~October.

Of note, recent work by New Zealand researchers identified the optimal temperature range for *C. rodgersii* larval development to be between ~17-23.5°C; which was essentially identical to that observed by the same researchers for *C. rodgersii* at Coffs Harbour in central NSW (Pecorino, *et al.*, 2013). Such a result seemingly contrasts with the above patterns of temperature dependency previously described for larvae from Tasmania and mid NSW whereby larvae were observed to develop to advanced plutei stage at temperatures as low as 12°C, albeit at a slower rate (Ling *et al.*, 2008). Notably, yields of Tasmanian 2-arm plutei crashed above 19 °C (Fig. 4b), suggesting the presence of heat shock at >~7 °C above am-

bient temperature. But moreover, for Tasmanian larvae, maximum yields were observed at $\sim 15^{\circ}\text{C}$ (Fig. 4b) and the optimal temperature range (as determined by rate of development) was $\sim 15\text{--}19^{\circ}\text{C}$ (Fig. 4c) indicating slight differences for development of early life history stages in cold environments. Importantly, while larval development occurs above 12°C , larval performance and survival of *C. rodgersii* larvae spawned within and advected to cooler Tasmanian waters (Fig. 4d) will indeed increase if winter sea temperatures warm above 12°C .

NO EVIDENCE FOR A GENETIC BOTTLENECK

Supporting the lack of difference observed for vital physiological rates of larval development between NSW and Tasmanian populations (Fig. 4c), investigation of *C. rodgersii* population genetics with allozyme and microsatellites revealed a lack of founder effect among the extended Tasmanian range as evidenced by low spatial genetic structure across the historical and range-extension zones (Johnson *et al.*, 2005, 2011; Banks *et al.*, 2010). That is, the range shift appears to be a poleward extension of the highly-connected range wide population of *C. rodgersii* involving continued advection and mixing of larvae from population centres within the native NSW range (Johnson *et al.*, 2005, 2011; Banks *et al.*, 2010). Suggesting that evidence for slight differences in thermal optima and heat shock responses between populations is phenotypic in nature (Ling *et al.*, 2008; see also Pecorino *et al.*, 2013). While there was a weak signal in genetic structuring across south east Australia, the underlying trend was for slightly reduced population-specific allele frequencies for the most southern populations in south-east Tasmania relative to central NSW populations (Banks *et al.*, 2010; Johnson *et al.*, 2005, 2011).

Genetic results therefore corroborate with the population age structure and patterns predicted from the vital physiological threshold for larval development across the extended range (Ling *et al.*, 2009a). That is, the broad range of *C. rodgersii* ages in north eastern Tasmania indicates that the range extension has not occurred as the result of a single, massive recruitment event. Rather, as supported by genetics (Johnson *et al.*, 2005, 2011; Banks *et al.*, 2010), age structure reveals multiple episodes of sea urchin recruitment with seemingly fewer and more recent recruitment events towards the southern limit of the extension-region (Fig. 2c). Thus combined, field, laboratory and genetic results support the recent nature of the *C. rodgersii* range-extension given that adaptive shifts to thermal tolerance would likely require many generations to evolve within the cooler Tasmanian environment. But moreover evidence for fixed temperature dependency of early development re-doubles the importance of environmental change in causing range-extension in this sea urchin species. That is, patterns of environmental change should largely determine the distribution and abundance of *C. rodgersii* and thus ultimately its abundance and propensity to cause widespread sea urchin barrens.

RESPONSE TO COASTAL WARMING

Long-term monitoring of sea surface temperature in eastern Tasmania has revealed an average warming of ~ 1.5 °C over the past 60 years, predominantly due to a greater influence of the EAC on this coast (Ridgway, 2007). Importantly, while the EAC is typically thought of as a summertime phenomenon, this warming trend in eastern Tasmania is also apparent during winter months, such that temperatures above the ~ 12 °C threshold for larval development are becoming frequent during the major spawning period (Fig. 5a) and are likely to arise with increasing frequency given anticipated ongoing coastal warming associated with global climate change (Cai *et al.*, 2005). Continued coastal warming will directly increase survival of *C. rodgersii* (Fig. 4d) plus also reduce overall larval development time (Fig. 4c) which may in turn enhance larval survival and increase the likelihood of self-recruitment of *C. rodgersii* within Tasmania due to decreased exposure to potentially hazardous planktonic conditions (e.g., Morgan, 1995).

Because eastern Tasmania represents the southern range extent where coastal waters are cold (~ 10 – 18 °C) relative to NSW (~ 13 – 25 °C), logically the observed distribution of *C. rodgersii* in Tasmania should track the moderating influence of the warm EAC along this coast (Ridgway, 2007; see Fig. 2a). Furthermore, any limiting effects of cold water on the development and survival of the sea urchin in Tasmania would most likely be felt during winter such that any temperature patterns driving distribution of *C. rodgersii* would likely manifest during winter. Indeed examination of *C. rodgersii* distribution with respect to winter water temperature revealed that the sea urchin generally occurs at sites existing above the 12 °C threshold. That is, examination of mean SST for 41 eastern Tasmanian sites during the known *C. rodgersii* spawning period of August (winter), revealed that the sea urchin is generally limited to sites experiencing relatively warm winter temperatures in eastern Tasmania (Fig. 5b). However, variability in this signal across warmer winter sites suggests that factors other than temperature *per se* are important in determining patterns in abundance such as reef habitat quality (particularly high relief boulder habitat where *C. rodgersii* is found in higher abundance and where the risk of predation is lower, Ling and Johnson, 2012), or there exists local barriers to dispersal of sea urchin larvae.

At local-scales in eastern Tasmania, *C. rodgersii* is observed to be abundant on headland areas with examination of sea temperature profiles revealing warmer winter temperatures at the local-scale of these features which demonstrated a greater proportion of winters > 12 °C relative to adjacent inshore sites where fewer or no *C. rodgersii* were established (Fig. 6a-c). Overall headlands expressed more moderate climates relative to inshore areas where seasonal temperature fluctuated with greater amplitude, with these shallower inshore environments appearing to be forced to a greater extent by seasonal atmospheric heating and cooling to become considerably warmer in summer but cooler in winter relative to headland sites (Fig. 6a-c). Closer to the EAC, headland sites were also more likely project

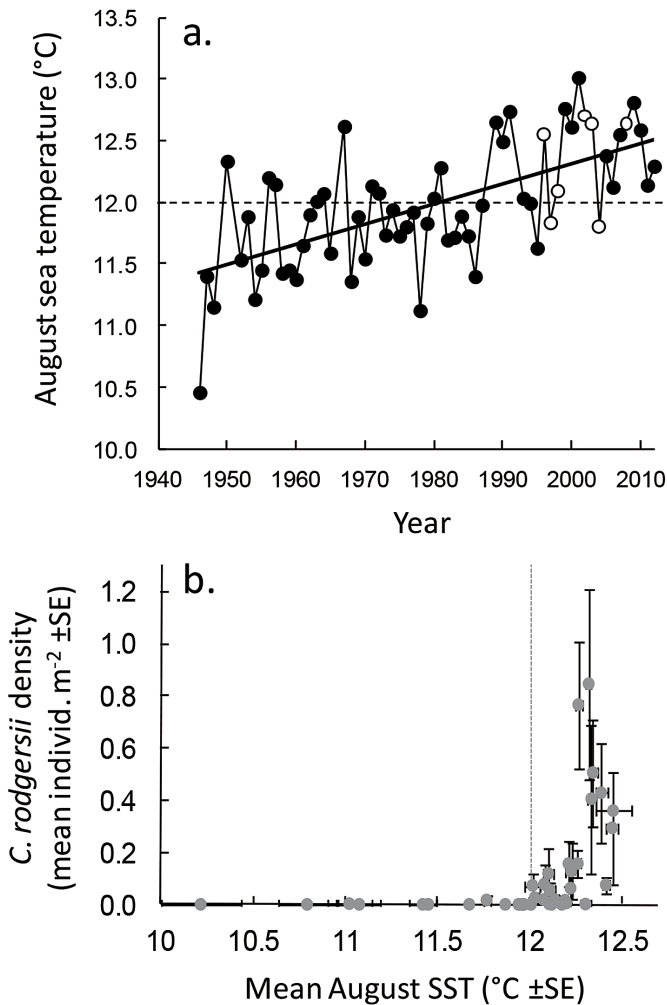


Figure 5. (a.) Long-term winter warming trend of coastal waters in eastern Tasmania, 1946-2012. Data are sea temperatures from the Maria Island coastal station (148° 13' E, 42° 36' S) averaged across depth (0-50 m) for August, i.e. the month of major spawning (data courtesy of CSIRO Marine & Atmospheric Research). Note that the water column is mixed across this depth range during August. Open symbols represent robust satellite derived estimates of sea surface temperature at the long-term station for recent years with missing *in situ* data (for demonstration of robust corroboration of SST with *in situ* temperature measurements see Ridgway, 2007). Dashed horizontal line at 12°C indicates the approximate minimum larval development threshold for Tasmanian *Centrostephanus rodgersii*. (b.). Abundance of *C. rodgersii* as a function of mean winter temperature (mean SST derived from satellite images for the period 1993-2006) for 41 sites in eastern Tasmania.

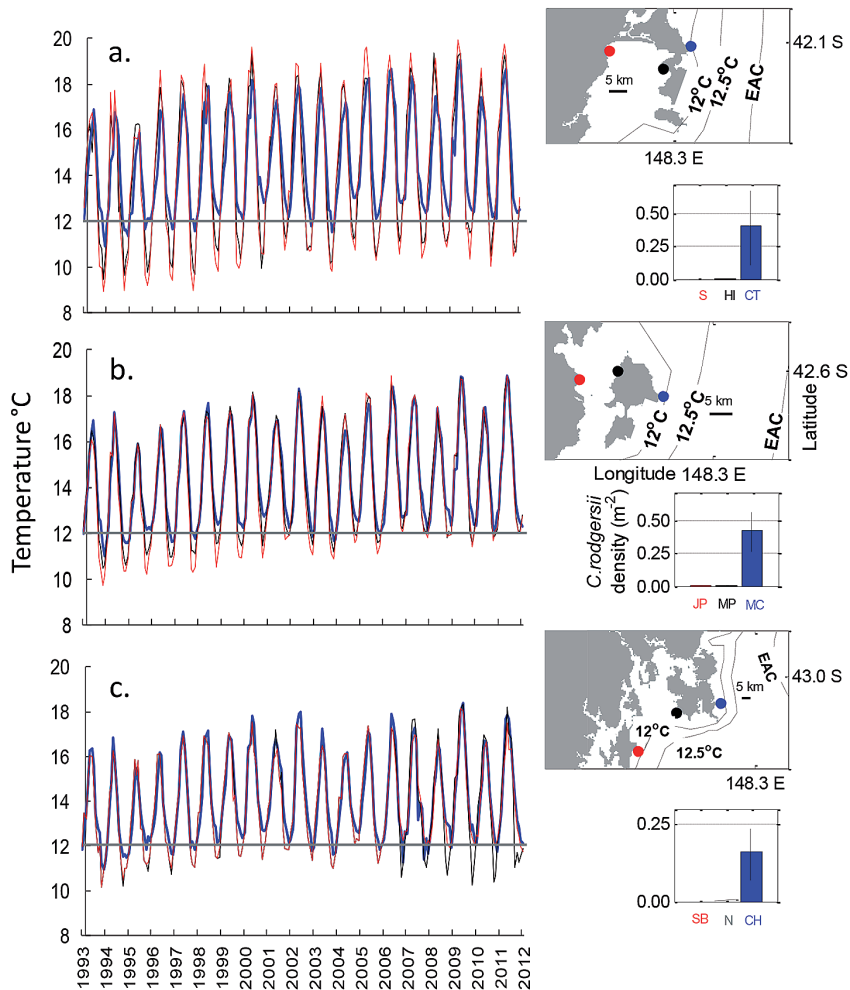


Figure 6. Seasonal temperature profiles and abundance of *Centrostephanus rodgersii* at 'headland' and adjacent inshore reefs. Data are SST for 1993-2012; thickened lines are data obtained from *in situ* temperature loggers. Horizontal bar on temperature plots indicates the lower temperature threshold (12 °C) for *C. rodgersii* larval development (after Ling *et al.*, 2008); numbers in parentheses below indicate proportion of winters > 12 °C at each site for 1993-2012. (a.) Freycinet Peninsula: CT=Cape Tourville (0.43); HI=Hazards Is. (0.00), S=Swansea (0.00); (b.) Maria Island: MC=Mistaken Cape (0.46), MP=Magistrates Pt. (0.00), JP=Johnson's Pt. (0.00); (c.) Tasman Peninsula: CH=Cape Huay (0.38), N=Nubeena (0.07), SB=South Bruny (0.07). For locations within Tasmania, refer to Figure 1. On maps, isotherms and western EAC margin represent mean positions for winter 1993-2006. *C. rodgersii* abundance data for HI and S, in panel (a.) courtesy of N. Barrett.

further beyond potential coastal boundary layers and so more frequently sample offshore currents (Ling *et al.*, 2009a). Thus, in eastern Tasmania the EAC appears to drive milder winters for offshore reefs and for north east Tasmanian reefs in general by having a greater influence on the thermal dynamics at such sites, essentially maintaining a temperature regime above the critical 12°C threshold for early development of *C. rodgersii*. Thus while the EAC is the chief vector for poleward transport of *C. rodgersii* larvae, as initially suggested by Dartnall (1980), purported by Edgar (1997) and concurred by Johnson and co-workers (2005, 2011) plus Banks and co-workers (2007, 2010), the dual role of this oceanic feature in providing a suitable thermal regime for *C. rodgersii* larval development is now also appreciated (Ling *et al.*, 2009a).

FUTURE TRENDS

Given that Tasmanian reared *C. rodgersii* displayed normal embryonic and larval development to the 2-arm pluteus stage within 12–20 °C (Fig. 4b), it is likely that the sea urchin successfully propagates larvae throughout its current Tasmanian range in years when the winter temperature during the major spawning period is ≥ 12 °C. As evidenced from laboratory studies in NSW, Tasmania and New Zealand, overall larval performance would also appear poised to further increase as eastern Tasmanian coastal waters continue to warm above this critical temperature threshold as predicted by general climate change models and specifically for the SE Australian region. Combining a trend of increasing population size with reproductive capability, suggests that aided by a new thermal regime, *C. rodgersii* has established viable populations along the eastern Tasmanian coastline. Thus in highlighting links between *C. rodgersii* population trends and the physical environment across the Tasmanian extension-region, ongoing climate change appears poised to have further positive effects on *C. rodgersii* abundance by 1) increasing the extent of thermally suitable reef habitat as a direct result of atmospheric forced ocean warming (Fig. 7c); and 2) by driving further poleward supply of larvae and accelerating a warmer coastal regime as a result of ongoing intensification of the EAC (as predicted by Cai *et al.*, 2005; Cai, 2006).

Of note, ongoing climate change driven by anthropogenic increase in CO₂ emissions will not only continue to warm sea temperatures owing to the greenhouse effect and overall amplification of global weather systems including ocean currents, but will also alter sea water chemistry due to the process of ocean acidification (OA; e.g., Feely *et al.*, 2004). While OA appears particularly dire for calcium carbonate “shell-forming” invertebrates, there appears a great amount of variability in the response of different marine shell-forming invertebrates to this stressor (reviewed by Dupont *et al.*, 2010; Byrne *et al.*, 2011). Scenarios of OA have been investigated in the laboratory for *C. rodgersii* with the response of fertilization and early larval development processes to lower pH levels, as predicted

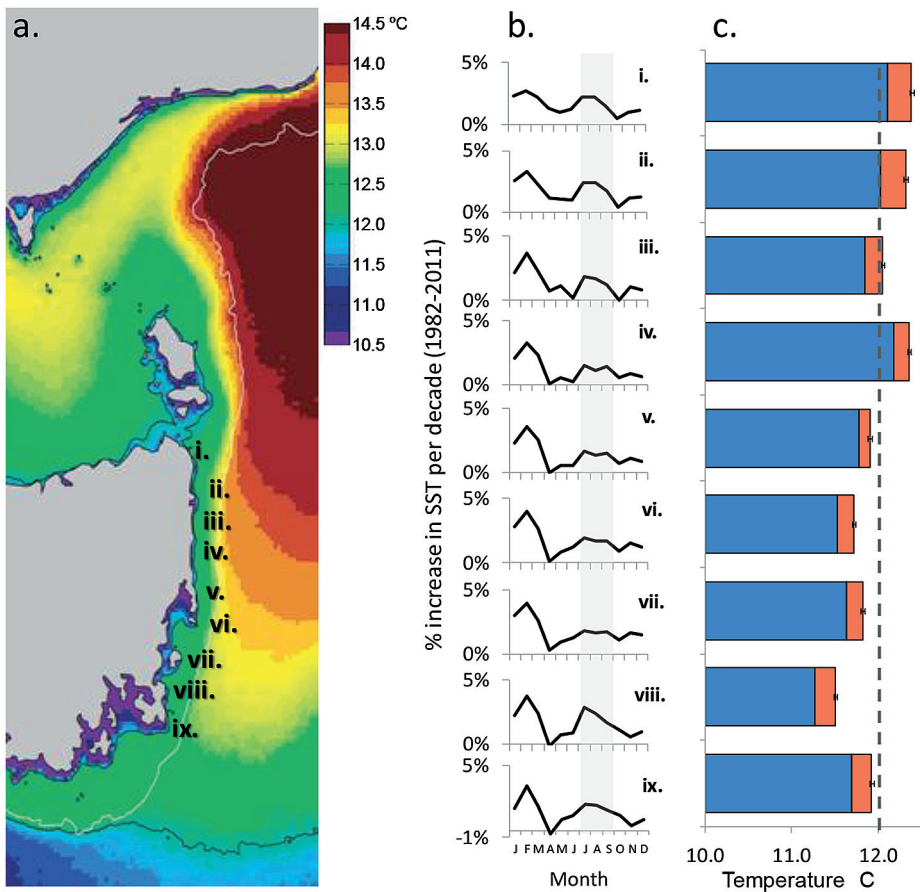


Figure 7. Spatial and seasonal patterns of sea warming across the Tasmanian east coast, 1982-2011. (a.) Map of eastern Tasmania showing sites (i-ix) examined for long-term SST change, SST map as per Fig. 1. (b.) Percent change in SST for each month of the year across eastern Tasmania revealing a clear pattern of summer and winter warming, grey band indicates the Austral winter (July-Sep) centred on the month of August when spawning by *Centrostephanus rodgersii* occurs. (c.) Mean August SST at each site during 2011, blue region of bar is SST in 1982 as back calculated (linearly) from observed level of warming (red region of bar) between 1982 and 2011. Dashed vertical line at 12°C indicates the approximate minimum larval development threshold for Tasmanian *C. rodgersii*. Coastal SST warming is based on the AVHRR V2 NOAA Optimum Interpolation 1/4 Degree Daily Sea Surface Temperature Analysis data (see Acknowledgments for data source).

for the year 2100, considered to be relatively robust compared to some other shell-formers and subtle relative to strong positive effects of ocean warming on rates of larval development (Byrne *et al.*, 2011; Pecornio, 2012; Foo *et al.*, 2012; reviewed by Byrne and Andrew, in press).

However inferring likely impacts of OA in nature is currently difficult as unlike the clear evidence of coastal warming and range-shift of *C. rodgersii* in eastern Tasmania (Figs. 5-7) there is at present a lack of field measurements of the current variability in pH levels across the distributional range of *C. rodgersii*. This is important as several coastal areas throughout the world show high urchin abundance yet demonstrate high daily variability in pH, with minimum pH readings often lower than that predicted to occur by the year 2100 (e.g., Hofmann *et al.*, 2011; J.C. Hernández, unpublished data). Given the potential for large spatial and temporal variability in pH, effects of OA are unlikely to be homogenous across the range of *C. rodgersii* and will not occur independently of changing thermal regimes with interactive effects between both these climate change stressors predicted to occur in the longer term (Foo *et al.*, 2012). Therefore a more complete understanding of current variability in pH across the distributional range of *C. rodgersii* (which clearly shows strong thermal variability) is required such that a firmer basis for predicting negative effects of OA at the individual (juvenile to adult stages), population and ultimately at the ecosystem level can be achieved.

While baseline surveys of *C. rodgersii* abundance conducted in eastern Tasmania in 2001/02 (Johnson *et al.*, 2005) have not been completely resurveyed, trained citizen scientists partially resurveyed all 9 baseline locations in eastern Tasmania in 2008/09 (on average 38% of all sites within a location were resurveyed). Importantly, there was no change in the rank abundances of *C. rodgersii* across locations between 2001/02 and 2008/09 with a slight, but not significant, overall increase in *C. rodgersii* abundance being observed (Ling and Jacques, 2009). The observed increase (while difficult to interpret given that not all sites within a location were re-surveyed) is consistent with an apparent gradual increase in sea urchin abundance within individual sites, which appeared largely accounted for by an apparent strong recruitment to the cryptic/ newly emergent size class (<70 mm TD) as such individuals became more frequently observed during 2008 at most sites (particularly among grazed rocky reef) that were regularly visited since 2001/02 (author's pers. obs.). Thus the anticipated pattern of population expansion is one of a gradual but steady increase in settlement, particularly for sites already containing the sea urchin, followed by emergence of sea urchins to the reef surface whereby such individuals can ultimately commence overgrazing once adequate size is attained (at ~ 7 years of age). Once such individuals become locally abundant then rates of grazing appear to become sufficient to overwhelm kelp beds and maintain widespread sea urchin barrens grounds. Indeed evidence from the age structure of populations in eastern Tasmania supports such a notion of gradual population building towards a critical transition in the rate of herbivory (Fig. 8).

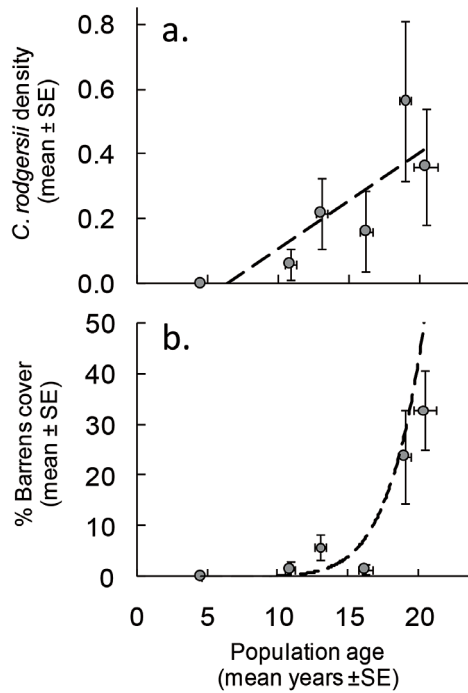


Figure 8. *Centrostephanus rodgersii* population density *versus* mean population age (a.), and percent cover of urchin barrens *versus* mean population age across the eastern Tasmanian range extension region. In (a.) linear fit described by $y = 0.029x - 0.187$, $R^2 = 0.70$; in (b.) power curve described by $y = 1E-09x^{8.15}$; $R^2 = 0.92$.

RESILIENCE OF KELP BEDS TO OVERGRAZING

A gradual build-up of *Centrostephanus rodgersii* within kelp beds prior to a critical tipping point towards sea urchin barrens is further supported by data collected across eastern Tasmania whereby a range of sea urchin biomasses can be sustained by kelp beds but then a critical tipping point in grazing is reached and catastrophic phase-shift to urchin barrens occurs (Fig. 9). That is, the transition between kelp beds and *C. rodgersii* barrens provides an example of a classic non-linear 'catastrophic shift' between alternative and stable reef states with a strong hysteresis effect, as return to the kelp dominated state requires reducing sea urchin biomass to much lower levels than the critical 'tipping' point at which destructive overgrazing occurred in the first place (see alternative 'forward' and 'reverse' phase shift paths in Fig. 9). Ultimately, *C. rodgersii* overgrazing in eastern Tasmania causes the underlying ecosystem dynamic to shift to an alternative

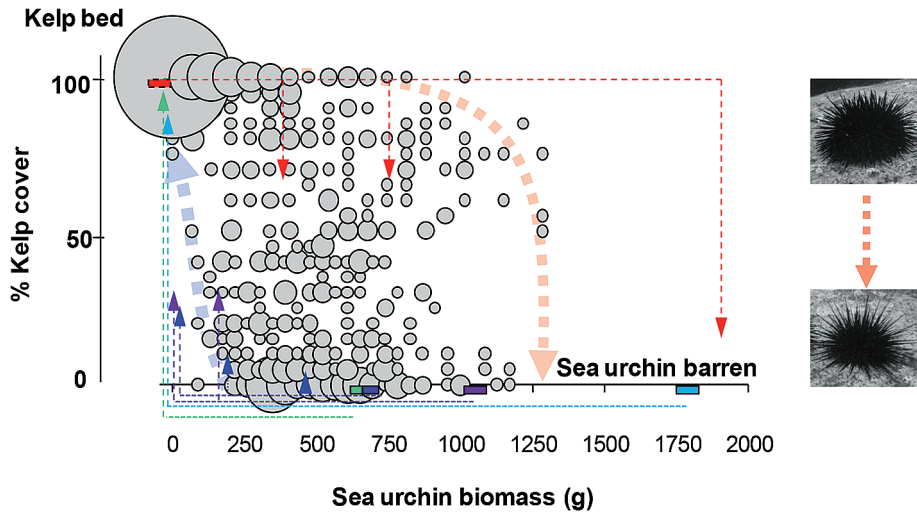


Figure 9. Catastrophic phase-shift between kelp beds and *Centrostephanus rodgersii* barrens. Bubble plot of kelp bed cover *versus* sea urchin biomass density per square metre for eastern Tasmania. Bubbles represent relative frequency of particular urchin density and seaweed cover combinations as measured in 575 individual 5 m² plots (data for 415 plots from Johnson *et al.*, 2005). Dashed arrows indicate magnitude and direction of ecosystem response to removals of *C. rodgersii* from a starting biomass density as indicated by rectangles; manipulated biomass density is where the arrow originating at rectangle takes a 90° turn from the x-axis, with the length of the arrow from the x-axis indicating the observed response in kelp cover after a given period of time (as specified below). Red rectangle/ arrows is that observed after ~5 months by Hill *et al.*, 2003 following additions of *C. rodgersii* to seaweed beds in NSW; dark blue is the response observed by Hill *et al.*, 2003 at ~5 months following sea urchin reductions on barrens in NSW; purple and light blue is response observed after 18 mths in NSW by Andrew and Underwood, 1993 and Andrew, 1998 respectively; light green is response after 18 mths observed in Tasmania by Ling, 2008. Broad dashed curves in background represent alternative «forward-shift» (kelp to barrens; red curve) and «reverse-shift» (barrens back to kelp) paths (after Scheffer *et al.*, 2001).

Images of *C. rodgersii* show alternative morphologies associated with seaweed-beds (short-spines) and barrens (long-spines) (after Ling and Johnson, 2009).

domain of attraction characterized by the sea urchin barrens state which by definition has its own self-maintaining feedback mechanisms (Ling *et al.*, 2009b). Such non-linear or “catastrophic phase shift” (reviewed by Scheffer *et al.*, 2001) between desirable and undesirable ecosystem states are of particular concern to natural resource management as recovery of ecosystems appears exceedingly difficult to achieve once change has occurred.

Given the threat of climate-driven increases in *C. rodgersii* abundance and increasing risk of catastrophic shift of kelp beds to extensive sea urchin barrens grounds, a key research question was to examine mechanisms of resilience of kelp beds against the climate-driven stressor of increasing sea urchin abundance. Indeed, coincident with the arrival and expansion of *C. rodgersii* is heavy fishing of Tasmanian rocky reef systems including fishing down benthic species capable of preying on sea urchins. Previously, Pederson and Johnson (2006) demonstrated that the spiny lobster (*Jasus edwardsii* – Palinuridae) was an important predator of the native Tasmanian sea urchin *Heliocidaris erythrogramma* (Echinometridae), but lobsters were only an effective predator of adult sea urchins when lobsters were larger than the legal-size limit of 110 mm carapace length. Furthermore, labrids (wrasse) were also observed to consume *H. erythrogramma* but per capita predatory effects were considered much lower than that caused by lobsters (Pederson and Johnson, 2006).

Similar to patterns described for *Heliocidaris erythrogramma* (Johnson *et al.*, 2004; Pederson and Johnson, 2006), broad-scale *in situ* surveys spanning eastern Tasmania indicated a negative ceiling distribution between lobster abundance and *C. rodgersii* (Johnson *et al.*, 2005, 2011). To explicitly test the influence of predation on the range-extending *C. rodgersii*, multiple experiments were used utilising comparisons between long-term research reserves (where predators had recovered post cessation of fishing) with sites open to fishing and thus experiencing ongoing harvest of lobsters to examine the possibility that a reduction in predators has reduced resilience of kelp beds and increased the likelihood of widespread barrens formation by *C. rodgersii*. Initially, remote video surveillance inside no-take Marine Protected Areas (MPAs) identified that the lobster *Jasus edwardsii*, frequently preyed on tethered and non-tethered *C. rodgersii* and was a more important predator of *C. rodgersii* than fish (Table 1a). Furthermore, from a calibrated field-of-view, video monitoring, in combination with caging and laboratory experiments, revealed that only supra-legal sized lobsters (carapace length \sim 140 mm) were capable of effectively preying on *C. rodgersii* (Ling *et al.*, 2009b).

Predation rates on *C. rodgersii* were much higher inside no-take MPA boundaries (Fig. 10) which contained a high abundance of large lobsters (\geq 140 mm CL) compared to adjacent fished reef with nil large lobsters (Table 1b). Notably, there was no difference between protected and unprotected reef in the abundance of predatory fishes that could potentially prey on the sea urchin, albeit observed for small size-classes of sea urchin only (Table 1b). Because of intensive fishing, large lobsters are now functionally extinct along much of the coastline (Fig. 11) with the combined evidence suggesting strongly that removal of large (supra-legal) predatory-capable lobsters has effectively reduced resilience of macroalgal beds and increased the risk of wide-spread barrens formation by the range extending *C. rodgersii* (Ling *et al.*, 2009b). In addition, experimental results inside and outside Tasmanian marine reserves clearly show that both size and habitat specific factors define the survival of *C. rodgersii* which indicates that

TABLE 1. (a.) Summary of predator identity and diel timing of predation on *in situ* *Centrostephanus rodgersii* as observed by video monitoring inside marine reserves in eastern Tasmania. a(i). Video monitoring of tethered *C. rodgersii* inside marine reserves [Maria Island Marine Reserve (MIMR) and Crayfish Pt. Marine Reserve (CPMR) (12 and 33 years protection at time of experimentation respectively)]; predator identity was discernable for a total of 26 predation events observed by monitoring a total of 47 individual sea urchins over a total of 28 days and nights. a(ii). Video monitoring of non-tethered, non-tagged *C. rodgersii* housed in partial cages at CPMR (Dec - Jan 2006); a total of 4 predation events were witnessed over 8 days and nights; for lobsters and wrasse, large corresponds to ≥ 140 mm Carapace Length and >300 mm TFL respectively. (b.) Mean abundance of large lobsters and wrasse averaged for experimental reefs inside and outside reserves; mean values are averages across MIMR & CPMR and adjacent fished sites with the value of each site obtained using $n=6$ fifty metre long belt transects (4 m wide for lobsters and 10 m wide for fish) assessed *in situ* by divers (*see* Ling & Johnson 2012 for details).

a.	Predator	% of total predation events witnessed	
		Diurnal	Nocturnal
i). Tethered <i>Centrostephanus rodgersii</i>			
	Large spiny lobster (<i>Jasus edwardsii</i>)	0 %	92 %
	Large Blue-throated wrasse (<i>Notolabrus tetricus</i>)	8 %	0 %
ii). Partially caged <i>Centrostephanus rodgersii</i>			
	Large spiny lobster (<i>Jasus edwardsii</i>)	0 %	100 %
Mean abundance 200m ⁻²			
b.	Predator	Reserve	Fished
	Large spiny lobster (<i>Jasus edwardsii</i>)	2.5 ± 0.9	0.0 ± 0.0
	Large blue-throated wrasse (<i>Notolabrus tetricus</i>)	± 0.3	0.9 ± 0.1

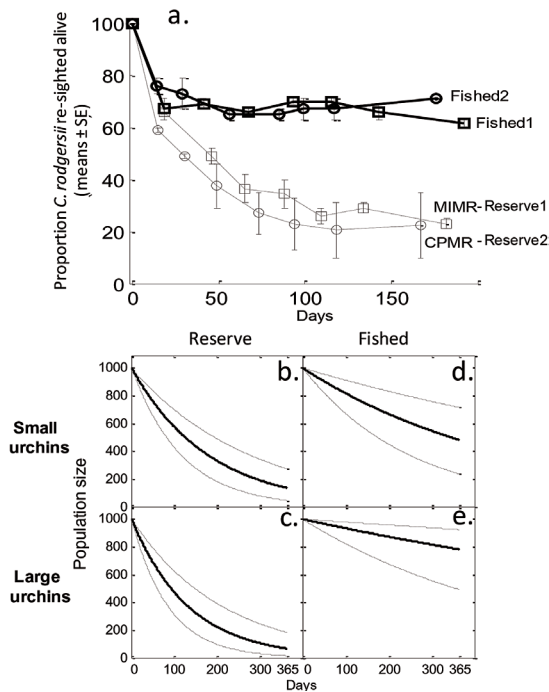


Figure 10. (a.) Percentage of tagged *Centrostephanus rodgersii* resighted through time at experimental reefs inside marine reserves (dotted lines; CPMR and MIMR) and at adjacent fished sites (solid lines) outside marine reserves, $n=96$ urchins per reef. Sites were located in Mercury Passage (Triangles); and the Derwent Estuary (circles). (b. - e.) Projection of annual population trajectories based on empirically observed mark-recapture survival rates applied to hypothetical populations of 1,000 small (b. - c.) and large (d. - e.) *C. rodgersii* 'invading' reef inside and outside marine reserves (after Ling and Johnson, 2012). Dotted lines indicate upper and lower 95% confidence intervals.

ecosystem impacts mediated by the climate driven range-extension of the sea urchin will be heterogeneous across different habitats, and that the likelihood and spatial extent of barrens will, all else being equal, be greater where urchin populations experience minimal predation risk within such novel systems (Ling and Johnson, 2012). That is, reefs protected from fishing, where the abundance of large predatory lobsters and predators in general (including labrids) is large, will maximise the resilience of kelp beds and reduce the likelihood and extent of catastrophic overgrazing.

While this clearly highlights the importance of predators for maximising resilience of kelp beds to overgrazing in the first instance, it is important to note

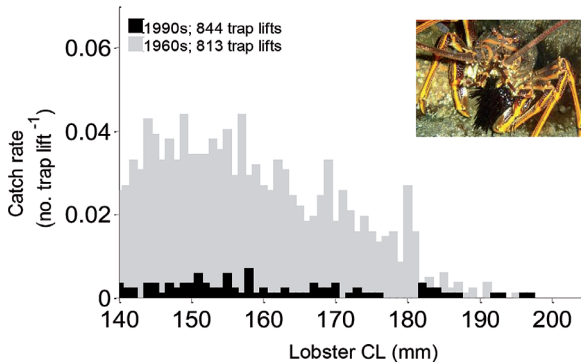


Figure 11. Change in size-frequency of the spiny lobster *Jasus edwardsii* pre- and post-intensive fishing in remote north eastern Tasmania for the large predatory capable size-class (CL ≥ 140 mm) observed to prey on *C. rodgersii* (data are for male lobsters which dominant larger size-classes, redrawn from Frusher, 1997). Inset image shows a large *J. edwardsii* (160 mm CL) preying on *C. rodgersii*; note prominent 1st pair of thoracic appendages used to grasp urchin.

that potential for predator driven recovery of barrens ground (once formed) appears to operate under a different dynamic due to the inherent hysteresis effect evident in this system (non-linear dynamics in the system). For example, take a starting sea urchin biomass of 850 g m^{-2} (~ 2 individuals m^{-2}) and assume strict adherence to the barrens formation ('forward-shift') and seaweed recovery ('reverse-shift') paths (Fig. 9). In the kelp bed dominated state, urchin biomass only needs to increase from $\sim 1000 \text{ g m}^{-2}$ to $\sim 1250 \text{ g m}^{-2}$ (an increase of 250 g m^{-2}) for the system to shift to the barrens state. Alternatively, assuming the same 1000 g m^{-2} starting biomass of urchins in the barrens state, and following the kelp recovery ('reverse-shift') path, urchin biomass must decrease to approx. $< 125 \text{ g m}^{-2}$ (a decrease of 875 g m^{-2}) for the system to return to the kelp dominated state. Thus conceptually, approx. 3.5 times as much urchin biomass must be consumed by predators to revert barrens to seaweed beds as that required to maintain the seaweed dominated state by keeping urchin density just below the 'forward-shift' threshold for barrens formation (Fig. 9).

Notably however, there appear other factors seemingly further stabilising the sea urchin barrens state once formed. That is, *C. rodgersii* on widespread barrens appear less vulnerable to predation as such individuals possess relatively long and more protective spines for a given test diameter (and age) compared to individuals observed within seaweed habitat where spines are frequently eroded by whiplash of robust seaweeds under the influence of ocean surge (Fig. 9). In addition, recruitment of juvenile sea urchins appears to be higher on urchin barrens compared to algal covered reef (e.g., Hernández *et al.*, 2010).

SUMMARY

The transition between the alternative seaweed dominated and sea urchin barrens states appears to be influenced by many processes operating across a wide spectrum of spatial and temporal scales. This includes oceanic processes affecting dispersal, larval development and settlement of urchins from the plankton (e.g., Hart and Scheibling, 1988; Ling *et al.*, 2008, 2009a); habitat preferences (e.g., Andrew, 1993; Ling and Johnson, 2012); storm events (e.g., Andrew, 1991); effects of sweeping macroalgae (e.g., Konar and Estes, 2003; Ling and Johnson, 2009); predation (e.g., Tegner and Levin, 1983; Estes and Duggins, 1995; Shears and Babcock, 2002; Ling *et al.*, 2009b; Ling and Johnson, 2012); and disease cycles (e.g., Lessios *et al.*, 1984; Scheibling and Hennigar, 1997). Thus, such reef assemblages are clearly complex and dynamic systems typified by high variability and shaped by interactions between physical and biological processes acting across multiple scales (e.g., Tegner and Dayton, 2000; Steneck *et al.*, 2002).

As evidenced from broad-scale field surveys, field manipulations and laboratory experiments the changing climate of eastern Tasmania has become increasingly suitable for *Centrostephanus rodgersii*. The timing of the sea urchins' arrival, age-structure and spatial distribution across the extension-region is consistent with patterns in warming sea temperatures and current-driven dispersal potential. Continued warming predicted for this region will favour increased larval survival, promoting ongoing population expansion and ultimately increased likelihood of populations reaching sufficient density to affect widespread overgrazing over a greater spatial extent of this coastline. Furthermore, heavy fishing of sea urchin predators also favours continuing population expansion and grazing impacts by the sea urchin. Thus while global climate change and overfishing may independently pose major threats to ecosystem dynamics, as reviewed here, the interaction between such broad scale perturbations demonstrates that it is the combined effects of multiple stressors that lead to unprecedented risk of catastrophic shifts in coastal ecosystems. Therefore, management of non-climatic local scale stressors, such as mediating the effects of heavy fishing on sea urchin predators, is an approach to increase resilience of kelp beds against overgrazing given climate-driven increases in this key sea urchin population.

ACKNOWLEDGEMENTS

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