Journal of Experimental Marine Biology and Ecology 400 (2011) 17–32

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

# Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania

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ARTICLE INFO

*Keywords:*
Cascading effects
Climate change
Eastern Tasmania
Marine ecosystems
Range expansion
Sea urchin

ABSTRACT

Several lines of evidence show that ocean warming off the east coast of Tasmania is the result of intensification of the East Australian Current (EAC). Increases in the strength, duration and frequency of southward incursions of warm, nutrient poor EAC water transports heat and biota to eastern Tasmania. This shift in large-scale oceanography is reflected by changes in the structure of nearshore zooplankton communities and other elements of the pelagic system; by a regional decline in the extent of dense beds of giant kelp (*Macrocystis pyrifera*); by marked changes in the distribution of nearshore fishes; and by range expansions of other northern warmer-water species to colonize Tasmanian coastal waters. Population-level changes in commercially important invertebrate species may also be associated with the warming trend.

Over-grazing of seaweed beds by one recently established species, the sea urchin *Centrostephanus rodgersii*, is causing a fundamental shift in the structure and dynamics of Tasmanian rocky reef systems by the formation of sea urchin 'barrens' habitat. Formation of barrens represents an interaction between effects of climate change and a reduction in large predatory rock lobsters due to fishing. Barrens realize a loss of biodiversity and production from rocky reefs, and threaten valuable abalone and rock lobster fisheries and the local economies and social communities they support. This range-extending sea urchin species represents the single largest biologically mediated threat to the integrity of important shallow water rocky reef communities in eastern Tasmania.

In synthesizing change in the physical ocean climate in eastern Tasmania and parallel shifts in species' distributions and ecological processes, there is evidence that the direct effects of changing physical conditions have precipitated cascading effects of ecological change in benthic (rocky reef) and pelagic systems. However, some patterns correlated with temperature have plausible alternative explanations unrelated to thermal gradients in time or space. We identify important knowledge gaps that need to be addressed to adequately understand, anticipate and adapt to future climate-driven changes in marine systems in the region.

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**Contents**

1. Introduction . . . 18
2. Materials and methods . . . 19
   2.1. Oceanographic change . . . 19
   2.2. Zooplankton communities, Tasmanian east coast . . . 19

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doi:10.1016/j.jembe.2011.02.032

2.3. Macroalgae: extent of giant kelp beds, Tasmanian east coast . . . 19
2.4. Macroinvertebrates: surveys of sea urchins, other invertebrates and barrens habitat . . . 19
2.5. Macroinvertebrates: sea urchin genetics . . . 20
2.6. Macroinvertebrates: blacklip abalone population parameters . . . 20
2.7. Macroinvertebrates: rock lobster growth and settlement . . . 20
2.8. Fish, Tasmanian east coast . . . 21
3. Changes in large scale oceanography . . . 21
4. Range expansion, and changes in population characteristics and community structure . . . 21
4.1. Plankton communities . . . 21
4.2. Macroalgae . . . 23
4.3. Macroinvertebrates . . . 24
4.4. Fish . . . 27
5. Evidence of cascading effects . . . 27
5.1. Rocky reefs . . . 27
5.2. Pelagic system . . . 29
6. Synthesis and future directions . . . 29
Acknowledgements . . . 30
Appendix A. Supplementary data . . . 30
References . . . 30

## 1. Introduction

An important predicted consequence of global warming is change in large scale patterns of ocean circulation (Meehl et al., 2007). These changes are likely to have flow-on effects to ecological communities through alteration of transport of planktonic stages and species (Harley et al., 2006; Brierley and Kingsford, 2009) and changes in biogeochemical cycling (Sarmiento et al., 2004; Schmittner et al., 2008) reflecting shifts in nutrients, temperature and community structure. In the eastern Pacific and the North East Atlantic, including the North Sea and English Channel, pronounced shifts in oceanic conditions linked to climate over the past century have been associated with large shifts in marine ecosystem structure and dynamics (e.g. Southward et al., 1995, 2005; McGowan et al., 1998; Benson and Trites, 2002; Hawkins et al., 2003; Alheit and Niquen, 2004; Beaugrand, 2004; Edwards and Richardson, 2004).

The rate of ocean warming off south eastern Australia over recent decades is ~3–4 times the global average (Holbrook and Bindoff, 1997; Ridgway, 2007b), making this one of the fastest warming regions in the southern hemisphere — a global 'hotspot'. Recent studies have shown that the decadal to multi-decadal warming in this region is consistent with a 'spin up' of the South Pacific gyre (Cai et al., 2005; Cai, 2006; Ridgway, 2007a,b; Roemmich et al., 2007), the western margin of which is the warm East Australian Current (EAC; Fig. 1). The EAC is the major boundary current off the east coast of Australia, with a substantial eastwards separation from the coast at ~32.5° S to form the Tasman Front which extends to New Zealand (Godfrey et al., 1980). Extension of the EAC south of this separation area now realizes longer and stronger incursions into waters off eastern Tasmania, which has the effect of transporting both heat (Cai, 2006; Ridgway, 2007a,b) and larvae of northern species (Johnson et al., 2005; Ling et al., 2009b; Banks et al., 2010) southward to Tasmania.

Increased incursions of the EAC in eastern Tasmania not only influence temperature and transport of larvae, but have also probably affected nutrient loading in the region. This is because the EAC is nutrient-poor (e.g. often ≤1 μM nitrate, particularly in summer) relative to the sub-Antarctic water masses that, until recently, dominated the oceanographic signature on the east coast of Tasmania (Harris et al., 1987; Ridgway, 2007a). EAC-driven ocean warming off eastern Tasmania is therefore likely to be strongly confounded with a decrease in nutrient availability, although it is worth noting that there is no evidence yet of a long term trend in nitrate levels at the single monitoring site in eastern Tasmania where nutrients have been sampled routinely (Thompson et al., 2009).

While there is unequivocal evidence of fundamental changes to ocean circulation and the physical parameters of waters off south eastern Australia, links to changes in species' distributions, with concomitant downstream effects on community structure and dynamics, and on local economies, are unclear (Poloczanska et al., 2007). These questions are important given the concentration of biodiversity, very high levels of endemism (Anon, 2008), and the high economic value of recreational and commercial fisheries in south east Australia in general and Tasmania in particular. In addition, in south eastern Australia the human population is strongly concentrated in coastal urban areas (Australian Bureau of Statistics, www.abs.gov.au). Fisheries in the region are among the most productive in the country, with New South Wales, Victorian and Tasmanian state waters together yielding ~33% (by value) of the total production of Australian state-based fisheries in 2008–09 (ABARE, 2010). Of individual states, Tasmania had the largest gross value of fisheries production (AUD

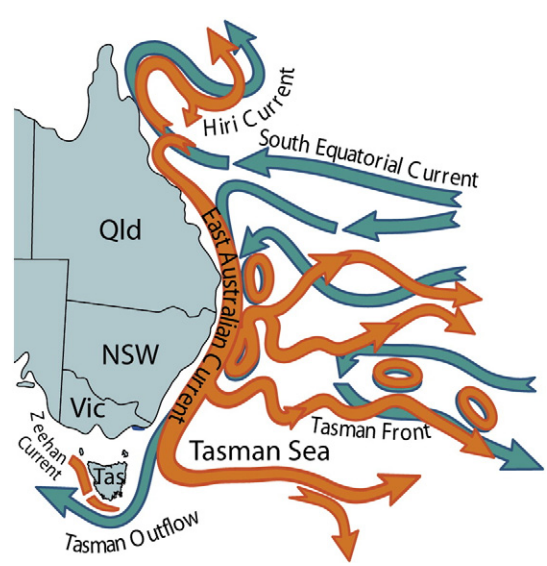


**Fig. 1.** Schematic representation of major current patterns off eastern Australia, including the East Australia Current (EAC) and the Tasman Front (TF). Surface currents are shown in orange and subsurface currents are in blue. Qld = Queensland, NSW = New South Wales, Vic = Victoria, Tas = Tasmania.

$522.2 M), accounting for 23% of total Australian fisheries production (ABARE, 2010).

For these reasons there is a strong imperative to understand ongoing oceanographic change and the implications of these changes for important ecological systems in the region. Here we synthesize existing knowledge of change in the physical ocean climate in eastern Tasmania, and concomitant shifts in species' distributions and ecological processes. We provide strong evidence that shifts in species' ranges and abundances, and in community structure, are associated with strengthening of the EAC and concurrent warming in eastern Tasmania, and demonstrate the cascading effects of ecological change. We also identify important knowledge gaps that need to be addressed in making predictions about future changes to marine systems in the region.

## 2. Materials and methods

### 2.1. Oceanographic change

Monthly temperature and salinity measurements have been collected by either bottle or CTD profiles at a location off eastern Tasmania near Maria Island (148° 13.8′ E; 42° 36′ S) since 1944. Simple quality control measures were applied to these data including range checking and gap-filling. To produce Fig. 2, the seasonal cycle was determined by harmonic analysis and removed from the series. Small gaps in the residual series were then filled by linear interpolation, and the original series was recovered by adding back the seasonal cycle. Resultant time series were low-pass filtered with a 5-year running mean.

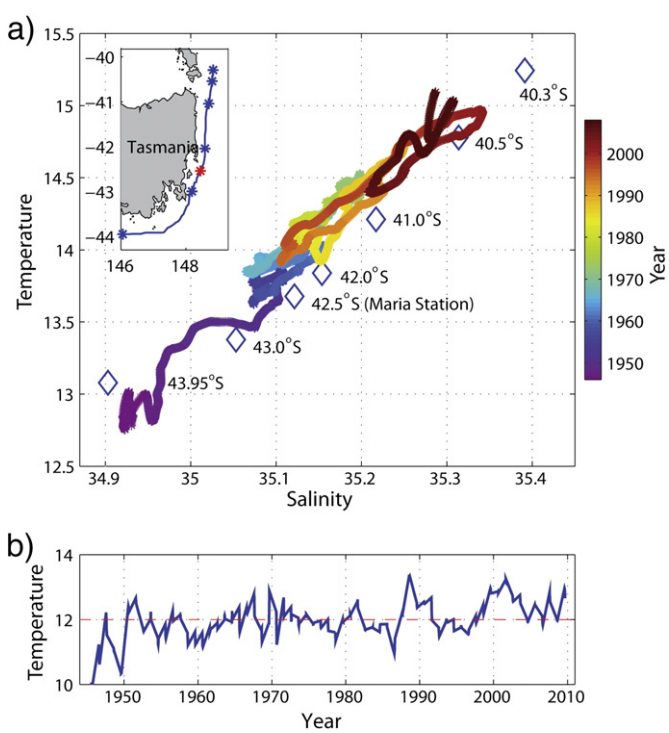


**Fig. 2.** (a) Changes in temperature and salinity off Maria Island 1944–2010; data are from the Maria Island Time Series station (location starred in red on inset map) and temperature refers to average water column temperature to 50 m depth. Diamonds represent temperature/salinity values at a series of seven locations along a track to the east of Tasmania (inset map) from a mean climatological field based on data obtained prior to 1970. Note that the temperature/salinity signature for Maria Island in 2010 is equivalent to the signature >2° further north prior to 1970. (b) The trajectory for August (winter) temperature collected at Maria Island from 1944 to 2010. The horizontal dashed line at 12 °C indicates the approximate minimum temperature for successful development of *Centrostephanus rodgersii* (long-spined sea urchin) larvae. There has been an increase in the frequency which this threshold has been exceeded since 1980.

### 2.2. Zooplankton communities, Tasmanian east coast

Zooplankton were sampled near Maria Island off eastern Tasmania during five different periods between 1971 and 2009. The absolute extent of the region sampled was from Schouten Island (42° 20′ S) to Tasman Island (43° 14′ S). Sampling regimes during the five data collection periods are summarized in Table A1 (Appendix A). All samples were preserved in 4–5% buffered formaldehyde and subsampled in the laboratory using plankton splitters. The analysis of zooplankton communities presented here includes only crustaceans (copepods and the ghost shrimp *Lucifer hanseni*) because of uncertainty regarding reporting at a species level for other common groups such as chaetognaths, salps, euphausiids and appendicularians. Analyses were conducted using PRIMER6 with the PERMANOVA add-on (Anderson et al., 2008).

### 2.3. Macroalgae: extent of giant kelp beds, Tasmanian east coast

The historical extent of *Macrocystis pyrifera* kelp beds was estimated using a GIS-based assessment of dense surface canopies visible from aerial photographs. The photographs (obtained from the photographic archives of the Tasmanian Department of Primary Industries, Parks Water and Environment) were examined to determine the historical distribution of *M. pyrifera* at seven coastal sites in eastern Tasmania from 1946 until 2007. Given potential problems with interpreting aerial photos of the sea surface depending on wind and light conditions, sites and times were selected on the basis of photos enabling unambiguous interpretation insofar as is possible. The geographic extent of the seven sites is provided in Table A2 (Appendix A). Photographs were scanned into GIS software to facilitate tracing of vectors around visible patches of *M. pyrifera* surface canopy, and shapefiles were generated using GenaMap (1946–1998) and ArcGIS (1999–2007). The main limitation of this approach is that water surface patterns can potentially mimic *M. pyrifera* bed cover. To exclude possible erroneous determinations, bed areas were checked against mapped reef areas and depth contour shapefiles from Seamap Tasmania.

### 2.4. Macroinvertebrates: surveys of sea urchins, other invertebrates and barrens habitat

Surveys of sea urchins (*Centrostephanus rodgersii*), abalone (*Haliotis rubra*) and rock lobster (*Jasus edwardsii*) and barrens habitat were conducted at sites in the Kent Group, Bass Strait, in 1974 and 1981 (diver searches from a depth of ~2 m up to a maximum of 50 m), 1993 (surveys at a depth of 5 m; Barrett and Edgar, 1993) and 2000 (diver searches from ~2 m to ~30 m depth and belt transects from ~6 m to ~18 m depth, as described below). Geographic coordinates for sites in the Kent Group are provided in Table B1 (Appendix B). Off mainland Tasmania, further surveys were conducted between 2000 and 2002 using a spatially hierarchical sampling design based on 13 primary locations, spaced at ~30 km intervals between Eddystone Point and Recherche Bay, on the east coast. Estimates of the density of *C. rodgersii*, *H. rubra* and *J. edwardsii* were collected using diver transects (belt transects set perpendicular to the shore, extending from ~6 m depth to a maximum depth of 18 m or a maximum total length of 100 m if the maximum seaward depth was less than 18 m), while percentage barrens cover was obtained using video transects (perpendicular transects covering a depth range from ~3 m to ~40 m and parallel transects within a depth range of 15–20 m). Further details on data collection methodology for sea urchins and barrens habitat in the Kent Group and on the east coast of Tasmania are provided in Johnson et al. (2005).

Individual age estimates (used to construct age frequency distributions for *C. rodgersii*) were generated from jaw lengths and test diameters using known age-at-size derived from a field-calibrated model of

*C. rodgersii* growth in eastern Tasmania (Ling et al., 2009b). The growth model was derived from annual growth increments (spanning 2004–2005) of tetracycline tagged individuals living in seaweed dominated habitat on rocky reefs in north eastern and south eastern Tasmania (St. Helens and the Tasman Peninsula, respectively). Further information on the derivation of age frequency distributions is provided in Ling et al. (2009b).

Abalone (*H. rubra*) and rock-lobster (*J. edwardsii*) populations were compared on *C. rodgersii* barrens and in adjacent algal-dominated habitat at the same depth and on the same substratum type at three sites in 2002 (Elephant Rock, 41° 15.30′ S, 148° 20.37′ E; St Helens Island, 41° 20.95′ S, 148° 20.15′ E; Mistaken Cape, 42° 38.86′ S, 148° 9.70′ E). At Elephant Rock and St Helens Island, barrens were extensive and well established in 2002, while at Mistaken Cape the barrens in 8–14 m were incipient, comprising small barren patches in the algal bed. Sampling involved four 50 × 2 m belt transects set within the 15–18 m depth strata in each habitat type at each site. Details of statistical analyses for data collected at these sites are provided in Johnson et al. (2005).

### 2.5. Macroinvertebrates: sea urchin genetics

Genetic diversity and genetic differentiation in *C. rodgersii* sampled from New South Wales (NSW), Bass Strait and Tasmania in 2000 were explored using two genetic marker types: microsatellites (as in Banks et al., 2010) and allozymes. It is useful to consider both microsatellites and allozymes since the two kinds of markers have different mutation rates and are thus likely to have different sensitivity to contemporary population processes, and allozymes are more likely to be under selection pressure and may reveal different patterns to microsatellite markers (Lemaire et al., 2000).

Sixty animals were collected from each of Bass Point, New South Wales (34° 35′ S, 150° 54′ E; August 2000); south side of East Cove, Deal Island, Bass Strait (39° 28.4′ S, 147° 18.4′ E; June 2000), and Fortescue Bay, Tasmania (43° 8.5′ S, 148° 0.0′ E; October 2000 and April 2001). Samples of gonad (free of other tissue) were excised from live animals, snap frozen in liquid nitrogen, and stored at −80 °C. Further information on sampling processing and the selection of allozymes and microsatellites for analysis is provided in Johnson et al. (2005) and Banks et al. (2010), respectively.

Genetic diversity was examined using Hardy–Weinberg tests (to detect deviations from expected genotype proportions) and generalized linear modeling (to test for differences in observed heterozygosity and allelic diversity between populations). Hardy–Weinberg tests and genetic diversity statistics were calculated in GenAlEx 6 (Peakall and Smouse, 2006), while generalized linear modeling was conducted using Genstat v11 (Payne et al., 2008). Individual ID was represented as a random term in a generalized linear mixed model to test for effects of locus and sampling site on the probability of a genotype being heterozygous. Allelic diversity data (number of different alleles sampled at each locus per population) were modeled as a normally distributed response variable with the number of individuals sampled at each site, locus and site as candidate explanatory variables.

The partitioning of genetic variation between NSW, Bass Strait and Tasmania was investigated with an Analysis of Molecular Variance (AMOVA) in Arlequin 3 for both microsatellite and allozyme data. $F_{ST}$ was estimated over all sites sampled in 2000 using Meirmans' (2006) approach to standardizing $F_{ST}$ to compare values between the microsatellite and allozyme datasets. Additional results from genetic analyses for microsatellite and allozyme datasets are available in (Banks et al., 2010) and Tables B2–B4 (Appendix B), respectively. Note that supplementary genetics data presented in Appendix B were obtained using BIOSYS (allelic diversity, heterozygosity and Nei's unbiased genetic distance; Swofford and Selander, 1981) and the software package TFPGA (Miller, 2000).

### 2.6. Macroinvertebrates: blacklip abalone population parameters

A large database of field observations on abalone held at the Tasmanian Aquaculture and Fisheries Institute made it possible to investigate across large scales the biology of blacklip abalone (*H. rubra*) under varying temperature conditions. Biological data for blacklip abalone used in the analyses were collected during fishery independent surveys conducted by research divers over a total period of 15 years from 1994 to 2008. Owing to different availability of samples, two subsets of the database were used: a subset relating temperature to maximum shell length and growth rate (30 samples at the scale of individual reefs) and a subset relating temperature to size at maturity (66 samples at the scale of statistical subregions of the abalone fishery). Sea surface temperature (SST) data were obtained from satellite readings (15-day median composite; CSIRO, 2004).

An inverse logistic growth model was used to derive maximum growth rates (MaxΔL) and maximum shell lengths (L95) from length increment data obtained from tag-recapture studies (following Haddon et al., 2008). Size at maturity was taken as the predicted shell length at which 50% of each population is mature (i.e. $SM_{50}$) based on logistic regression of shell length and maturity data from fishery independent surveys. Relationships between SST and maximum growth rate, size at maturity and maximum shell length for east coast and west coast *H. rubra* populations (where a 147° E longitude line was used as the east/west divide) were explored using 1-way ANCOVAs.

### 2.7. Macroinvertebrates: rock lobster growth and settlement

Size at maturity was obtained for female rock lobsters from the east coast of Tasmania at shallow water (42° 44.34′ S, 148° 0.54′ E; 8–30 m depth) and deep water (42° 20.1′ S, 148° 13.02′ E; 35–45 m depth) sites at or near Maria Is during surveys undertaken in March, July and November of each year from 1992 to 2004 (see Gardner et al., 2006 for methodology). Growth increments were obtained from mark-recapture studies of male lobsters between 1992 and 2003 (see Frusher and Hoenig, 2001 for tagging methodology). Lobsters were tagged in March and recaptured the following March to ensure that tagging and recapture did not overlap with a moulting period. Residual growth increments for the east coast region (42° 20.1′ S, 148° 13.02′ E) were obtained from linear regression of growth increment against carapace length for individual lobsters. Residuals were averaged for each year of sampling to obtain mean residual growth increments.

The puerulus stage is the last of a long period of oceanic larval stages of southern rock lobsters, and puerulus larvae settle on benthic habitat and provide the first indications of recruitment to regional reef habitats. In eastern Tasmania artificial larval collectors were used to monitor monthly settlement from 1994 to 2007 (see Gardner et al., 2001 for methodology). Mean monthly settlement data and monthly SST data (from satellite imagery) for Bicheno (41° 52.14′ S, 148° 18.00′ E) and Recherche Bay (43° 35.40′ S, 146° 55.08′ E) were 'filtered' to remove seasonal signals. SST for each site was interpolated from a surrounding 4 × 4 km pixel and was offset seaward by 4 km to avoid distortion from coastal landmass. Filtering of the seasonal signal involved fitting sine curves to settlement and temperature data, and then subtracting the periodic component to obtain the remaining (filtered) trend (Fig. A1, Appendix A).

Size at maturity and mean residual growth increment were plotted against temperature data from the Maria Island Time Series station (average water column temperature to 50 m depth). For size at maturity, we used average temperatures over the past four years (i.e. the assumed period of growth prior to the year of each record). Mean residual growth increment was plotted against mean temperature for the period between marking and recapture (i.e. from March to March). Filtered mean puerulus settlement over the peak settlement

months (July–January inclusive) was plotted against filtered monthly SST data for Bicheno and Recherche Bay.

### 2.8. Fish, Tasmanian east coast

Shifts in coastal fish species distributions on the Tasmanian east coast since the early 1980s were determined by updating data from Last et al. (2010) with additional records from the Australian National Fish Collection and Redmap (http://www.redmap.org.au). Distribution changes were classified according to the following criteria:

1. *New record for eastern Tasmania*
   Any change from 'absent' to the observation of juveniles, or a status of 'rare', 'uncommon' or 'extralimital vagrant'.
2. *Newly established in eastern Tasmania*
   Any change from 'absent' or the presence of juveniles to established adult populations (but only if the initial state was 'absent' or presence of juveniles in all four eastern Tasmanian bioregions).
3. *Range expansion into eastern Tasmania*
   Any of (a) change from 'rare' or 'uncommon' to the presence of juveniles or adult populations, (b) change from 'absent' to 'rare', 'uncommon', presence of juveniles or established adult populations, or (c) change from the presence of juveniles to established adult populations (note that change to established adult populations was only considered as range expansion if the initial state *was not* 'absent' in all four east Tasmanian bioregions).
4. *Increase in abundance*
   Any change from 'rare', 'uncommon' or the presence of juveniles to established adult populations.

## 3. Changes in large scale oceanography

There has been a marked shift in the temperature and salinity regime in south eastern Australian coastal waters over the past six decades. Data from the Maria Island Time Series station (42.6° S, 148.23° E) off the east coast of Tasmania, which shows both increasing temperature and salinity in surface waters since 1950 (Fig. 2a), unambiguously identifies the increased influence of the EAC in the region (Ridgway, 2007b; Hill et al., 2008). Given the combined temperature/salinity trace, it can be concluded that warming of surface waters has occurred largely due to changes in ocean circulation with increasing influence of the EAC, and not as a direct transfer of heat energy from the atmosphere to the surface ocean. This explains why the mean rate of ocean warming off eastern Tasmania is 2.28 °C/century, compared with a global average rate of 0.6 °C/century (Ridgway, 2007b).

There are several lines of evidence suggesting a mechanism behind the poleward extension of the EAC in recent decades. Sea surface heights derived from satellite altimetry together with in situ subsurface temperature and salinity measurements from World Ocean Circulation Experiment (WOCE) hydrographic data, a repeat Expendable Bathythermograph (XBT) survey, and data from the global Argo array, confirm that there has been an overall intensification of the South Pacific subtropical gyre circulation (Willis et al., 2004; Qiu and Chen, 2006; Roemmich et al., 2007). Evidence of a multi-decadal upper ocean warming of the southwest Tasman Sea to the east of Tasmania (Holbrook and Bindoff, 1997; Ridgway, 2007b) suggests that the 'spin-up' of the South Pacific Gyre circulation since the early 1990s is part of a multi-decadal, or longer term, increase in gyre intensity.

Gyre intensity is of fundamental importance in influencing the EAC, but there are several possible mechanisms that might affect it. Positive changes in the Southern Annular Mode (SAM) and associated increases in wind stress in the Southern Ocean may result from greenhouse warming (e.g. Kushner et al., 2001) and/or ozone depletion (e.g. Shindell and Schmidt, 2004). Results from Cai's (2006) modeling study suggests that Antarctic ozone depletion and positive changes in the SAM may be responsible for the southward shift and decadal spin-up of the 'super-gyre' since the 1990s, with concomitant strengthening and southward penetration of the EAC. Multi-decadal changes in circulation were also identified in an ocean general circulation model simulation forced by changes in the Southern Hemisphere sub-polar westerly winds (Oke and England, 2004). Both Roemmich et al. (2007) and Qiu and Chen (2006) show evidence to suggest that observed changes in the South Pacific Gyre also reflect changes in South Pacific winds, with a delay of several years. Hill et al. (2008) extended this work by showing a correlation between the low-frequency South Pacific wind forcing and ~3-year lagged temperature/salinity changes observed at the Maria Island Time Series station.

Most recently, it has been shown that Tasman Sea sea-level and EAC baroclinic transport changes are modulated by decadal variations in El Niño-Southern Oscillation (ENSO), most likely due to incoming westward propagating Rossby waves forced in the central South Pacific, east of New Zealand (Sasaki et al., 2008; Holbrook, 2010). Holbrook et al. (2010) demonstrate that Rossby waves forced by wind stress changes in the central South Pacific provide the important mechanism for the ocean-adjusted multi-decadal increasing trend in EAC intensity and sea level that has been observed at Fort Denison (FDSL) in Sydney Harbour since 1960. They also report a highly significant 3-year lag between low-frequency (five-year smoothed) FDSL and the Southern Oscillation index, demonstrating the connection between FDSL and large-scale decadal ENSO variability. In this context it is noteworthy that there are substantial and highly significant connections between the large-scale climate, interannual to multi-decadal changes in EAC intensity and FDSL on the continental shelf that may be a manifestation of multi-decadal ENSO (Holbrook, 2010; Holbrook et al., 2010).

Whether the observed changes in the EAC are due to increased wind stress in the Southern Ocean or multi-decadal changes in the wind stress curl in the central South Pacific, and what the relative contributions are of anthropogenic greenhouse warming, ozone depletion and natural multi-decadal variability as the ultimate causal mechanism, is still not completely clear. Nevertheless, it is clear and very evident that marine systems in south eastern Australia have experienced dramatic multi-decadal changes in environmental conditions since 1960. Further, global climate models indicate that there will be continued change into the future (Ridgway and Hill, 2009).

In the following section we demonstrate compelling correlations between changes in physical characteristics of coastal waters in eastern Tasmania and ecological changes. We review and integrate changes already reported alongside novel observations to demonstrate that ecological changes linked to increased EAC intensity over recent decades apply across a broad range of species/groups.

## 4. Range expansion, and changes in population characteristics and community structure

### 4.1. Plankton communities

Thompson et al. (2009) reported a ~50% decline in the spring bloom biomass and growth rate (determined from remotely sensed chlorophyll *a*) at Maria Island from 1997 to 2007, but they did not detect any change in the degree of surface water stratification or nitrate concentrations over the same period. Since recent annual mean concentrations of silicate at Maria Island are below the half saturation value for diatom uptake, they suggest that a long-term decrease in dissolved silicate concentrations in east coast waters, driven by poleward transport of warm low silicate EAC water, could be restricting phytoplankton growth. Thompson et al. (2009) anticipate shifts in east coast diatom species, long-term declines in east coast diatoms as a proportion of the total phytoplankton community, and a reduction in primary productivity if the decline

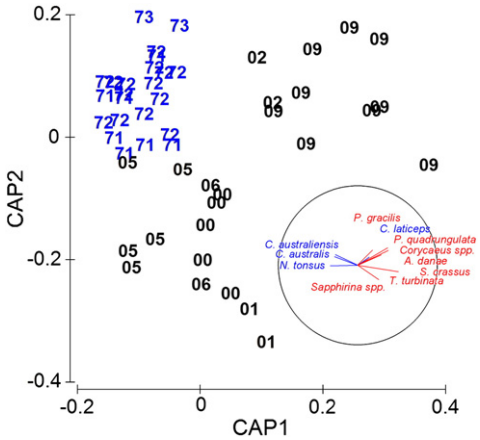


**Fig. 3.** CAP (Canonical Analysis of Principal coordinates) ordination of zooplankton community composition in samples collected off Maria Island in 'cool' (1971, 1972, and 1973) and 'warm' (2000, 2001, 2002, 2005, 2006, and 2009) years (based on a Bray Curtis similarity matrix of square-root transformed data for 34 species). The CAP analysis was constrained to differentiate among years, and shows clearly that community composition in the 1970s is distinct from that over the past decade (2000–2009). There is also some evidence that zooplankton assemblages in 2002 and 2009 differ from other sampled years within the past decade. The vector overlay represents Pearson correlations between the ordination axes and abundances of recognized cold water 'signature' species (blue) and warm water EAC 'signature' species (red). Genus names for signature species are provided in Fig. 4. Note that most years are represented by samples across several months, while all of the 2005 and 2006 samples were from October. However, CAP analyses performed on data sets filtered by season, and for the data set containing signature species only, generated qualitatively equivalent ordinations to that shown, i.e. with a distinctive grouping of 'cold' years from the 1970s.

in silicate concentrations continues. In a related study, Thompson et al. (2008) suggest that the observed rise in local dominance of dinoflagellates in the Huon Estuary (southeastern Tasmania) from 1996 to 2005 may also be related to intensification of the EAC, but the idea requires critical testing.

This is not to suggest that all observed broad scale shifts in phytoplankton composition over recent decades imply intensification of the EAC as the underlying mechanism. Hallegraeff et al. (2008) report apparent range expansion of the red-tide dinoflagellate *Noctiluca scintillans* from New South Wales into southern Tasmanian waters since 1994. However, it is difficult to unequivocally attribute this to changes in oceanographic conditions as eutrophication and ship ballast water translocations continue to alter species distributions for microalgae such as *N. scintillans* (Hallegraeff, 2010). Furthermore, northward spread of *N. scintillans* from Sydney to Cairns on the east coast of Australia, and to Port Esperance on the west coast of Australia, since 2005 (Hallegraeff, 2010) is consistent with the epidemiological spread of an invasive species aided by anthropogenic vectors, and is unlikely to reflect effects of climate change.

Information on the impacts of climatic change on zooplankton communities in Australia is extremely limited (Richardson et al., 2009), and there is no documentation of long-term changes in species assemblages in the region. Here, we present new evidence for distinct shifts in zooplankton communities off the east coast of Tasmania (Maria Island) between the 1970s and the period from 2000 to 2009 (Figs. 3 and 4). This shift is noticeable both in terms of overall community composition (Fig. 3) and in the relative dominance of recognized 'signature species' of cold and warm water masses. Cold water signature species are generally more abundant in samples collected off Maria Island during the 1970s, while warm water (i.e. EAC associated) species are far more prominent in samples collected

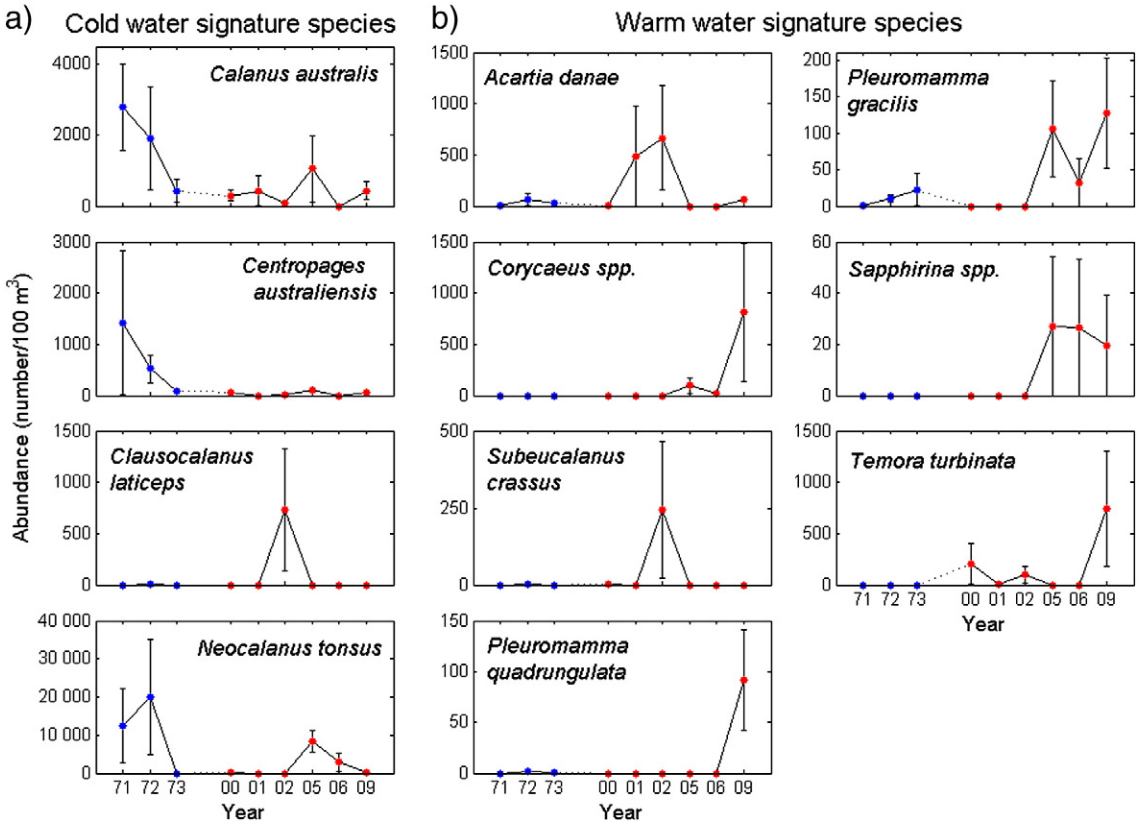


**Fig. 4.** Changes in zooplankton abundance (mean ± SE) in samples collected off Maria Island for (a) cold water 'signature' species (first column of plots) and (b) EAC 'signature' species (second and third columns of plots). Cold water species are generally more abundant in samples collected during the 1970s, while EAC associated species have become more prominent in samples collected between 2000 and 2009. Results for signature species with low abundances (maximum <30 individuals/100 $m^3$) are not presented.

between 2000 and 2009 (Fig. 4). Occasional spikes in cold water species (e.g. a peak in abundance of *Clausocalanus laticeps* in 2002; Fig. 4) emphasize the highly labile nature of oceanography in eastern Tasmania (e.g. Ridgway, 2007a), and we should expect to detect ongoing occasional pulses of cold water, e.g. that may reflect northward movement of sub-Antarctic water driven by periods of strong westerly wind (Harris et al., 1991, 1992), overlaying an otherwise overall warming trend.

### 4.2. Macroalgae

One of most notable changes to macroalgal communities in Tasmania in recent decades is the dramatic decline in the extent of giant kelp (*M. pyrifera*) forests (first documented by Sanderson, 1990). Giant kelp in Australia is found predominantly in the southeast where water conditions are cool and relatively nutrient rich. Dense *M. pyrifera* beds forming a closed or semi-closed surface canopy represent a distinctive and important habitat type on shallow (to ~25 m depth) Tasmanian subtidal reefs. These beds were once sufficiently large to be harvested commercially (Sanderson, 1987; Edyvane, 2003) but in many areas in eastern Tasmania, and particularly in the northeast, their extent has declined dramatically, especially since the 1980s.

The decline in extent of *M. pyrifera* beds forming dense surface canopies is clearly evident from a series of aerial photographs (from the photographic archives of the Department of Primary Industries, Parks Water and Environment) of seven regions taken from 1946 to 2007 (Fig. 5). Across all seven sites, average canopy extent in the last decade is ~9% of average canopy extent in the 1940s, with declines of 95% around Freycinet Peninsula and Maria Island (regions (b) and (c) in Fig. 5), and a 98% decline around Bruny Island further south (region (f) in Fig. 5). It is worth noting that there is presently extensive cover of *M. pyrifera* surface canopy in the Southport area (region (g) in Fig. 5), indicating recent recovery not yet surveyed. In general, declines in surface canopy cover are less pronounced in southern regions than in northern regions in eastern Tasmania. This is consistent with progressive southward penetration of warm, salty, nutrient-poor EAC water, which is now found ~350 km further south than 60 years ago (Fig. 2; Ridgway, 2007b), and greater likelihood of relatively cooler and more nutrient rich water influencing the southern rather than the northern parts of the east coast of Tasmania (Harris et al., 1992). These trends are not readily explained by the usual 'boom and bust' dynamics of *M. pyrifera* populations (e.g. Dayton et al., 1984), although large inter-annual fluctuations in cover are nonetheless evident in some of the areas we analyzed (Fig. 5).

While increased influence of the EAC is very likely to be the ultimate cause of declines in extent of dense stands of *M. pyrifera* in Tasmania, the proximal cause remains unclear because warm temperatures and low nutrients are confounded under EAC influence. It is well established that growth and survival of seaweeds is strongly influenced by temperature, salinity and nutrient levels (Lobban and Harrison, 1997). While no seaweed is known to be affected by increases in salinity as small as those associated with the advent of EAC water in eastern Tasmania (only ~0.5‰ over ~50 years; Hill et al., 2008; Fig. 2), laminarian species in particular have been reported to be sensitive to the relatively small absolute increases in temperature (Gunnill, 1985; Lüning and Freshwater, 1988; Dayton et al., 1999) and declines in nutrient concentration (Dean and Jacobsen, 1986; Graham et al., 2007) of the order experienced in eastern Tasmania.

Notably, unlike other laminarian species (e.g. Chapman and Craigie, 1977; Gangé et al., 1982), adult *M. pyrifera* sporophytes have limited capacity to store nitrogen (Gerard, 1982a), and so this species is likely to be particularly affected by decreased nutrient loading. Growth in *M. pyrifera* is likely to be greatly limited in nitrate concentrations <1 μM (Gerard, 1982b), which is typical of EAC water over most of the year. Some experimental work suggests that reduced growth of *M. pyrifera* during El Niño is through nutrient limitation and not elevated temperatures (Dean and Jacobsen, 1986), although it seems clear that both warming and reduced nitrate levels during events such as El Niño can both significantly reduce growth and photosynthesis (Gerard, 1984). Results from experimental manipulations conducted by Hernández-Carmona et al. (2001) indicate that nutrients directly affect recruitment and survival of *M. pyrifera* at its southern limit in Baja California, Mexico, and that plants may be affected by synergistic nutrient and temperature stress. Certainly it is well established that the advent of warm nutrient-poor water can cause widespread decline in *M. pyrifera* (e.g. Edwards and Estes, 2006).

Valentine and Johnson (2004) suggested that an unusual dieback of the shallow sublittoral brown macroalga *Phyllospora comosa* along the east coast of Tasmania in 2001 may have been in response to above-average seawater temperatures coupled with nutrient stress. However, with few exceptions (e.g. Edwards and Estes, 2006),

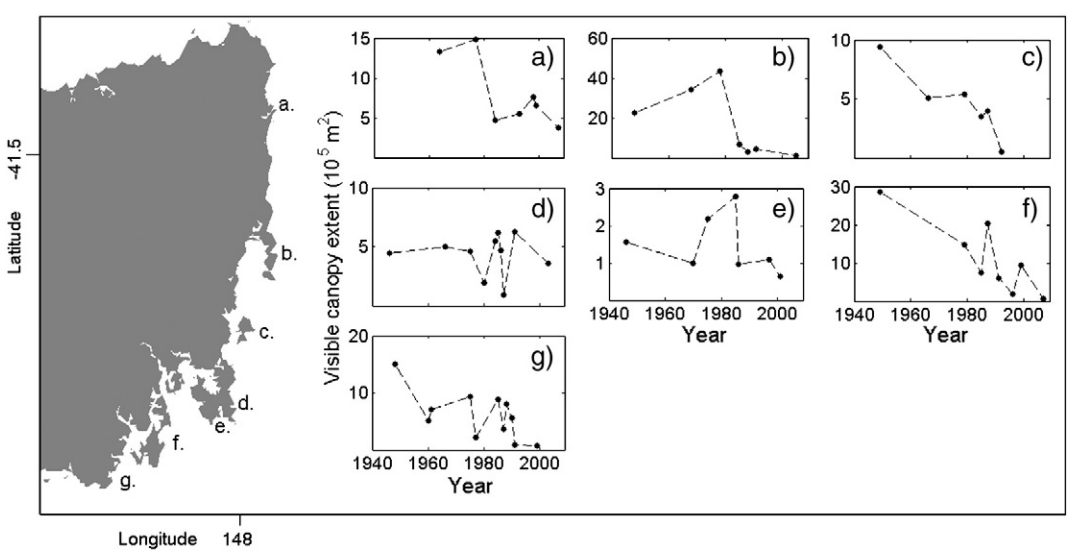


**Fig. 5.** Change in extent of visible surface canopy of *Macrocystis pyrifera* in seven regions (a)–(g) on the east coast of Tasmania, 1940–2007. Visible dense surface canopy was digitized from aerial photographs. Average canopy extent in the last decade is ~9% of average canopy extent in the 1940s, with 95% declines in regions (b) and (c), and a 98% decline in region (f). Note that extensive cover of *M. pyrifera* beds has been observed in region (g) over the 2009–2010 period, however quantitative survey data are not available.

responses of seaweeds to simultaneous changes in temperature and nutrients have not been adequately addressed in the context of long-term oceanographic change. The response of individual species, and of macroalgal communities as a whole, to the individual and combined effects of chronic warming and nutrient depletion is clearly an important direction for future research. Changes in the density, distribution, or production of canopy-forming macroalgae are likely to have widespread 'downstream' effects on the structure and functioning of seaweed-based communities as a whole (Dayton et al., 1984; Reed and Foster, 1984; Johnson and Mann, 1988; Schiel, 1988), but it may be difficult to separate the effects of changes in nutrients, temperature and other characteristics influenced by shifts in oceanography and/or climate. In Tasmania, the effects of oceanographic changes on macroalgal habitats are confounded with dramatic ecological change brought about through overgrazing by the barrens-forming sea urchin *C. rodgersii* (Johnson et al., 2005; Ling, 2008; Ling and Johnson, 2009; see below).

### 4.3. Macroinvertebrates

Among macroinvertebrate species in Tasmanian rocky reef habitats, *C. rodgersii* (the long-spined sea urchin), *H. rubra* (blacklip abalone) and *J. edwardsii* (the southern rock lobster) are important both economically and ecologically. All three show evidence of biological responses to recent climate-driven oceanographic change. There is now strong evidence that the barrens forming sea urchin *C. rodgersii* has undergone a poleward range expansion from New South Wales to Tasmania over the past ~40 years (Johnson et al., 2005; Ling et al., 2008, 2009b). Surveys in the Kent Island Group in Bass Strait (between Tasmania and mainland Australia) from 1974 to 2000 indicate initial establishment of *C. rodgersii* in the 1960s followed by reasonably rapid spread (Fig. 6 and Table B1, Appendix B). The first individual recorded in north eastern Tasmania was in 1978 (Edgar, 1997), and data from surveys conducted between 2000 and 2002 at locations along the entire east coast of Tasmania (Johnson et al., 2005) demonstrate subsequent expansion of populations to the urchin's current status as a common and, in some places, dominant invertebrate on shallow subtidal rocky reefs (Fig. 7).

Developmental and genetic studies support the notion that range expansion of *C. rodgersii* has been mediated by poleward extension of the EAC. Successful larval development of this sea urchin species requires water temperatures ≥12 °C, and warming of eastern Tasmanian waters has resulted in more favourable conditions for the reproduction and development of *C. rodgersii*, particularly since ~1980 (Ling et al., 2008; Fig. 2b). The clear indication of the combined results from microsatellites (Banks et al., 2010) and allozymes is equivalent genotype proportions and little genetic differentiation between New South Wales, Bass Strait and Tasmanian populations of *C. rodgersii* (Table 1 and Tables B2–B4, Appendix B). Genotypes do not deviate from expected Hardy–Weinberg proportions and there is no evidence of significant differences in observed heterozygosity or allelic diversity between populations (Table 1). Overall $F_{ST}$ (i.e. for all populations combined) was higher than pairwise $F_{ST}$ estimates for the microsatellite dataset, but not for the allozyme dataset. For both datasets, pairwise $F_{ST}$ between the southern Tasmanian population at the edge of the range and the New South Wales population was greatest, although this was non-significant after adjustment for multiple comparisons.

These results indicate absence of a founder effect, and support the concept of sustained transport of *C. rodgersii* larvae from the native range in New South Wales rather than a single chance dispersal event (or small number of events) to Tasmania, with subsequent recruitment. There has been no loss of genetic diversity or increased genetic differentiation during the southward range expansion of *C. rodgersii*. Populations established via a founder event are likely to exhibit both a reduced number of alleles as well as heterozygote deficit compared with long-established populations within the main range. The consistent combined results suggest a demographic scenario of repeated immigration and recruitment events from pre-expansion source populations in New South Wales.

Range expansion in and of itself need not necessarily greatly influence community structure or ecosystem processes and, of course, range boundaries can be dynamic in natural circumstances. However, the southward incursion of *C. rodgersii* into Tasmania represents a critical threat to the integrity of nearshore subtidal reef systems because this species is able to overgraze productive macroalgal

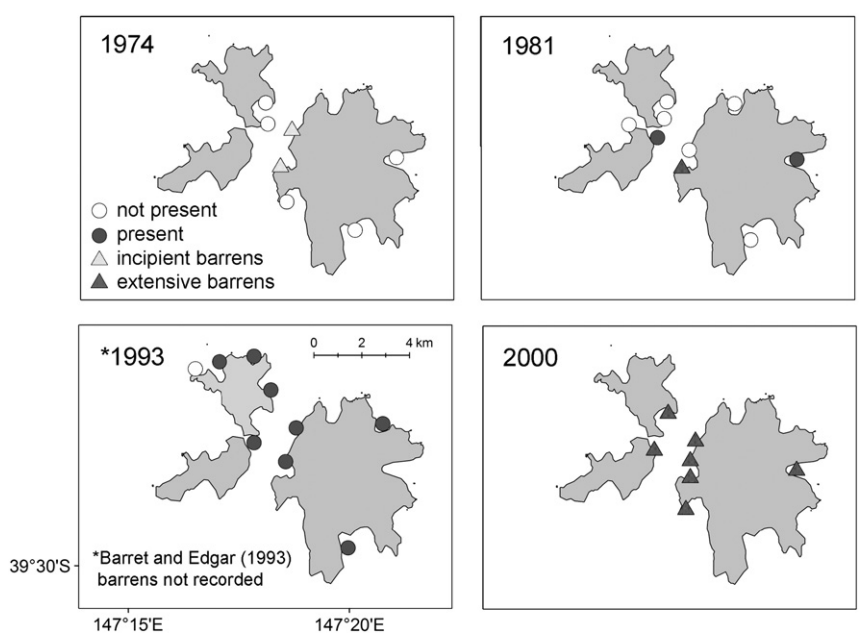


**Fig. 6.** Distribution of *Centrostephanus rodgersii* and barrens habitat in the Kent Island Group, Bass Strait, from surveys in 1974, 1981, 1993 and 2000. The observed pattern is consistent with range expansion of *C. rodgersii* over a 20–30 year period, and a pronounced, concurrent increase in the extent of sea urchin barrens. Note that surveys conducted by Barrett and Edgar (1993) quantified densities of *C. rodgersii* but did not record the presence or extent of any *C. rodgersii* barrens habitat. Quantitative data used to generate these maps are provided in Table B1 (Appendix B).

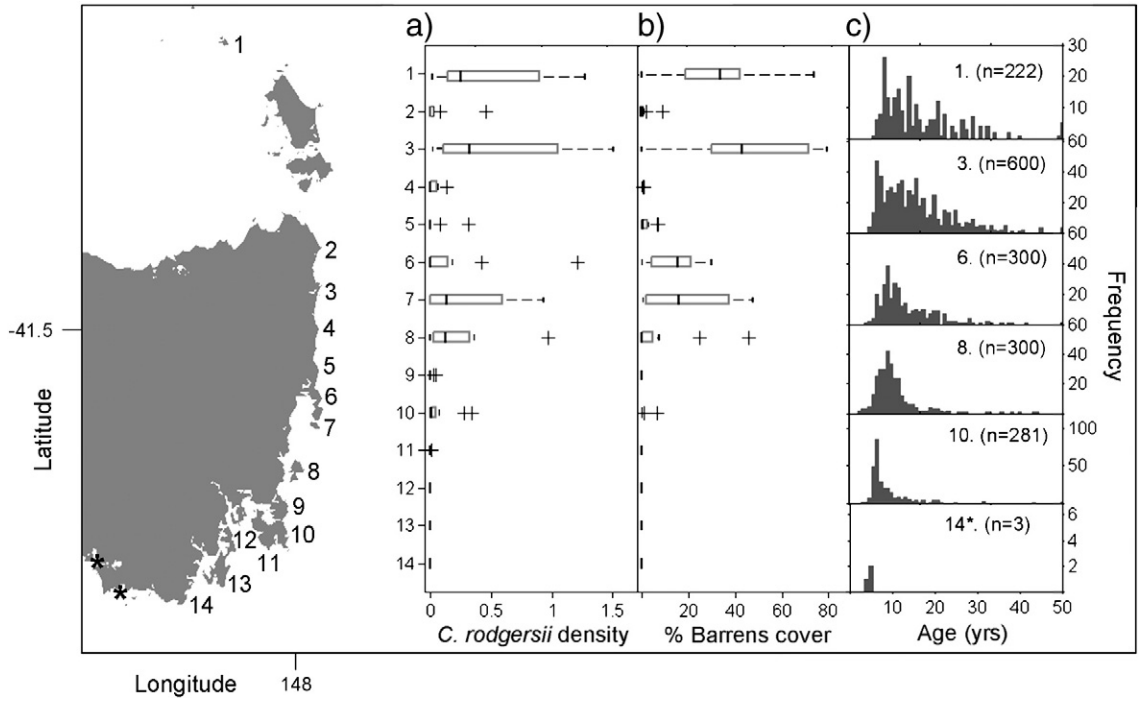


**Fig. 7.** Evidence for range expansion of *Centrostephanus rodgersii* from 14 survey locations in eastern Tasmania. Box plots showing (a) mean density of *C. rodgersii* (individuals $m^{-2}$) and (b) percentage cover of barrens habitat indicate that both sea urchin abundance and barrens habitat decline southwards along eastern Tasmania. Age frequency distributions (c) reflect initial colonization in the north east and support the hypothesis of recent range expansion mediated by increasing southward larval transport. The number of individuals sampled to generate age frequency distributions is indicated in parentheses in panel (c). Data were collected in 2000–2002 (density and barrens cover) and 2005 (age frequency data).

habitat to form 'sea urchin barrens' supporting high densities of sea urchins, but largely devoid of macroalgae (Andrew, 1989, 1993; Figs. 6 and 7b). *C. rodgersii* barrens covers ~50% of nearshore reef in New South Wales (Andrew and O'Neill, 2000) and around some Bass Strait islands and St. Helens in northeast Tasmania (Fig. 7b). Extensive *C. rodgersii* barrens occur at several locations in the northern half of the Tasmanian east coast, but decline with latitude and do not yet occur in southeast Tasmania (south of Tasman Peninsula) where the sea urchin is nonetheless present (Fig. 7a and b). At the southern extent of barrens habitat on the open coast, barrens are incipient and occur as small patches in otherwise intact macroalgal beds (Johnson et al., 2005).

Importantly, strengthening of the EAC, which is the ultimate cause of range extension of *C. rodgersii* into Tasmanian waters, is not responsible for the subsequent population expansion to the point where destructive grazing commences. The primary predator of *C. rodgersii* in eastern Tasmania is the southern rock lobster (*J. edwardsii*), and there is clear evidence that only large individuals – the supra-legal size classes – are capable of successful predation on emergent *C. rodgersii* (Ling et al., 2009a). Thus, formation of *C. rodgersii* barrens in Tasmania arises as an interaction between climate change, which facilitated the incursion in the first instance (Johnson et al., 2005), and ecological overfishing of large rock lobsters, which eroded resilience of the seaweed beds and enabled densities of the sea urchin to build to the point where destructive grazing could occur (Ling et al., 2009a).

Climate change may not only affect marine invertebrates by facilitating establishment of new species, but may also significantly affect the population characteristics of long established residents. Nowhere is interest in this question more keenly focused than on harvested species. Tasmania's two most valuable fisheries are black-lip abalone (*H. rubra*, valued at ~AUD$100M pa before processing; Tasmania supplies ~30% of the global wild caught abalone market), and southern rock lobster (~AUD$70M pa; ABARE, 2010). Should climate change significantly affect key parameters such as recruitment, growth, reproduction or survivorship of these important commercial species, there is the likelihood of serious socio-economic

**Table 1**
Summary of genetic diversity and differentiation analyses of allozyme and microsatellite genotypes from *Centrostephanus rodgersii* sampled in New South Wales, Bass Strait and Tasmania in 2000. Values for genetic diversity statistics $H_E$ (expected heterozygosity), $F_{IS}$ and AD (allelic diversity — the number of alleles sampled per site) are presented as means with standards deviations in parentheses. $F_{ST}$ values were estimated from an Analysis of Molecular Variance in Arlequin 3.11 and standardized according to Meirmans (2006).

| | | Allozyme data | | | | Microsatellite data[(a)] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Site | Overall | NSW | Bass Strait | Tasmania | Overall | NSW | Bass Strait | Tasmania |
| Genetic diversity | $H_E$ | 0.53 (0.29) | 0.57 (0.29) | 0.54 (0.28) | 0.49 (0.3) | 0.56 (0.2) | 0.55 (0.2) | 0.56 (0.21) | 0.56 (0.21) |
| | $F_{IS}$ | 0.18 (0.17) | 0.12 (0.16) | 0.22 (0.3) | 0.09 (0.14) | 0.07 (0.19) | 0.08 (0.28) | 0.06 (0.18) | 0.07 (0.2) |
| | AD | 5.5 (2.2) | 5.75 (2.5) | 5.5 (2.08) | 5.25 (2.06) | 7.79 (5.85) | 5.88 (4.39) | 9.13 (7.24) | 8.38 (6.16) |
| | | Overall | NSW — Bass Strait | Bass Strait — Tasmania | NSW — Tasmania | Overall | NSW — Bass Strait | Bass Strait — Tasmania | NSW — Tasmania |
| AMOVA | $F_{ST}$ | 0.0003 | 0 | 0 | 0.005 | 0.011 | 0.004 | 0.006 | 0.019[(b)] |
| | Standardized $F_{ST}$ | 0.0007 | | | | 0.029 | | | |

[(a)] Modified after Banks et al. (2010).
[(b)] P = 0.0168. Not significant after P value adjustment for multiple comparisons.

consequences, particularly in rural regions given that the major ports for these fisheries are distributed widely. Moreover, both species play significant roles in influencing the dynamics of the rocky reef communities in which they reside.

There is good evidence that water temperature directly affects the population biology of *H. rubra* in Tasmania. Maximum growth rates of juveniles, size at maturity and maximum shell length of populations of wild blacklip abalone populations were estimated for a large number of sites spanning a natural temperature gradient (Fig. 8). Because abalone growth rates decline rapidly after the onset of maturity, maximum lifetime growth rates are achieved during the juvenile stage. While there is no evidence that temperature over the range currently experienced in Tasmania affects maximum growth rate (Fig. 8a), increasing mean annual temperature significantly reduces size at maturity and therefore maximum shell length in wild populations (Fig. 8b and c). These trends suggest that production in the fishery will decrease with ongoing warming, however these data represent only an initial exploration of the question. The effects of changed EAC conditions on abalone population biology and the consequences for community ecology and the fishery are still unclear.

The influence of oceanic change off eastern Tasmania on the growth and recruitment dynamics of southern rock lobster (*J. edwardsii*) is also somewhat uncertain, although initial assessments have predicted significant effects of climate change on the fishery (Pecl et al., 2009). Given a strong latitudinal cline in growth rate, with relatively rapid growth and much larger sizes in the north than in the south of the State (Frusher, 1997), it might be tempting to suggest a role for temperature given relatively cooler waters in the south. However, there are potential alternative mechanisms to explain this: the differences in growth rate may stem from density dependent intra-specific competition since densities are much greater in the south (Frusher, 1997), or there may be differences in the type of food available (Guest et al., 2009).

Interestingly, there appear to be no strong relationships between some key population characteristics and temperature across years at particular sites, suggesting relatively minor effects of temperature within the range experienced over the last 1–2 decades. For example, no relationship is evident between size at maturity of female lobsters and mean water temperature (averaged over the four year growth period prior to maturity) for data collected between 1992 and 2004 at two sites (Fig. 9a). Mean residual annual growth increments for male lobsters (from tag/re-capture studies conducted between 1992 and 2003) are negative at low and high temperature extremes, and positive at intermediate temperatures (Fig. 9b). This is suggestive of an optimal mean temperature for growth between ~13 °C and 14.5 °C, however further research is required to confirm this relationship and to explore possible physiological mechanisms. Interpretation is complicated by the capacity of some young lobsters within the size range examined to moult twice within a year; these are the individuals that generate the large positive residuals between about 13.3 °C and 14.4 °C mean annual water temperature (Fig. 9b).

Monitoring rock lobster recruitment (i.e. settlement of final-stage puerulus larvae) indicates lack of any relationship between puerulus settlement and temperature in south eastern Tasmania (Recherche Bay; Fig. 9c) but a significant negative relationship in north eastern Tasmania (Bicheno; Fig. 9d). While the drivers for settlement of rock lobster puerulus throughout its distribution in south eastern Australia are uncertain, the position of the sub-tropical convergence (STC), where the EAC meets cooler Southern Ocean water, does appear to be important for puerulus recruitment in eastern Tasmania (Pecl et al., 2009). These authors suggest that extension of the STC northward during autumn and winter provides puerulus recruits to the Tasmanian east coast. If so, then a stronger EAC which results in reduced northerly penetration of the STC is likely to result in fewer larvae reaching north easterly and mid-easterly regions of Tasmania. As the EAC penetrates further southwards, northeastern and eastern regions of Tasmania are likely to experience continued decline in puerulus settlement. It is unclear why purelus settlement in south-easterly regions is unaffected by increasing temperature, or is even slightly positive (Fig. 9c), and whether this will eventually change to the pattern of declining puerulus settlement with temperature found in northern regions. Changes in puerulus recruitment rates may also reflect reduced survival of mid-stage *J. edwardsii* larvae under higher water temperatures (Bermudes and Ritar, 2008).

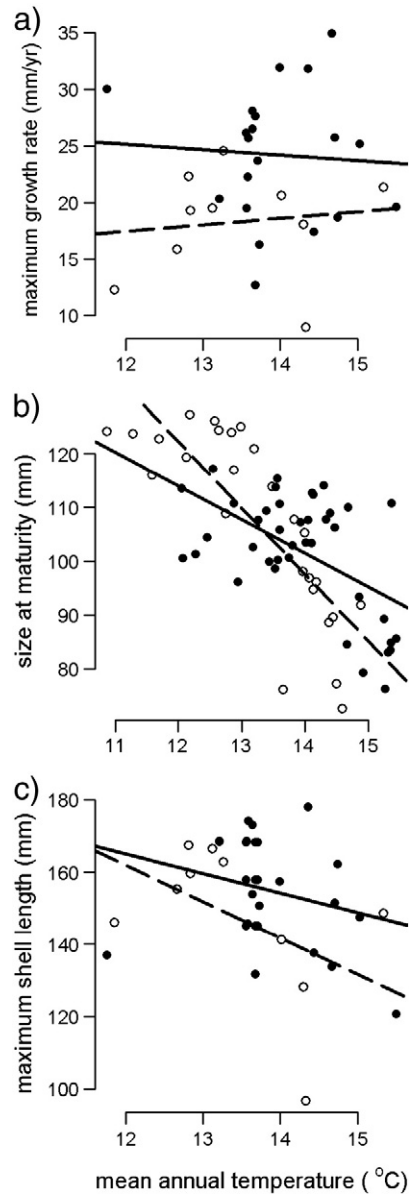


**Fig. 8.** Correlations of mean annual water temperature with (a) maximum growth rate (n = 30), (b) size at maturity (n = 66) and (c) maximum shell length (n = 30) of blacklip abalone (*Haliotis rubra*) in Tasmania. Mean annual sea surface temperatures were obtained for a total of 252 populations divided into east coast (filled circles) and west coast (open circles) by the 147.0° E longitude meridian. Regression lines were determined through linear correlation for both the east coast populations (solid line) and west coast populations (dotted line). Plots (a) and (c) refer to averages for individual reefs, while plot (b) presents data for statistical subregions of the abalone fishery. 1-way ANCOVAs indicate that temperature has no significant effect on maximum growth rate, but the effect of temperature on both size at maturity ($P<0.001$) and maximum shell length ($P<0.05$) is significant. The effect of temperature on size at maturity differs for east and west coasts ($P<0.05$), and there is a significant difference in maximum growth rates between east and west coast populations (i.e. lower maximum growth rates in west coast populations).

While we have focused on range expansion and population-level changes for ecologically and economically significant macroinvertebrates, it is worth noting that distributional changes are being

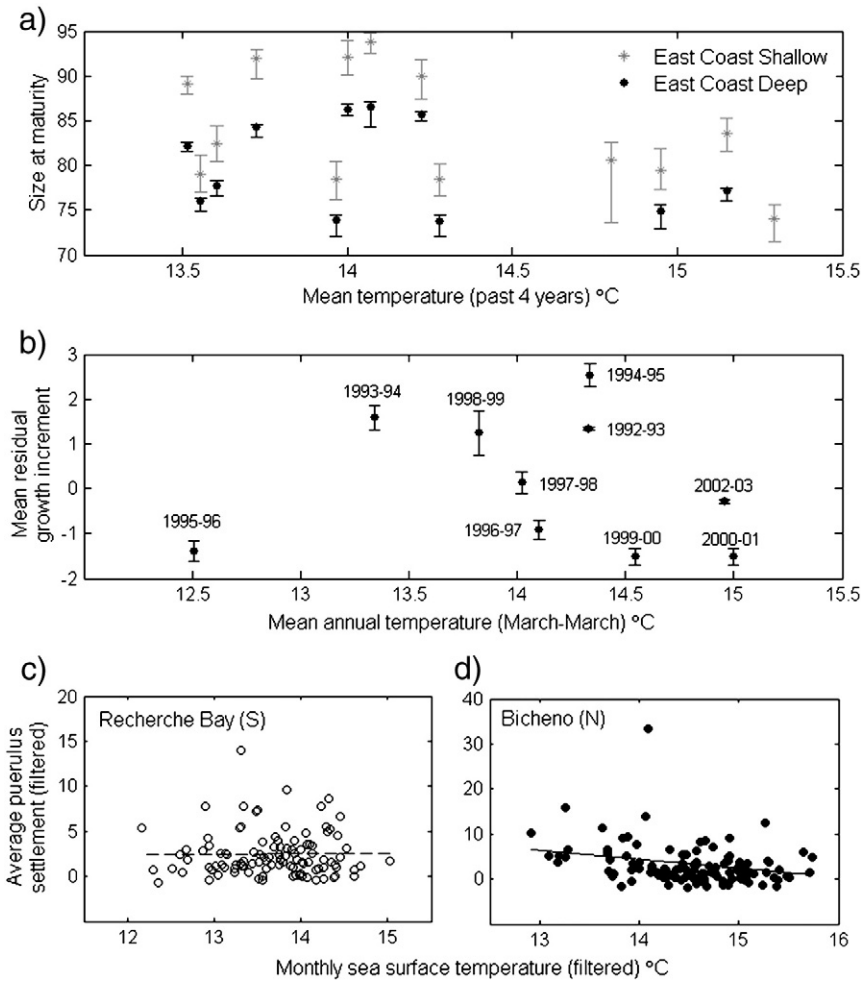


**Fig. 9.** Relationships between water temperature and rock lobster (*Jasus edwardsii*) population parameters in eastern Tasmania. (a) Mean size at maturity (±SE) of female lobsters versus average water temperature (water column to 50 m) over the previous four years (i.e. the assumed growth period prior to achieving maturity) at two sites at or near Maria Island on the east coast of Tasmania; data span from 1992 to 2004. The (linear) relationship between temperature and size at maturity is not significant at either site. (b) Mean residual growth increment (±SE) versus average temperature (water column to 50 m) over the year between tagging and recapture (March–March). Residuals are obtained from the linear regression of growth increment against carapace length. Data are for 1992–2003 from a single site. Average rock lobster puerulus larvae retrieved from standardized collectors (monthly, July–January inclusive across peak puerulus settlement) versus monthly sea surface temperature (SST) from 1994 to 2010 are presented for two sites: (c) Recherche Bay in the south east and (d) Bicheno in the north east. The seasonal signal was filtered out from both settlement and SST data (see Fig. A1, Appendix A). The linear relationship between total puerulus collected and SST is not significant for Recherche Bay ($P = 0.94$) and significantly negative for Bicheno ($P < 0.001$).

identified for other macroinverterbrates. Recent verified records (with photographic evidence) from 'RedMap' (http://www.redmap.org.au/) indicate southerly excursions for *Octopus tetricus*, *Plesiastrea versipora* (a tropical scleractinian coral) and *Jasus* (*Sagmariasus*) *verreauxi* (eastern rock lobster) in the order of 350–650 km, 80–100 km and 80–100 km, respectively.

### 4.4. Fish

Last et al. (2010) recently synthesized data from a range of sources – including published accounts, scientific surveys, spearfishing and angling competitions, commercial catches and under water photographic records – covering from the late 1800s to the present, to determine shifts in the distribution of coastal fish in south eastern Australia. Forty-five species, representing 27 families (about 30% of the inshore fish families occurring in the region), exhibited major distributional shifts, which the authors tentatively attributed to climate factors, and in particular recent intensification of the EAC. Addition of data to update Last et al. (2010), including additional records from the Australian National Fish Collection and RedMap, and focusing only on the east coast of Tasmania, reveals a total of 8 new records for fish species (assumed in most cases to be extra-limital vagrants), 7 newly established species, 20 cases of apparent range expansion (with good evidence that this has occurred in a southward direction for all but one of these species), and 21 cases of abundance increase since the early 1980s (Table B5, Appendix B). These changes apply across a broad range of fish families and functional groups, and at least 13 of the species for which changes have occurred are typically associated with *C. rodgersii* barrens habitat in New South Wales.

## 5. Evidence of cascading effects

### 5.1. Rocky reefs

A sequence of changes in rocky reef communities over recent decades emanating from the climate-driven establishment of *C. rodgersii* in eastern Tasmania provides the first documented example for Southern Hemisphere temperate reef systems of cascading ecological effects stemming, at least in part, from oceanographic change. The critical issue associated with the advent of *C. rodgersii* in Tasmania is the formation of barrens habitat caused by their overgrazing of macroalgae and intense predation on a wide range of sessile benthic invertebrates. Even at small spatial scales, barrens formation realizes a direct loss of ~150 macroscopic species (Ling,

2008), as well as loss of habitat and productivity. Formation of barrens habitat also negatively affects the two key commercial fisheries associated with Tasmanian rocky reefs (Fig. 10). In keeping with observations in New South Wales (Shepherd, 1973; Andrew and Underwood, 1992; Andrew et al., 1998), in eastern Tasmania there is a negative relationship between the abundance of *C. rodgersii* and the density of blacklip abalone (*H. rubra*; Fig. 10b), and there is a similar negative relationship with southern rock lobster (*J. edwardsii*; Fig. 10a). The density of abalone is significantly lower on barrens habitat than in adjacent macroalgal beds at the same depth and on the same substratum type (Fig. 10c), and it seems clear that both abalone and rock lobster are unlikely to occur in commercial quantities on *C. rodgersii* barrens. Furthermore, Strain and Johnson (2009) show that increased densities of *C. rodgersii* have negative effects on *H. rubra* in intact kelp beds before any sign of overgrazing and barrens formation. When densities of *C. rodgersii* were experimentally increased in intact algal beds, within 6 months abalone showed decreases in reproduction, growth and survivorship relative to controls.

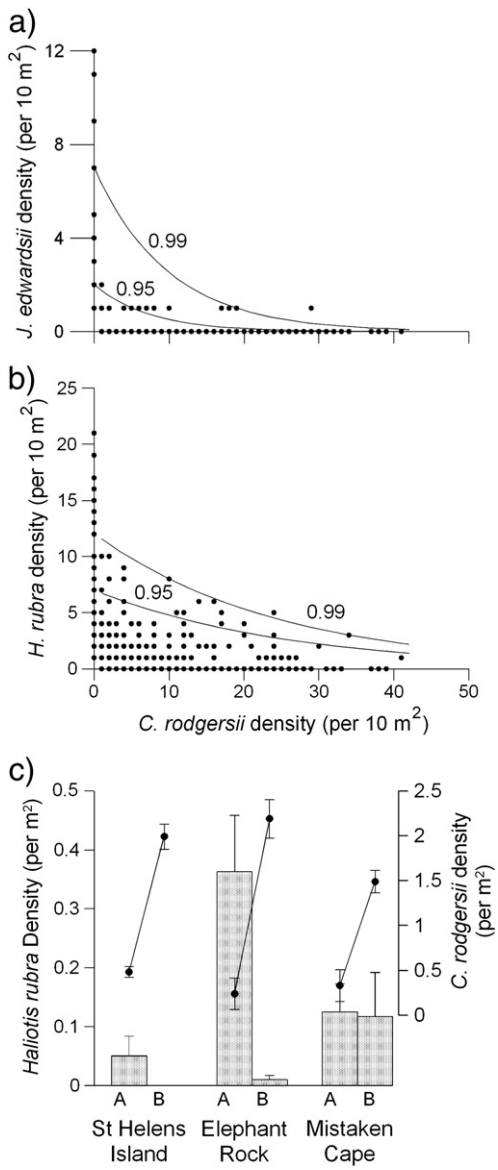


**Fig. 10.** Relationship between abundances of *Centrostephanus rodgersii* and (a) abalone (*Haliotis rubra*) and (b) rock lobsters (*Jasus edwardsii*) across locations 2–10 (as shown in Fig. 7). Quantile regressions (95th and 99th quantiles) reveal significant negative relationships in both cases. Paired-site data in (c) provides a comparison of *H. rubra* (bar chart, left hand axis) and *C. rodgersii* (line chart, right hand axis) densities in macroalgal habitat (A) and in adjacent barrens habitat (B) at 15–18 m depth at Elephant Rock (41° 15.30′ S, 148° 20.37′ E), St. Helens Island (41° 20.95′ S, 148° 20.15′ E) and Mistaken Cape (42° 38.86′ S, 148° 9.70′ E). *H. rubra* are significantly less abundant in barrens habitat than at adjacent sites supporting dense macroalgal cover at St. Helens Island and Elephant Rock (Model III 2-way ANOVA: transformation = $Y^{0.19}$; habitat (= fixed), $F_{1,1} = 264.4$, $P = 0.039$; site (= random) $F_{1,12} = 11.51$, $P = 0.005$; habitat*site, $F_{1,12} = 0.18$, $P = 0.677$). At Mistaken Cape, differences in abalone abundances inside and outside of small patches of barrens were not significant, reflecting the early stage of barrens formation at this site (i.e. 'incipient barrens').

The transition to barrens habitat is particularly problematic because, unlike other herbivores that overgraze, sea urchins are able to maintain populations on barrens (Johnson and Mann, 1988; Andrew and Byrne, 2007; Ling and Johnson, 2009) where they feed on microalgae, non-geniculate coralline algae and occasional drift algae. The stability of barrens habitats as an alternative community state to productive and diverse kelp beds has led Ling et al. (2009a) to refer to the transition as a catastrophic phase shift. Although expansion of *C. rodgersii* barrens arguably represents the single largest immediate environmental threat to rocky reef communities in eastern Tasmania, the distribution of barrens in the region is patchy, suggesting that the likelihood of barrens habitat formation is dependent on substratum and depth (Fig. 11). In Tasmanian waters, large continuous tracts of *C. rodgersii* barrens do not develop in shallow water (2–10 m) as occurs in New South Wales, but they largely occur within a depth range of ~10–20 m in Bass Strait, and ~15–35 m on the east coast of Tasmania (Johnson et al., 2005). Barrens habitat is more prevalent on boulder substratum than other types of consolidated reef, extending to cover >75% of the seafloor on this substratum at some locations, and averaging ~33% cover on boulder substratum across all survey locations in Tasmania where barrens occur. Given these collective observations, and estimates that boulders comprise ~55% of consolidated reef in depths ≤18 m and 34% of consolidated reef to ~40 m depth (Johnson et al., 2005), barrens habitat could potentially expand to cover ~50% of rocky reef on the east coast of Tasmania, as currently occurs in Bass Strait and New South Wales. This scenario has serious implications for the abalone and rock lobster fisheries on this coast.

The sequence of oceanographic change (i.e. intensification of the EAC) effecting local warming and increased larval transport, which facilitates range expansion of a key species acting as an 'ecosystem engineer' leading to a fundamental shift in ecological dynamics with concomitant threats to fisheries and sections of the local Tasmanian economy, is a clear example of cascading effects. While the role of anthropogenic climate change as a driver in this cascade is not fully certain, the proximate ecological mechanisms (reduction in predation of sea urchins due to fishing of large lobsters (Ling et al., 2009a), with subsequent formation of barrens habitat by *C. rodgersii* (Figs. 6, 7 and

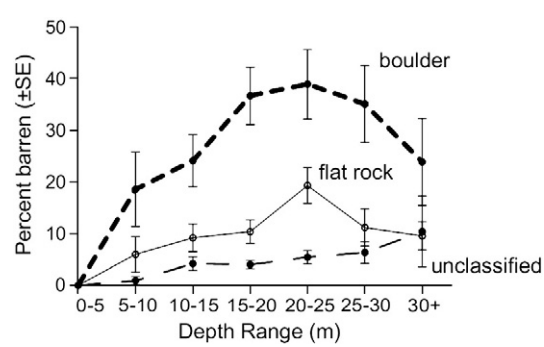


**Fig. 11.** Distribution of *C. rodgersii* barrens by depth for three main substratum types (boulder, flat rock and unclassified; unclassified indicates where the substratum type cannot be clearly interpreted from video transects). Data represent combined estimates from survey locations 2–10 (as shown in Fig. 7). Barrens are most common in the 15–30 m depth range, and occur most frequently on boulder substratum. Note that for the purposes of this figure, barrens refer to both extensive contiguous barrens and 'incipient' barrens, i.e. areas where barrens habitat occurs as distinct patches in seaweed beds.

10)), and proximate oceanographic mechanisms (intensification and poleward extension of the EAC effecting larval transport) are well understood. An associated but otherwise independent effect on rocky reef systems is the massive decline in the distinct and important habitat created by dense stands of giant kelp (*M. pyrifera*; Fig. 5). Coupled with potential effects on population parameters of key commercial species such as abalone (Fig. 8) and rock lobsters (Fig. 9) dependent on reef ecosystems, the combined influence of climate change on eastern Tasmanian rocky reefs, and the humans that depend on them, is already manifestly large.

It is important to mention that the large shifts in rocky reef communities documented here may not be evident in all parts of the system, particularly in shallow water. Stuart-Smith et al. (2010) report relative stability in shallow reef systems, largely surveyed at 5 m depth, around Tasmania over the past decade. This lack of change is not necessarily evidence of long-term stability, but may reflect that ecological change occurs in 'bursts' when thresholds of acclimatization and adaptation are exceeded (as discussed in Wernberg et al., 2010). In this context it is noteworthy that Pitt et al. (2010) document that 16 of 29 (=55%) intertidal species they examined demonstrated a mean southerly range shift of ~116 km since the 1950s.

### 5.2. Pelagic system

While our focus has been largely on the cascading ecological effects associated with range expansion and overgrazing by *C. rodgersii*, there is also evidence for 'bottom-up' driven change in the coastal pelagic system off eastern Tasmania, ostensibly stemming from reduced nutrient supply with increased influence of the EAC. Changes in phytoplankton and zooplankton communities in Storm Bay (south-east Tasmania) are strongly associated with changes in nutrient conditions forced by wind-driven circulation (Harris et al., 1991, 1992). Latitudinal changes in the position of subtropical high pressure cells over south-eastern Australia influence oscillations in Zonal Westerly Wind (ZWW) strength. High ZWW stress causes advection of colder, nutrient-rich sub-Antarctic water up the eastern side of Tasmania and reduces water column stability. This results in periodic overturn of the water column and increased production, with phytoplankton communities characteristically dominated by large diatoms. Reduced ZWW stress (under the influence of high pressure) leads to incursions of subtropical (EAC) water, increased water column stability and reduced biological production. In calm years, spring blooms tend to be weaker, and phytoplankton communities are dominated by small dinoflagellates, indicative of regenerated production (Harris et al., 1991). Although the physical mechanism described by Harris and colleagues that realized differential supply of nutrients to Storm Bay was not necessarily underpinned by climate change, we expect similar responses to intensification of the EAC increasingly delivering warm, low nutrient water to eastern Tasmania.

The observed changes in phytoplankton production and, in particular, size structure in response to declining nutrients have cascading effects for both zooplankton and the baitfish that feed on them. Reduced nutrient availability in warm years leads to reduced production and a shift to smaller phytoplankton species, resulting in a drastic reduction in the biomass of larger zooplankton, especially krill (*Nyctiphanes australis*). In summer, jack mackerel (*Trachurus declivis*) feed on krill in coastal waters but, in years of reduced availability of krill, *T. declivis* do not school in commercial quantities and the fishery fails (Harris et al., 1991, 1992). Failure of the jack mackerel fishery occurred at ~10-year intervals (during La Niña periods) off the east coast of Tasmania during the 1970s and 80s. However, since the 1980s an absence of swarms of *N. australis* and relatively low levels of jack mackerel have become the norm, not the exception, off eastern Tasmania. Over this period there has been a progressive replacement of *T. declivis* by redbait (*Emmelichthys nitidus*), which is recognized by Hobday et al. (2009) as an EAC-associated species. This long term trend suggests a directional shift in pelagic food chains associated with increased influence of nutrient-depleted EAC water on coastal eastern Tasmania, again with effects promulgating through the ecosystem to ultimately impact an established fishery. We point out that, despite its documented importance in the ecology of the pelagic system in eastern Tasmania, we did not include *N. australis* in our analysis of shifts in the zooplankton community (Figs. 3 and 4) because this species was treated differently across the several studies (some enumerated juveniles, others only adults) whose data we pooled for analysis.

## 6. Synthesis and future directions

We have presented evidence of distinct ecological changes across a range of marine taxa and communities in eastern Tasmanian in recent decades. These changes are associated with the increased influence of EAC water in the region, a high likelihood of reduced nutrient loading, and associated transport of heat and larvae (and, potentially, of metamorphosed individuals).

The observed changes encompass range expansions (*C. rodgersii* and a diverse array of fish species, some of which are associated with *C. rodgersii* barrens), and changes in abundance of key species (decline of *M. pyrifera* giant kelp beds and pelagic species such as *N. australis* and *T. declivis*, and increased abundance of a range of coastal fishes) and in overall community composition (shifts in zooplankton assemblages and other components of pelagic systems). In addition, trends in population parameters associated with temperature imply population-level changes in the commercially important blacklip abalone (*H. rubra*) and possibly in southern rock lobster (*J. edwardsii*).

Despite strong evidence that poleward extension of the EAC is the ultimate cause of ecological change in Tasmanian marine ecosystems, our understanding of proximate mechanisms varies depending on the species or functional group in question. In the case of *C. rodgersii*, there is a coherent body of evidence, including a myriad of manipulative experiments as well as broadscale surveys, showing southward range expansion facilitated by warmer water temperatures and successful development of *C. rodgersii* larvae transported from northern populations in New South Wales and Bass Strait. Overlaying this is the demonstrated synergistic interaction between oceanographic change and ecological overfishing of large predatory rock lobsters, leading to decreased resilience of kelp beds and their conversion to barrens habitat (Ling et al., 2009a) with subsequent loss of biodiversity and production.

To better interpret the relationship between increased influence of the EAC with decline in *M. pyrifera* in Tasmania, and building on the preliminary findings of Sanderson (1990), experiments are currently underway to separate the effects of increasing temperature from decreasing nutrients, and their possible synergistic interaction, on growth in *M. pyrifera*. Indeed, there is need across a variety of important ecological and commercial species for more experimental and modeling work to quantify the effects of temperature and/or nutrients on growth and other life history parameters, and to determine whether pronounced latitudinal patterns (e.g. in growth of lobsters) arise because of differences in temperature or in response to other factors associated with climate or factors unrelated to the physical environment. It is certainly well appreciated that many of the observations on biota in the Tasmanian context are simply broad correlations over relatively short time frames, and that these correlations do not imply cause and effect with climate change. While water temperature is clearly a major driver of the distribution, abundance, phenology and life-history of marine species (e.g. Harley et al., 2006; Cochrane et al., 2009), it is nonetheless only one of a suite of climate variables that can drive ecological change in marine systems (Harley et al., 2006). While there is good progress in south east Australia to identify climate related effects other than those directly related to temperature, more effort is warranted.

A notable gap in understanding concerns regional patterns in availability of nutrients, trace metals and other elements that may limit growth of photosynthetic species in the context of climate change. For example, although it is widely appreciated that (i) the EAC is characteristically oligotrophic, (ii) intensification of the EAC has realized much greater influence of EAC water in eastern Tasmania (Fig. 2), and (iii) declines in *M. pyrifera* (Fig. 5) and shifts in phytoplankton (Harris et al., 1991, 1992; Thompson et al., 2009) are consistent with declining nutrients, the only long term monitoring data (from the Maria Island Time Series station) does not show a trend in nitrate concentrations, although silicate has declined markedly (Thompson et al., 2009). This apparent paradox requires resolution; it is unclear whether trends in nutrients at Maria Island are representative of the entire Tasmanian east coast, and whether there are mechanisms that act to decouple the temperature and nutrient signals in this region.

Additional knowledge gaps that impede improved predictions about climate driven change in eastern Tasmanian marine systems include (i) uncertainty about mechanisms for change in pelagic ecosystems and the broad-scale implications of 'bottom-up cascades' for commercially important fish species, and (ii) effects on growth and recruitment dynamics of commercially important invertebrate species, in particular blacklip abalone (*H. rubra*) and the southern rock lobster (*J. edwardsii*). While temperature-related changes in size at maturity and maximum shell length of *H. rubra* are compelling (Fig. 8b and c), the direct effects of changed EAC conditions on abalone population biology are still unclear. The fact that relatively few years' of data are available to assess temperature driven changes in growth and recruitment of *J. edwardsii* (Fig. 9) means that it is difficult to detect patterns and to assign causal mechanisms with certainty.

Other potential climate change impacts on south eastern Australian marine ecosystems not adequately addressed include the effects of increasing acidification on marine organisms (Kroeker et al., 2010), the potential for increased risk of disease outbreaks with increasing temperatures (Harvell et al., 2002), and changes in growth rates of juvenile fish (Thresher et al., 2007). Temperate marine environments, such as south eastern Australia, may also be particularly vulnerable to phenological mismatches in predator–prey relationships, with potential impacts on food-web structures (Edwards and Richardson, 2004). As our findings have shown, impacts of climate change are influenced strongly by local- and meso-scale phenomena (e.g. fishing, oceanography; see also Wernberg et al., this issue), and ongoing work is attempting to better resolve interactions of these multiple influences. A critical issue for eastern Tasmania is the lack of contiguous land mass to the south, and thus southern Tasmanian species in particular are vulnerable in having nowhere to retreat in the face of ongoing warming and southerly expansion of northern species. Whether Tasmania's endemic species adapt to ongoing warming or decline remains to be seen.

In summary, pronounced changes have occurred in Tasmanian marine ecosystems over the past seven decades that correlate with multi-decadal, large-scale oceanic change in the region. In all of the examples presented, changes are associated with southward extension of the EAC, but improved understanding of proximate mechanisms is needed in several cases. Better understanding of the interactions between effects of climate change on individual taxa and the way that interactions between species mediate these effects is critical, both for marine resource management and our ability to make projections regarding future change (Hulme, 2005; Brown et al., 2010). Cascading ecological effects in marine ecosystems triggered by climatic change, and the manner in which direct climate change impacts promulgate to determine emergent ecological behaviors clearly have significant implications for marine ecosystem dynamics and functioning, and the nature and supply of marine resources into the future.

## Acknowledgements

We are grateful to Fiona Brodribb for providing information on out-of-range records for fish species from RedMap, and to Tasmanian recreational and commercial fishers and SCUBA divers for providing photographic records. Comments from two anonymous reviewers and the editor improved the manuscript. **[SS]**

## Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.jembe.2011.02.032.

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