

Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming

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Abstract

Despite increasing scientific and public concerns on the potential impacts of global ocean warming on marine biodiversity, very few empirical data on community-level responses to rising water temperatures are available other than for coral reefs. This study describes changes in temperate subtidal reef communities over decadal and regional scales in a location that has undergone considerable warming in recent decades and is forecast to be a 'hotspot' for future warming.

Plant and animal communities at 136 rocky reef sites around Tasmania (south-east Australia) were censused between 1992 and 1995, and again in 2006 and 2007. Despite evidence of major ecological changes before the period of study, reef communities appeared to remain relatively stable over the past decade. Multivariate analyses and univariate metrics of biotic communities revealed few changes with time, although some species-level responses could be interpreted as symptomatic of ocean warming. These included fishes detected in Tasmania only in recent surveys and several species with warmer water affinities that appeared to extend their distributions further south. The most statistically significant changes observed in species abundances, however, were not related to their biogeographical affinities. The majority of species with changing abundance possessed lower to mid-range abundances rather than being common, raising questions for biodiversity monitoring and management. We suggest that our study encompassed a relatively stable period following more abrupt change, and that community responses to ocean warming may follow nonlinear, step-like trajectories.

Keywords: climate change, community-level, East Australian current, latitudinal range, reef fishes, UVC

Received 12 January 2009 and accepted 25 February 2009

Introduction

Anthropogenically induced impacts are increasingly evident in marine communities, with climate change, removal of key predators and grazers by fishing, invasive species and pollution causing substantial alterations to community structure (Jackson *et al.*, 2001; Steele, 2004; Hays *et al.*, 2005; Southward *et al.*, 2005; Piazzzi & Ceccherelli, 2006). The need for long-term monitoring at the community level and over broad spatial scales has been recognized as crucial for understanding the nature and scale of these impacts (Hawkins *et al.*, 2003; Helmuth *et al.*, 2006; Halpern & Cottenie, 2007), yet datasets that fit these needs are rare for benthic marine commu-

nities, particularly in comparison to terrestrial, pelagic and intertidal marine communities (Beaugrand *et al.*, 2002; Thompson *et al.*, 2002; Walther *et al.*, 2002; Helmuth *et al.*, 2006; Richardson & Poloczanska, 2008). Growing evidence suggests that climate change, in particular, is having more substantial and rapid effects on marine communities than terrestrial ones (Richardson & Poloczanska, 2008), making the need for such data even greater and more urgent if a more comprehensive understanding of community responses to climate change is to be achieved.

Much current knowledge of the effects of climate change on marine organisms has resulted from either studies confined to a small number of species (Southward & Crisp, 1954) or locations (Sagarin *et al.*, 1999), or has been based on modelling studies (Poloczanska *et al.*, 2008). The exceptions largely relate to coral reef

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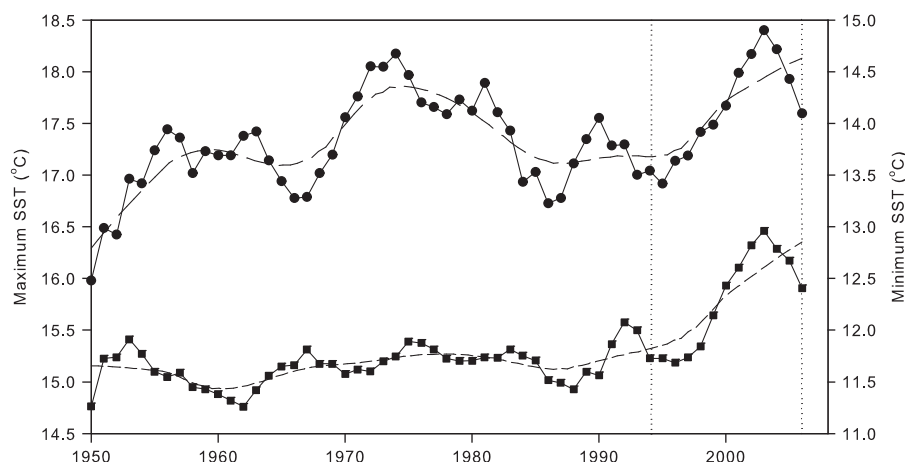


Fig. 1 Trend in maximum (circles, left axis) and minimum (square symbols, right axis) sea surface temperatures (5-year running means) on Tasmania's east coast with loess smoothers superimposed (dashed lines) to show the long-term trends. Raw data from CSIRO monitoring station off Maria Island, 148.23°E, 42.6°S (see Ridgway 2007 for more on trend).

associated taxa, plankton and fishes (Genner *et al.*, 2004; Hays *et al.*, 2005; Graham *et al.*, 2007b). Very few empirical studies have investigated decadal long term changes in benthic marine habitats at the community level (e.g. Tegner *et al.*, 1996; Currie & Parry, 1999; Bradshaw *et al.*, 2002; Lima *et al.*, 2007; Hiddink & ter Hofstede, 2008), and even fewer have done this over regional spatial scales. We undertook a study of subtidal reef communities over a decadal time scale, comparing data on fishes, macroinvertebrates and macroalgae collected at 136 sites, spanning hundreds of kilometres around the island of Tasmania (south-eastern Australia) in the early to mid 1990s, with data from the same sites in 2006/2007. The general objective was to examine broad-scale patterns of change in temperate reef communities; here we address specific hypotheses regarding anticipated impacts of climate change.

The south-eastern Australian coastline has experienced relatively rapid warming during the last century as a consequence of a strengthening of the warm East Australian Current (EAC) (Ridgway, 2007). The summer phenomenon of warm EAC water influencing the Tasmanian east coast has become more prominent due to ocean circulation changes linked in part to Antarctic ozone depletion (Cai *et al.*, 2005; Cai, 2006). The net outcome has been an increase in sea surface temperature (SST) of $2.28 \pm 0.35^\circ\text{C}$ per century for the period 1944–2002 (Fig. 1) (Ridgway, 2007), which is considerably more rapid than the global mean of $0.6 \pm 0.2^\circ\text{C}$ per century estimated by Smith & Reynolds (2003), and a mean increase in surface air temperature of $0.6\text{--}0.8^\circ\text{C}$ (Salinger, 2005; Hansen *et al.*, 2006). This warming off the Tasmanian east coast has exceeded warming

observed off the Tasmanian west coast [Japan Meteorological Agency, data accessed through the NOAA PMEL Live Access Server (<http://ferret.pmel.noaa.gov/LAS/home>)].

Although given less attention, winter minimum temperatures on Tasmania's east coast have also increased substantially, particularly over the last decade (Fig. 1), during the period of our study. Considering the logical importance of minimum temperatures in limiting the poleward endpoints of species ranges (e.g. Hutchins, 1947; Valiela & Bowen, 2003), it could be hypothesized that this sharp increase in Tasmanian winter SST during the last decade could lead to alterations in the ranges of south-east Australian reef species.

We tested the following hypotheses to assess whether this environmental change has directly altered Tasmanian subtidal reef communities between the early to mid 1990s and 2006/2007:

Hypothesis 1: Tasmanian subtidal reef communities have substantially changed over the past decade, with changes on the east coast greater than on the west and north coasts due to greater warming in the east. If supported, the south east community type identified in the 1990s should have converged towards the north east community type and the north east community type towards that found further north off the eastern Bass Strait islands (i.e. communities should have become more like those originally present in warmer regions to the immediate north).

Hypothesis 2: Changes over the past decade in the abundance of species correspond to their biogeographical affinities, such that warm-water species have

become more abundant and cool water species less abundant.

Hypothesis 3: Differences are evident in the highest and lowest latitude at which species were observed, such that the southern latitude limits of warm water species, and the northern latitude limits of cool water species, should have moved south (polewards) over the past decade.

Hypothesis 4: Eastern Australian species previously unrecorded from Tasmanian reefs should be detected in the recent survey.

Materials and methods

Data collection

Underwater visual censuses were used to assess changes in subtidal reef communities between 1994 and 2006. Censuses at 136 shallow reef sites around the Tasmanian coastline (Fig. 2) were undertaken during late austral summer and autumn in 1992, 1993, 1994 and 1995 (hereafter collectively referred to as 1994, as the majority of sites were censused in 1994), recording the abundance and size structure of fishes and mobile benthic macroinvertebrates (>2.5 cm) and cover of macroalgae (see Edgar *et al.*, 1997). Each of these sites was recensused in 2006/2007 (hereafter referred to as

2006). The 2006 surveys were primarily undertaken by a dive team that differed from, but was trained by, the original dive team.

Underwater census protocols have been described in detail by Edgar & Barrett (1997) and Edgar *et al.* (1997). In brief, the method involved divers laying four 50 m transect lines at each site, either along the 5 or 10 m isobath, depending on availability of reef habitat and local conditions (with transects laid at the same depth in both 2006 and 1994 surveys). The number and size of all fishes sighted within 5 m of the line during a swim up each side of the transect line were recorded, as were mobile macroinvertebrates within 1 m on one side of the line, where divers brushed aside the algal canopy. Thus, the number of fishes recorded at each site represented their relative abundance per 2000 m², and macroinvertebrates per 200 m². Fish sizes were estimated after practising with objects of known size, and were believed to be accurate and consistent (Edgar *et al.*, 2004). The size of rock lobster (carapace length) and abalone (shell length) were measured underwater to the nearest millimetre using callipers. The area covered by macroalgal species and sessile invertebrates was assessed by placing a 0.25 m² quadrat at 10 m intervals along the transect lines and estimating the percent cover of each species within the quadrat. This was achieved objectively by counting the number of times each species occurred directly under the 50 positions in the quadrat at which perpendicularly placed wires crossed each other. Understorey algae and sessile invertebrates were assessed after the canopy algae had been assessed and brushed aside; thus it was possible for estimated macroalgal cover to exceed 100%.

Data analysis

Taxa investigated. For all analyses, fish, invertebrate and macroalgal species for which taxonomy was uncertain or not recorded at the species level were combined with congeners. Data for schooling pelagic fishes such as *Arripis* spp., *Trachurus declivis*, atherinids and clupeids were omitted due to their highly patchy distributions. Cover of encrusting algae and sessile invertebrates was also omitted because methods of recording these taxa changed between monitoring periods.

Seasonal and interannual variability. Individual sites were censused in a similar season in the two survey periods whenever logistically possible in order to minimize seasonal biases in results. To assess whether conclusions were potentially influenced by temporal anomalies associated with a particular year of survey (see Barrett *et al.*, 2007), we tested whether the years used in the decadal analyses were different from the

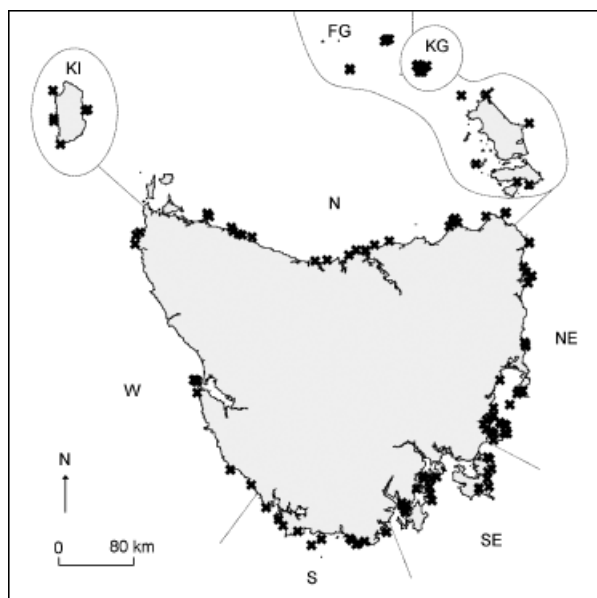


Fig. 2 Map of Tasmania showing location of reef sites censused in 1994 and 2006 (black crosses) and near-shore reef bioregions (boundaries indicated by dotted lines) as identified by Edgar *et al.* (1997). FG, Furneaux, Hogan and Curtis Groups; KG, Kent Group; KI, King Island; N, North coast; W, West coast; S, South coast; SE, Southeast coast, and NE, Northeast coast.

years immediately preceding or following them. For this assessment, we used data from a subset of 10 sites on the east coast of Tasmania, plus additional data collected at these same sites in the year before and following the 1994 and 2006 surveys using the same methods. These data were analysed using non-parametric analysis of variance (PERMANOVA; Anderson, 2001, McArdle & Anderson, 2001) and permutational analysis of multivariate dispersions (PERMDISP; Anderson, 2004a,b). The McArdle-Gower measure of dissimilarity with a base of 10 (Anderson *et al.*, 2006) was chosen for these analyses as we wished to test for changes in both abundance and composition, and this dissimilarity measure explicitly weights order-of-magnitude changes in abundance and change in species composition equally.

Only fish and invertebrate data were analysed for interannual variability because algal data were not available for all sites in the relevant years. A nested design was used with data from the year before, the year of, and the year after our surveys ('Year' factor) nested within the factor 'Decade' (1994 vs. 2006) to test whether the survey data we used differed from data collected at the same sites the year before and after. Dissimilarity values were ranked and *P*-values were obtained by permutation (4999 restarts).

Tasmanian reef community change – Hypothesis 1. To examine patterns of community change between 1994 and 2006, a combination of ordination procedures and hypothesis tests were conducted on the full dataset for fishes, invertebrates and algae. MDS and CAP (canonical analysis of principal coordinates; Anderson & Willis, 2003) based on Bray–Curtis dissimilarity of $\ln(x + 1)$ transformed data were used to visualize and test patterns in the data. Changes in univariate descriptors of community characteristics such as species richness, total fish abundance and cover of different functional groups of algae (i.e. canopy-forming brown, under-story brown, red and green macroalgae) were also analysed by one-way ANOVAS, with bioregion (as defined by Edgar *et al.*, 1997, shown in Fig. 2) as a fixed factor.

Change related to species' biogeographical affinities – Hypotheses 2 and 3. For analyses of changes associated with species' biogeographical affinities, species were categorized into four groups; eastern, western, southern and widespread species, based on their Australian distributions on inshore reefs reported in the literature (Womersley, 1984, 1987, 1994, 1996, 1998, 2003; Hutchins & Swainston, 1986; Kuiter, 1996; Edgar, 1997) and widely accepted temperate Australian biogeographical boundaries, as first described by Bennett & Pope (1960) and

more recently summarized by Waters & Roy (2003).

To explore changes in relative abundances of species, the abundances of species which showed the strongest indication of change between decades in CAP analysis (i.e. those for which correlation between first CAP canonical axis and 'decade' $|r|$ exceeded 0.2) were separately analysed using *t*-tests. Data were $\ln(x + 1)$ transformed as for CAP. Only sites at which a species was found in at least one of the survey years were used in paired *t*-tests. The large number of correlations investigated here, and *a posteriori* selection of species based on CAP results, likely generates some Type I statistical errors associated with significant indication of a change when no real change has occurred. We did not apply an adjustment to the *P*-value (such as Bonferroni's correction) to avoid inflating Type II errors (i.e. missing a real change because of poor power of tests), following the recommendation of Anderson *et al.* (2008) to consider the set of tests as a whole, in probabilistic terms. Regardless, individual *t*-test results must be interpreted with caution, particularly those with marginally significant results ($P > 0.01$).

A second analysis was conducted to determine whether changes in species abundances were related to their biogeographical affinities. For this, the mean differences in the relative abundance of species across sites between decades [$\ln(x + 1)$ transformed] were used as replicates in separate one-way ANOVAS for fishes, invertebrates and algae, with biogeographical affinity as a fixed factor (four levels).

Changes in the southern-most and northern-most latitudes that species were recorded were also analysed by one-way ANOVA, with the biogeographical affinity of species again a fixed factor and the change in the southern-most or northern-most latitude at which each species was recorded between decades as the response variable. Fishes, invertebrates and algae were separately investigated, with the omission of species recorded in only 1 year (species recorded only in 1 year were considered separately).

Results

Interannual variability

Based on the subset of 10 sites studied over many years, no evidence of substantial interannual variability was found among years before and after those that we used for comparison of communities between 1994 and 2006. While fish communities differed between 1994 and 2006 in the subset of sites, neither fish nor invertebrate communities differed in multivariate location or dispersion among the years 1993, 1994 and 1995, nor among the years 2005, 2006 and 2007 (Table 1). Pair-wise tests

showed no significant differences between any of the 3 years within either decade (all $P > 0.257$). These results suggest that reef communities in 1994 and 2006 were representative of the applicable 3-year period (i.e. they were not anomalous years) and comparisons of communities based on the full dataset are unlikely to be strongly confounded by variability on short interannual scales in community characteristics.

Tasmanian reef community change – Hypothesis 1

Analyses based on the full data set of 136 sites around Tasmania suggested that the magnitude of change in reef communities has been relatively small, with fish, invertebrate and algal communities in 2006 largely similar to those observed in 1994. Nonmetric MDS ordinations (Fig. 3) clearly show that spatial differences in communities (between bioregions), which have been previously described (Edgar *et al.*, 1997), are far greater

than the differences between years in each bioregion. Also clear from the ordinations is that, while the NE and SE bioregions became slightly more similar, they actually differed less between surveys than other bioregions, and the NE bioregion showed no indication of converging with the eastern Bass Strait islands (FG and KG). The NE and SE bioregions encompass the eastern Tasmanian coast and have experienced the greatest warming during the last few decades. In general, no consistent trends were evident in the trajectories of the bioregions plotted.

Similar to the MDS, univariate community characteristics showed stability between decades, with no differences observed in species richness or total fish abundance between 1994 and 2006, with the exception of algal species richness (Table 2, Figs 4 and 5). Algal species richness was consistently higher in 2006 than 1994 across all bioregions. The cover of all functional groups of macroalgae was also significantly greater in 2006 than 1994, but the level of change varied between bioregions (Fig. 6).

CAP, however, revealed significant differences associated with decade for fishes, invertebrates and algae

Table 1 Multivariate tests of location and dispersion differences in communities between years using a subset of 10 sites

			PERMANOVA		PERMDISP	
Factor	df	Error df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Fishes</i>						
Decade	1	54	3.405	0.037	0.569	0.454
Year	4	54	1.139	0.359	1.475	0.213
<i>Invertebrates</i>						
Decade	1	54	2.260	0.110	1.745	0.192
Year	4	54	0.905	0.526	1.009	0.422

The factor 'decade' has two levels 1994 and 2006 and represents the test for differences between the survey periods 1993–1995 and 2005–2007. The 'year' factor tests for differences between each of the 6 years used in these analyses (pair-wise comparisons all nonsignificant, see text). Analyses were based on ranked McArdle-Gower Dissimilarity with a base of 10. Dispersion in PERMDISP was measured from group centroids. *P*-values less than 0.05 are italicised.

Table 2 Results of *t*-tests assessing overall difference between 1994 and 2006 in species richness, total fish abundance [$\ln(y + 1)$ transformed] and cover of different functional groups of algae (arcsine transformed)

Dependent variable	<i>P</i>
<i>Species richness</i>	
Δ Fishes	0.709
Δ Invertebrates	0.422
Δ Algae	0.001
Δ Total fish abundance	0.273
<i>Algae functional group cover</i>	
Δ Canopy-forming browns	<0.001
Δ Under-story browns	0.032
Δ Red algae	0.015
Δ Green algae	<0.001

P-values less than 0.05 are italicised.

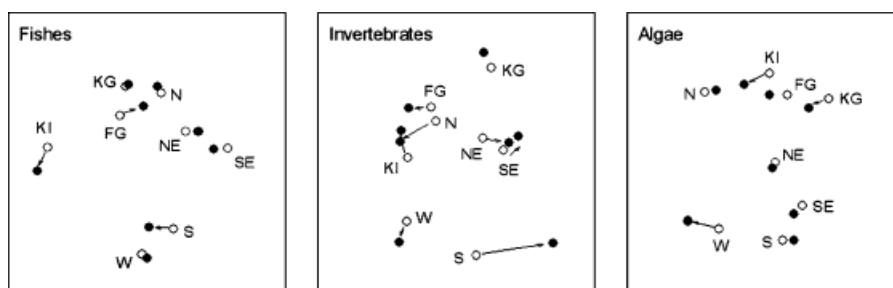


Fig. 3 Nonmetric MDS ordinations of fish, invertebrate and algal communities based on Bray–Curtis dissimilarity of $\ln(y + 1)$ transformed data (stress values = 0.05, 0.12 and 0.07, respectively). Open symbols represent communities in 1994 and closed symbols communities in 2006.

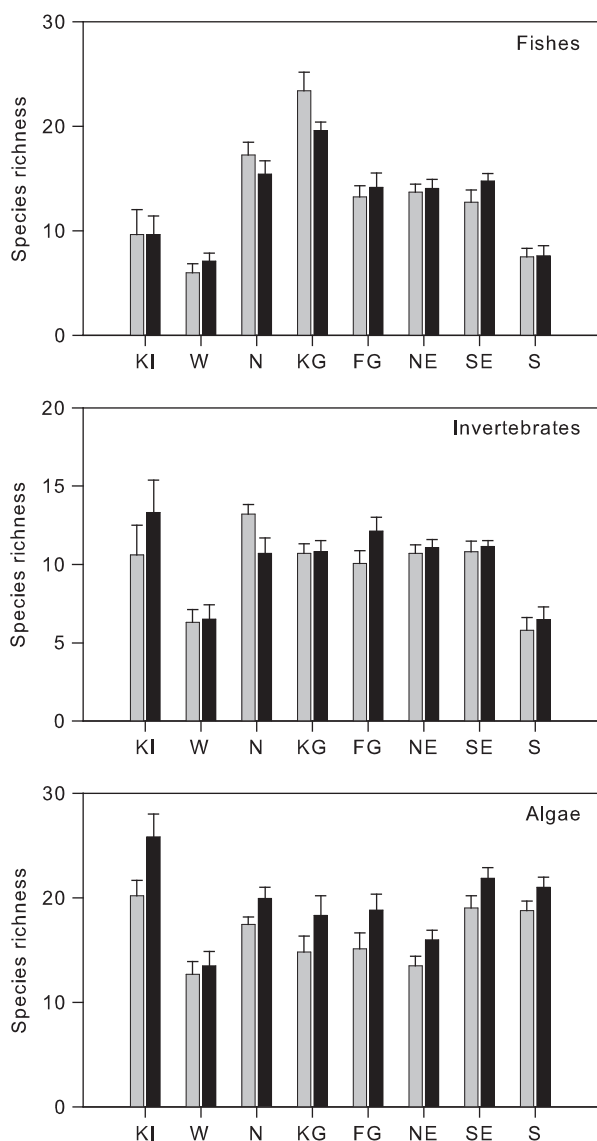


Fig. 4 Mean (+SE) species richness recorded at sites in each bioregion in 1994 (grey fill) and 2006 (black fill). Overall differences in species richness between years were only significant for algae.

(Table 3). Analysis of changes in the relative abundance of individual species identified by CAP as having the greatest correlation between first canonical axis and 'decade' ($|r| > 0.20$) generated numerous significant differences (Table 4).

Change related to species' biogeographical affinities – Hypotheses 2 and 3

Changes in density were nonsignificant for species with different biogeographical affinities for fishes, invertebrates and algae (Table 5, Fig. 7). Importantly, the

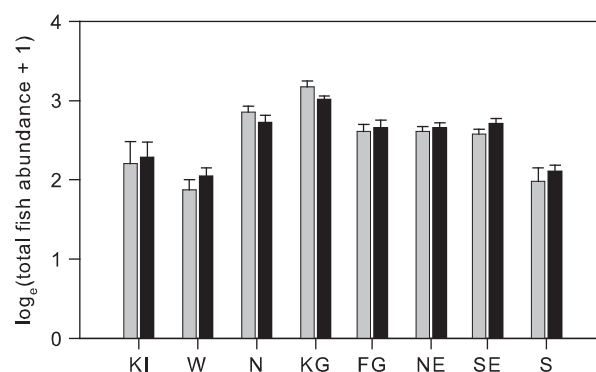


Fig. 5 Mean (+SE) total fish abundance (log transformed) recorded at sites in each bioregion in 1994 (grey fill) and 2006 (black fill).

differences identified in CAP appeared to be a result of changes in less abundant species (e.g. the fishes *Aracana aurita* and *Diodon nichthemerus*), or in the patchiness of more abundant species (e.g. *Latridopsis forsteri*). Regression of the 10th percentile of *P* values from *t*-tests of fish and invertebrate abundance changes against their mean abundance (in the 1994 surveys) was performed and confirmed that species with lower to mid-range abundance values showed changes of greatest statistical significance (Fig. 8). Statistical outcomes from a random population would be predicted to show the opposite results, with relatively minor but consistent change among common species showing higher probability than for rarer species, because patterns for the latter include more stochastic noise.

Although the observed southern limit of some species appeared to have extended southwards since 1994 (e.g. the southern-most observation of *Girella tricuspidata* shifted from 40.3020° in 1994 to 42.5255° in 2006), no significant differences were evident in changes in minimum or maximum observed latitudes for species with different biogeographical affinities for fishes, invertebrates or algae (Table 6, Fig. 9). Specifically, eastern species did not show greater southwards shifts than western or widespread species. The overall mean southern-most latitude of sightings for fishes was 42.5789° south in 1994 and 42.7313° south in 2006, a difference of only approximately 16.9 km further south. A large proportion of fish species that appeared to have shifted in their southern or northern observed limit were rare, small or cryptic species, for which observations of distributional endpoints are difficult to estimate as they are affected by fortuitous sightings of individuals. Specifically, 25% of species that were found >0.4° further south, and 57% of species whose southern-most observations were >0.4° further north, were rare, small or cryptic species.

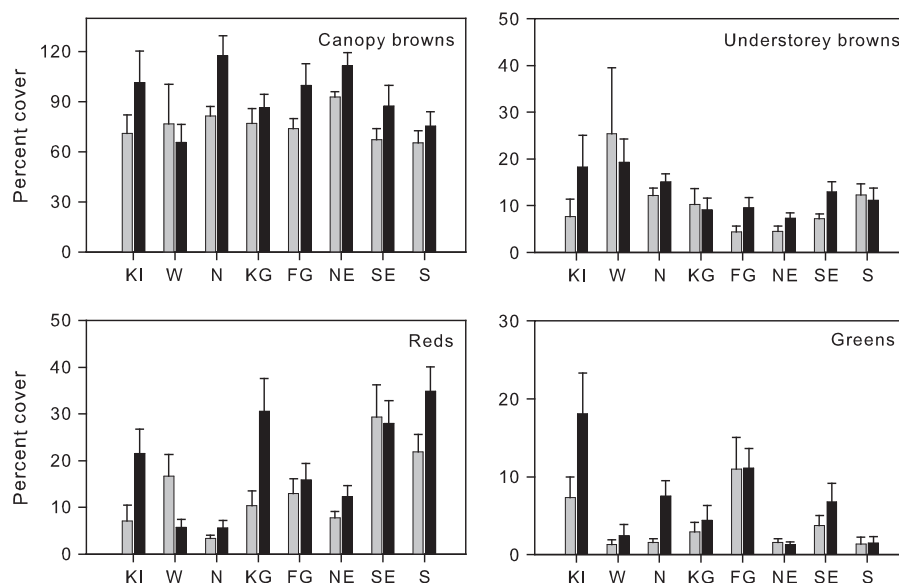


Fig. 6 Mean (+ SE) percent cover of different functional groups of macroalgae recorded at sites in each bioregion in 1994 (grey fill) and 2006 (black fill). Percent cover of canopy-forming brown algae can exceed 100% at sites in which species within this group co-occur at various canopy heights and thus overlay each other. Percent cover differed between years for all groups (Table 4).

Table 3 Results of canonical analysis of principal coordinates (CAP) examining the effect of decade on the full data set of 136 sites and all species (fishes = 104 species, invertebrates = 56 species, and algae = 79 species or species groups)

	<i>m</i>	% Var	Allocation success (%)	<i>P</i>
Fishes	15	90.63	60.662	<i>0.009</i>
Invertebrates	15	99.32	56.107	<i>0.013</i>
Algae	20	99.09	68.462	<i><0.001</i>

%Var = the percentage of the total variation explained by the first *m* principal coordinate axes. Allocation success = the percentage of sites correctly allocated to each survey year. *P*-values less than 0.05 are italicised.

New records of NSW species – Hypothesis 4

Several species were only recorded in one of the survey years (Table 7). Some of these species were actually observed in the other year while undertaking the field-work (e.g. *Aracan ornata* and *Hypoplectrodes maccullochi*), but by chance were not recorded along any transects, and others were small or cryptic species or vagrants from other habitats (e.g. *Stigmatopora nigra*), for which reliable determination of presence would require surveys in other habitats or the use of different survey methods. There were two species, however, that were recorded on transects in 2006 that were new sightings in Tasmania. These were the eastern species *Notolabrus gymnogenis*, and *Aplodactylus lophodon*.

Discussion

Tasmanian shallow rocky reef communities have been relatively stable over the past decade, despite a substantial rise in minimum SST during this period and the continuation of a considerable warming trend in oceanographic conditions over the last 50 years. Ordinations revealed a lack of consistent trajectories of communities in multivariate space through time. In particular, the NE and SE bioregions, which are most influenced by the EAC and hence have experienced the greatest warming over the last century, appeared to have actually changed very little. Thus, our results did not support Hypothesis 1 that communities should have changed substantially and that community types should have become more like those in adjacent lower latitude regions.

This general lack of community change through time contrasts with outcomes of studies elsewhere. Holbrook *et al.* (1997) reported substantial changes in temperate reef fish community structure that were linked to a climate regime shift that saw SST rise by 1 °C over a 2-year period, while Schiel *et al.* (2004) found a substantial shift in benthic community structure on a subtidal rocky reef over 10 years of warming. Helmuth *et al.* (2006) also summarized significant reported changes in Californian intertidal communities during a long-term 2 °C increase in SST, and Hiddink & ter Hofstede (2008) noted significant changes in fish species richness over 22 years and ~1.9 °C of warming of bottom temperatures in the North Sea.

Table 4 Differences in the mean density of species with the greatest correlation ($|r| > 0.20$) with the first CAP axis

Species	Correlation coefficient	Mean		P	Increase (↑) or decrease (↓)	BA
		1994	2006			
Fishes						
<i>Latridopsis forsteri</i> †	0.3552	0.8	1.0	0.244	–	S
<i>Aracana aurita</i>	0.3451	1.1	2.5	<0.001	↑	WS
<i>Scorpius lineolata</i>	0.3157	2.3	13.5	<0.001	↑	E
<i>Forsterygion varium</i> *	0.2488	1.2	7.2	<0.001	↑	Intr
<i>Siphonognathus beddomei</i>	–0.2765	11.0	5.2	0.002	↓	W
<i>Diodon nicthemerus</i>	–0.2449	1.8	1.3	0.030	↓	WS
<i>Heteroclinus johnstoni</i>	–0.2288	0.5	0.4	0.399	–	S
<i>Cheilodactylus spectabilis</i> †	–0.2039	3.8	2.7	0.025	↓	S
Invertebrates						
<i>Patiriella calcar</i>	0.2631	1.1	2.7	0.033	↑	WS
<i>Astrosole scabra</i> *	0.2570	0.3	2.1	<0.001	↑	Intr
<i>Pentagonaster dubeni</i>	–0.3632	0.6	0.6	0.944	–	WS
<i>Nectria ocellata</i>	–0.3476	2.6	1.4	0.002	↓	S
<i>Petricia vernicina</i>	–0.3220	2.1	1.2	0.002	↓	WS
<i>Goniocidarid tubaria</i>	–0.2798	7.4	4.5	0.003	↓	S
Algae						
<i>Caulerpa scalpelliformis</i>	0.2948	0.1	0.9	0.005	↑	WS
<i>Codium pomoides</i>	0.2786	0.1	0.5	0.001	↑	W
<i>Halopteris</i> spp.	0.2637	1.2	2.2	0.001	↑	
<i>Cystophora moniliformis</i>	0.2575	5.3	9.7	0.002	↑	WS
<i>Caulerpa brownii</i>	0.2365	1.4	3.9	<0.001	↑	W
<i>Caulocystis</i> spp.	0.2326	0.7	1.1	0.101	–	
<i>Plocamium</i> spp.	0.2238	3.2	5.4	<0.001	↑	
<i>Dictyopteris muelleri</i>	0.2219	0.5	1.4	0.006	↑	WS
<i>Callophyllis</i> spp.	0.2196	1.2	2.8	<0.001	↑	
<i>Carpomitra costata</i>	0.2008	0.2	0.6	0.010	↑	E
<i>Seirococcus axillaris</i>	–0.2283	1.6	1.2	0.086	–	W

*Species not native to Tasmania.

†Commercially or recreationally harvested. Bioregional affinity has been left blank for species that have been pooled with congeners. *P* values are from paired-sample, two-tailed *t*-tests on $\ln(x + 1)$ transformed data. Means presented are untransformed numbers (or % cover) per site at which they occurred in at least one of the survey years. BA, biogeographical affinities (based on traditional temperate Australian distributions on inshore reefs); WS, widespread; E, eastern Australian; S, southern Australian; W, western Australian; Intr, introduced; CAP, canonical analysis of principal coordinates.

Table 5 Results of one-way ANOVAS using data on the difference in relative abundance of fish [$\ln(x + 1)$ transformed], invertebrate and algal species between years for species with different biogeographical affinities

	Biogeographical affinity				Error	
	df	MS	<i>F</i>	<i>P</i>	df	MS
Fishes	3	0.992	0.885	0.452	99	1.120
Invertebrates	3	0.396	1.023	0.391	47	0.387
Algae	2	0.441	2.222	0.116	74	0.199

Our analyses of communities between 1994 and 2006 had a large degree of spatial replication, and should be considered relatively robust, yet we did not identify substantial changes at the community level. Not only

were Tasmanian reef communities remarkably similar between 1994 and 2006 in a multivariate sense, but univariate community characteristics such as species richness and total fish abundance were also consistent.

The only substantial change between decades was identified by CAP. This outcome resulted from a combination of changes in the abundance of less common species and differences in the degree of patchiness in other species. CAP can identify differences that occur on a different axis to that in which the most variation occurs, and can thus identify differences due to changes that are sometimes hidden in other multivariate analyses, particularly when little change occurs in some of the highly abundant species (Anderson, 2004a,b). Quantile regression of species' abundances against their *P*-values from *t*-tests agreed with the contention that the

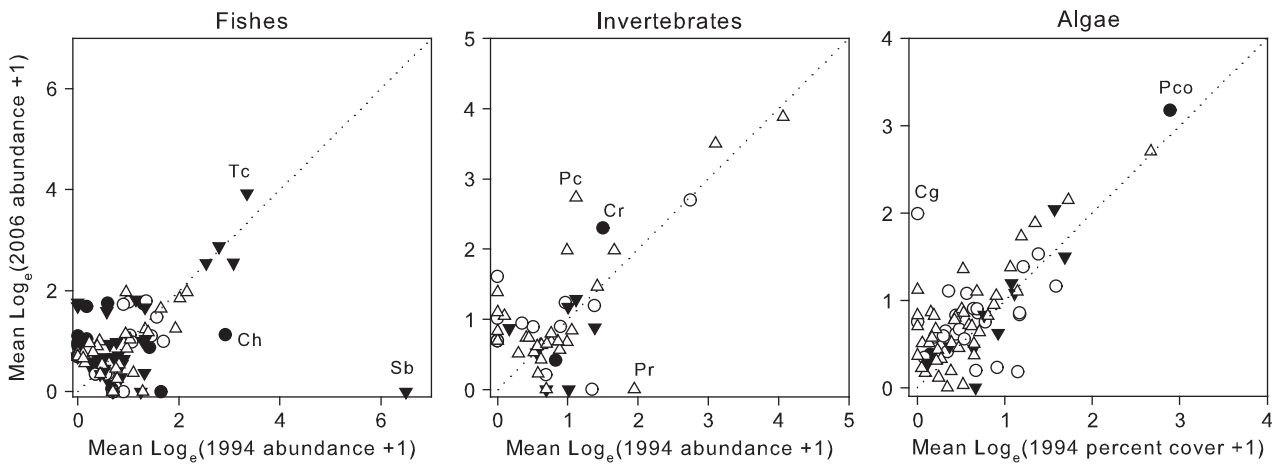


Fig. 7 Changes in the relative abundance of species with different biogeographical affinities. Filled circles, eastern species; open circles, western species; closed triangles, southern species; open triangles, widespread species. Dotted line represents no change. Species name abbreviations: *Trachinops caudimaculatus* (Tc), *Chromis hypsilepis* (Ch), *Seriolella brama* (Sb), *Patiriella calcar* (Pc), *Centrostephanus rodgersii* (Cr), *Patiriella regularis* (Pr - introduced), *Cystophora grevillei* (Cg), *Phyllospora comosa* (Pco).

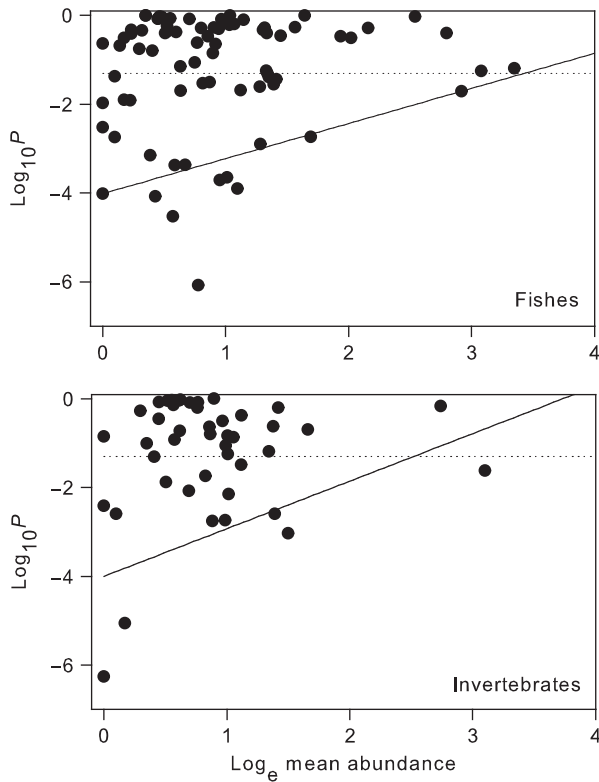


Fig. 8 Relationships between species abundance and the significance of changes in abundance. P -values (on y -axis) are from two-tailed, paired sample t -tests and are log-transformed. The dashed line represents significance of changes in abundance between 1994 and 2006 at the 0.05 level, with points lying below this line being species that differed significantly in abundance between surveys. The solid lines represent significant regression of the 10th percentile (fishes $P = 0.004$, invertebrates $P = 0.023$).

Table 6 Results of one-way ANOVAs using data on the difference in southern and northern latitudinal range limits of fish, invertebrate and algal species between years for species with different biogeographical affinities

	Biogeographical affinity				Error	
	df	MS	F	P	df	MS
<i>ΔSouthern limit</i>						
Fishes	3	1.299	1.619	0.193	66	0.802
Invertebrates	3	0.005	0.013	0.998	36	0.389
Algae	3	0.022	0.082	0.970	56	0.264
<i>ΔNorthern limit</i>						
Fishes	3	1.430	1.827	0.151	66	0.783
Invertebrates	3	0.123	0.229	0.876	36	0.538
Algae	3	0.131	0.128	0.943	63	1.027

most significant changes in species abundances, and hence those that were identified by CAP as being important in describing the differences between years, were in fact in those species with lower to mid-range abundance.

The disproportionate level of change detected among the less common species raises concerns from the perspective of biodiversity management. Few monitoring studies include population estimates of rare species, and, within these, very little data on rare species are sufficiently detailed to enable tracking of population trends. As a consequence, the number of rare species exhibiting population decline and threatened by anthropogenic disturbance or climate change is unknown, but could well be large. Moreover, reliance on

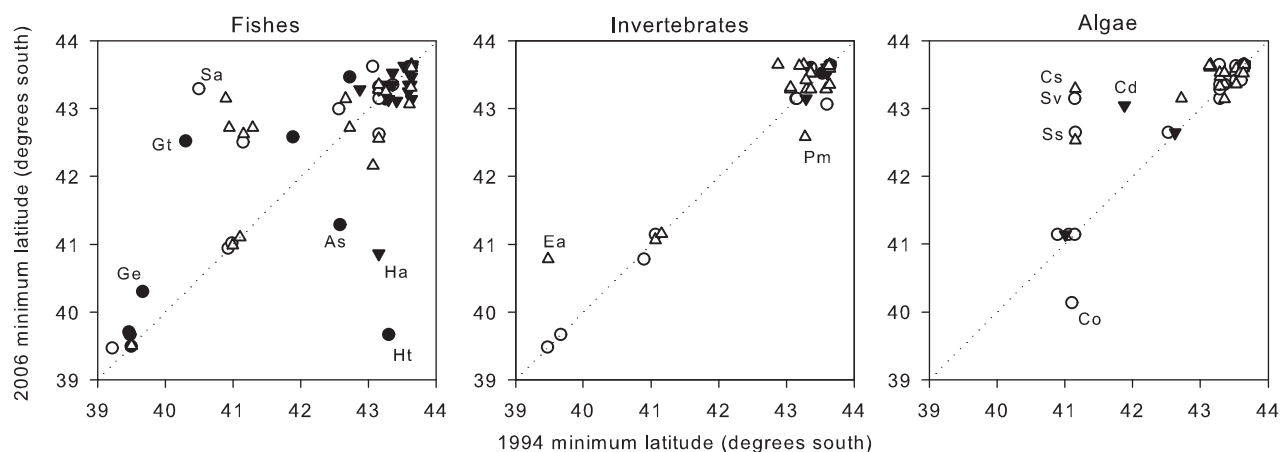


Fig. 9 Changes in the southern latitudinal limits of species with different biogeographical affinities. Filled circles, eastern species; open circles, western species; closed triangles, southern species; open triangles, widespread species. Dotted line represents no change and symbols above the line represent species that were observed further south in 2006. Species name abbreviations: *Siphonognathus attenuatus* (Sa), *Girella tricuspidata* (Gt), *Girella elevata* (Ge), *Atypichthys strigatus* (As), *Hippocampus abdominalis* (Ha), *Heteroclinus tristis* (Ht), *Echinaster arcystatus* (Ea), *Penion mandarinus* (Pm), *Caulerpa scalpelliformis* (Cs), *Sargassum varians* (Sv), *Sargassum sonderi* (Ss), *Codium dimorphum* (Cd), *Caulerpa obscura* (Co).

Table 7 Fish and invertebrate species only found in one survey year and mean abundance at sites where found

Species only in 1994	Geographical affinities	Sites	Mean <i>N</i>	Species only in 2006	Geographical affinities	Mean <i>N</i>	Sites
<i>Fishes</i>							
<i>Aracana ornata</i>	W	1	1	<i>Aploactisoma milesii</i> †	WS	1	1
<i>Gymnothorax prasinus</i> †	WS	1	1	<i>Aplodactylus lophodon</i> *	E	1	1
<i>Hypoplectrodes maccullochi</i>	E	2	5	<i>Asymbolus analis</i> †	E	1	1
<i>Hypoplectrodes nigrorubrum</i>	WS	2	1	<i>Chironemus georgianus</i> †	W	1	1
<i>Meuschenia scaber</i>	WS	7	3	<i>Chironemus marmoratus</i>	E	3	2
<i>Meuschenia venusta</i>	WS	1	1	<i>Eocallionymus papilio</i> †	WS	1	1
<i>Omegophora armilla</i>	W	1	1	<i>Eupetrichthys angustipes</i>	WS	5	1
<i>Parascyllium variolatum</i> †	W	2	1	<i>Nemadactylus macropterus</i>	S	3	14
<i>Seriotelebra brama</i>	S	1	665	<i>Notolabrus gymnogenis</i> *	E	5	2
<i>Stigmatopora nigra</i> †	WS	1	1	<i>Parascyllium ferrugineum</i> †	S	2	1
<i>Thamnaconus degeni</i>	S	2	3	<i>Paratrachichthys</i> sp.†	S	3	1
				<i>Tetractenos glaber</i>	E	3	1
<i>Invertebrates</i>							
<i>Amblypneustes</i> sp. 1	–	5	2	<i>Carcinus maenas</i>	Intr	2	1
<i>Patiriella regularis</i>	Intr	1	6	<i>Fusinus australis</i>	W	1	1
<i>Smilasterias multipara</i> †	S	1	1	<i>Maoricolpus roseus</i>	Intr	1	2
				<i>Nectria multispina</i>	W	3	1
				<i>Scutus antipodes</i>	WS	12	1

*Species not previously recorded in Tasmania.

†Rare or cryptic species.

Biogeographical affinities: WS, widespread; E, eastern Australian; S, southern Australian; W, western Australian; Intr, introduced.

abundant species as indicators of ecosystem health could well be misleading.

Our initial hypotheses not only related to changes in community structure associated with warming of the east coast of Tasmania, but also in shifts in ranges and abundance that relate to species' biogeographical affi-

nities (Hypotheses 2, 3 and 4). However, none of these hypotheses were supported, as discussed below.

Much of the literature on the effects of ocean warming on plant and animal communities suggests that the ranges of species should shift polewards in warmer conditions, and that some warmer-water species should

increase in population abundance whilst some cooler-water species should decrease in abundance (Zacherl *et al.*, 2003; Genner *et al.*, 2004; Helmuth *et al.*, 2006; Hobday *et al.*, 2006; Poloczanska *et al.*, 2008). Some changes in species' latitudinal limits and relative abundance were observed; however, these changes were slight and apparently unrelated to biogeographic affinity, with the exception of some western and widespread species that appeared to extend further south and the presence of new eastern species in the 2006 surveys. Regardless, the lack of significant extensions in range or increases in abundance of eastern species compared with western and southern species was contrary to expected effects of the strengthening EAC.

For macroalgae, higher species richness and changed percentage cover of the major functional groups were recorded in 2006 surveys. The change in species richness likely reflected, at least in part, bias associated with divers improving their knowledge of algal taxonomy, and thus being able to identify increasing numbers of algal species in the field through time. Field identification of macroalgae is typically difficult in southern Australia due to the high diversity of species and phenotypic variation within species (e.g. Womersley, 2003). The fact that algal species richness was consistently higher across all bioregions in 2006, and that different divers recorded algal data in different years, suggests this source of bias.

When algal data were pooled within functional groups (canopy browns, under-story browns, reds and greens), however, thus eliminating potential confounding from diver error in identification, significant differences remained evident between years, and these did vary spatially in some cases. More data are needed to evaluate potential causes of these changes, particularly whether the increase in the cover of brown and green macroalgae and the decrease in red algae in the south-east bioregion represents a response to a reduction in shading following a decline in giant kelp.

Although our observations indicate general stability of reef communities off Tasmania over the past decade, previous studies indicate that Tasmanian coastal communities can undergo pronounced change. Numerous fish species that were formerly common and once supported major fisheries, including striped trumpeter (*Latris lineata*) and warehou (*Seriolella brama*), are now rare and functionally extinct from inshore reefs (Harries & Croome, 1989; Edgar *et al.*, 2005). In particular, giant kelp (*Macrocystis pyrifera*) forests off the northeast Tasmanian coast significantly declined during the 1980s (Edyvane, 2003), and loss of this habitat-forming species will have greatly affected community composition (Clark *et al.*, 2004; Graham *et al.*, 2007a,b).

We interpret our results as indicating that temporal change in community structure in response to stressors such as climate change can occur at different levels. One level may consist of a range of episodic abundance and distributional changes at an individual species level during years of rapid warming, only some of which persist beyond the years in which SST peaks. Such changes have commonly been recorded during ENSO events in the Northern Hemisphere (e.g. Pearcy & Schoener, 1987; Stephens *et al.*, 1994). The other level, which is of greater magnitude and importance, comprises substantial, long-term community-level change between periods of relative stability (i.e. a regime shift, *sensu* Hare & Mantua, 2000; Scheffer *et al.*, 2001). We suggest that our study encompassed a relatively stable intermediate between periods of significant change, with only signs of short-term or smaller-scale changes evident. Some of these changes, such as those in less abundant species and in the arrival of new species, may still be important, but no evidence was found of substantial change at the community level.

Our analysis of fish and invertebrate communities at a small subset of sites supported the legitimacy of comparing the two snapshots of subtidal communities, indicating that in the subset of sites, the snapshots were representative of 3 year periods in which they were taken. Apart from inter-annual stochasticity, another major reason why comparing snapshot data may be biased is that the comparison may be made of communities at different stages of cyclical patterns, like ENSO for example. The fact that there were no differences that were consistent across different taxonomic groups (e.g. fishes and invertebrates), not only suggests that we were not observing any community-level changes in response to a long-term trend in ocean warming, but also that comparisons were not heavily influenced by any common factor that differed between snapshots.

This study has identified that while small changes have occurred in Tasmanian shallow rocky reef communities between 1994 and 2006, communities were fairly similar overall, despite a long-term trend of increasing SST that is greater than many other parts of the world. Warming conditions are expected to continue globally, with the Tasmanian east coast predicted to experience the greatest warming in the Southern Hemisphere during the next century (Cai *et al.*, 2005). Thus, future continuous monitoring of Tasmanian rocky reef communities is needed to build on these data to create a detailed and robust long-term dataset capable of detecting the community changes that appear likely, and further explore potential impacts on less abundant species. Given that our results appear to be unusual in a global context, not only in relation to the warming trend, but also when the full range of anthropogenic

pressures on near-shore marine communities are considered, more research is clearly needed to test hypotheses specific to these other pressures, like fishing and pollution, as well as determine differences and similarities between Tasmanian reef communities and those in other parts of the world that appear to be sensitive to rises in SST. Such research would provide further insight into the stability reported in this study.

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