

## ACCEPTED VERSION

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3 Running head: Climate impacts and temperate coasts

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5 **Impacts of climate change in a global hotspot for temperate**  
6 **marine biodiversity and ocean warming**

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26  
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28 extension, range-contraction, community ecology, multiple stressors, phase shift.

29  
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## 32 **Abstract**

33 Temperate Australia is a global hotspot for marine biodiversity and its waters have  
34 experienced well-above global average rates of ocean warming. We review the observed  
35 impacts of climate change (e.g. warming, ocean acidification, changes in storm patterns) on  
36 subtidal temperate coasts in Australia and assess how these systems are likely to respond to  
37 future warming. Observed impacts are region specific with the greatest number of species  
38 responses attributable to climate change reported in south-eastern Australia, where recent  
39 ocean warming has been most pronounced. Here, a decline of giant kelp (*Macrocystis*  
40 *pyrifera*) and poleward range-extension of a key herbivore (sea urchin) and other  
41 trophically important reef organisms has occurred. Although, evidence of changes on other  
42 coastlines around Australia is limited, we suggest that this is due to a lack of data rather  
43 than lack of change. Because of the east-west orientation of the south coast, most of  
44 Australia's temperate waters are found within a narrow latitudinal band, where any  
45 southward movement of isotherms is likely to affect species across very large areas. Future  
46 increases in temperature are likely to result in further range-shifts of macroalgae and  
47 associated species, with range-contractions and local extinctions to be expected for species  
48 that have their northern limits along the southern coastline. While there is currently no  
49 evidence of changes attributable to non-temperature related climate impacts, potentially  
50 due to a lack of long-term observational data, experimental evidence suggests that ocean  
51 acidification will result in negative effects on calcifying algae and animals. More  
52 importantly, recent experiments suggest the combined effects of climate change and non-  
53 climate stressors (overharvesting, reduced water quality) will lower the resilience of  
54 temperate marine communities to perturbations (e.g. storms, diseases, introduced species),  
55 many of which are also predicted to increase in frequency and/or severity. Thus climate  
56 change, both singularly and synergistically, imposes change to southern Australian coastal

57 species, including important habitat-forming algae and the associated ecological  
58 functioning of temperate coasts. Management of local and regional scale stresses may  
59 increase the resistance of temperate marine communities to climate stressors and as such,  
60 provides an attractive management tool for building resilience in temperate systems.

## 61 **Introduction**

62 Global biodiversity is under increasing pressure from environmental change caused by  
63 human activities. Despite recent attention towards defining the biological impacts of  
64 climate change, the effects of this global physical forcing on marine organisms are still  
65 poorly understood (Richardson and Poloczanska, 2008; Rosenzweig, *et al.*, 2008).

66

67 The biodiversity of Australia's marine life is globally unique. With almost 40% of the  
68 world's species of macroalgae, the algal flora of southern Australia is the most speciose in  
69 the world (Bolton, 1994; Kerswell, 2006), and it is estimated that up to 50% of its species  
70 are endemic (Phillips, 2001). Rates of endemism in Australia are similarly high for  
71 predominantly marine invertebrates such as echinoderms (31%), molluscs (38%), annelids  
72 (67%), and marine sponges (56%) (Cork, *et al.*, 2006), and this endemism is even higher  
73 for some temperate species. For example, southern Australia has 2-3 times as many species  
74 of molluscs as any other temperate coast in the world (Crame, 2000), and in some places up  
75 to 60% of these are endemic (Benkendorff and Davis, 2002). The evolution of this globally  
76 unique biodiversity has been attributed to a combination of the extensive rocky coasts, the  
77 unique oceanography associated with Australia's boundary currents (cf. Fig. 1), and  
78 climatic stability over geological time scales (Adey and Steneck, 2001; Phillips, 2001;  
79 Kerswell, 2006).

80

81 A characteristic feature of the Australian continent is that it is bound to the south by the  
82 longest east-west running coastline in the world. Together with the east and west coasts  
83 south of ~27 °S, the temperate coastline of Australia covers >3,000 km. It straddles three  
84 biogeographic provinces (Waters, *et al.*, 2010) and includes some of the most pristine  
85 temperate coast in the world, as well as several areas which are heavily populated. Rocky

86 coasts dominated by macroalgae (seaweeds) are a defining feature across these coasts (e.g.,  
87 Underwood et al. 1991, O'Hara 2001, Wernberg et al. 2003, Connell & Irving 2008, Smale  
88 et al. 2010). Because of its east-west orientation, Australia's temperate coastline is found  
89 within a narrow latitudinal band where even a small southward shift in isotherms will affect  
90 a very large area. Indeed, because of the lack of habitat to the south of the Australian  
91 mainland, most species will have limited opportunity to shift their geographical ranges  
92 poleward in response to warming, resulting in a narrowing of geographical ranges if  
93 distribution limits shift poleward.

94

95 Southern Australia has experienced some of the fastest increases in ocean temperatures  
96 globally, but climate signals have been variable within the region. In south-eastern  
97 Australia, strengthening of the East Australian Current has caused warming at a rate of  
98  $0.023^{\circ}\text{C year}^{-1}$  which is approximately four times the global ocean warming average  
99 (Ridgway, 2007). Coastal waters in south-western Australia have also warmed appreciably,  
100 increasing by  $0.013^{\circ}\text{C year}^{-1}$  since 1951 (Pearce and Feng, 2007), while south coast waters  
101 have warmed  $\sim 0.011^{\circ}\text{C year}^{-1}$  since 1950 (Suppiah, *et al.*, 2006). Warming of Australia's  
102 temperate coasts are set to continue with another 1-3  $^{\circ}\text{C}$  predicted for the coming century  
103 (Lough, 2009). In addition, compounding stressors such as increasing pressure from human  
104 populations, changes to storm and rainfall patterns, terrestrial based inputs (e.g. nutrients  
105 and turbidity) and fishing will reduce the resilience of desirable ecosystem states (Ling, *et*  
106 *al.*, 2009a; Wernberg, *et al.*, 2010).

107

108 There is now great concern for the continued existence of Australia's unique temperate  
109 marine biodiversity under current rates of global climate change. Thus, relative to  
110 temperate rocky shores elsewhere, its unique evolutionary history and high levels of

111 endemism, occurring within a relatively narrow climate envelope, makes the biota of  
112 southern Australia highly vulnerable in terms of potential for total species losses as the  
113 marine environment warms, the seas become more acidic, storm patterns change, sea levels  
114 rise or consumers shift their distributions. Here, we review the current evidence for impacts  
115 of climate change across Australia's temperate rocky coasts and consider future needs for  
116 understanding ecological change. In recognition of the need to understand the range of  
117 potential impacts even if providing unequivocal evidence is near impossible, we have  
118 included a broad range of published, unpublished and anecdotal evidence across southern  
119 Australia. We first recognise known changes that may have been forced by climate and  
120 then forecast future change that may be managed by policy. Much of this review is based  
121 on the idea that large scale process such as climate change cannot be studied or prepared  
122 for unless the compounding or mediating effects of local-scale influences (e.g.  
123 eutrophication, over-fishing) on climate change responses are also recognised.

124

## 125 **Observed impacts**

126 Southern Australia is particularly under-represented in terms of documented impacts of  
127 climate change in marine systems (Poloczanska, *et al.*, 2007; Rosenzweig, *et al.*, 2008). A  
128 lack of long-term data to assess change against has been identified as one of the primary  
129 reasons for this paucity of documented impacts. However, warming over the past ~50 years  
130 has been identified as a primary or contributing cause of a number of ecological changes.

131

### 132 *Range contractions*

133 Perhaps the most visible impact has been the decline of the surface-canopy of the giant kelp  
134 *Macrocystis pyrifera*. Archival aerial photographs, admiralty charts and anecdotal accounts  
135 by fishermen and marine naturalists document that previously widespread *M. pyrifera*

136 forests have disappeared from many sites in eastern Tasmania (Edyvane, 2003, Johnson et  
137 al this issue). Ocean warming and an associated influx of nutrient poor water driven by a  
138 strengthening of the East Australian Current appears the most plausible cause of this  
139 decline (Jonson *et al.*, this issue).

140

141 The distribution of other large macroalgae may also have been affected. Herbarium records  
142 suggest that the distribution of the three habitat-forming species *Ecklonia radiata*,  
143 *Phyllospora comosa* and *Durvillaea potatorum* have shifted southwards on the east coast  
144 over recent decades (A.J. Millar pers. obs.). Massive declines of large habitat-forming  
145 algae have also been recorded around urban centres, such as for *P. comosa* around Sydney  
146 (Coleman, *et al.*, 2008) and *E. radiata* around Adelaide (Connell, *et al.*, 2008). The  
147 processes responsible for these changes are currently under study but are likely to be  
148 directly or indirectly driven by climate and local anthropogenic stressors such as reduced  
149 water quality (Connell, 2007; Connell, *et al.*, 2008). For example, an unusual dieback of *P.*  
150 *comosa* and *E. radiata* in eastern Tasmania in 2001 was attributed to above-average  
151 seawater temperatures coupled with nutrient stress during calm sea conditions (Valentine &  
152 Johnson 2004).

153

#### 154 *Range-extensions*

155 The barren-forming sea urchin *Centrostephanus rodgersii* has extended its range poleward  
156 by ~160 km decade<sup>-1</sup> over the past 40 years, from New South Wales to eastern Tasmania  
157 (Ling, *et al.*, 2009b). There is strong evidence that a strengthening of the East Australia  
158 Current and associated ocean warming (Ridgway, 2007) has been responsible for this  
159 southward range extension as ocean temperatures across much of eastern Tasmania now  
160 exceeds the 12°C threshold for successful development of *C. rodgersii* larvae (Ling, 2008).



161 *C. rodgersii* is a voracious grazer, and in New South Wales ~50 % of all near-shore rocky  
162 reefs are urchin barrens where urchins have eaten most erect vegetation, leaving behind  
163 bare rock (Andrew and Byrne, 2007; Connell and Irving, 2008). In the three decades since  
164 its arrival, previously absent urchin barrens are now extensive throughout north-eastern  
165 Tasmania, and these are expected to expand further (Johnson et al. 2005). This habitat  
166 transition has been estimated to cause a minimum local loss of ~150 taxa associated with  
167 macroalgal beds (Ling, 2008).

168

169 Similar southern (poleward) range expansion has also been documented for 16 intertidal  
170 species in south-eastern Australia, including the giant rock barnacle *Austromegabalanus*  
171 *nigrescens* which has expanded into Tasmania, albeit with a slower mean expansion rate of  
172 ~29 km decade<sup>-1</sup> since the 1950's (Pitt, *et al.*, 2010).

173

174 Southward (poleward) range extensions have been documented for 45 species of fish on the  
175 south-east coast (Last, *et al.*, 2010). These represent ~15% of coastal fishes in temperate  
176 southeastern Australia and include several herbivorous, territorial and predatory species  
177 with the potential to significantly influence macroalgal habitats. For example, the  
178 damselfish *Parma microlepis*, known to influence other organisms by defending local  
179 territories (e.g., Buckle and Booth, 2009), was extremely rare in north-eastern Tasmania in  
180 the early 2000's, where it now constitutes one of the most conspicuous benthic fishes,  
181 particularly on *C. rodgersii* barrens (S. Ling *pers. obs*). Of the predators, the Port Jackson  
182 shark (*Heterodontus portusjacksoni*) and the eastern blue grouper (*Acherodus viridis*) have  
183 extended their ranges into north-eastern Tasmania, though both are still rare. Both species  
184 are known predators of *C. rodgersii* (Andrew and Byrne, 2007), but at their present  
185 densities and size structure it is unlikely that they are impacting on sea urchin populations.

186

187 While increasing frequency of sightings of south-eastern Australian mainland marine  
188 species has occurred in north-eastern Tasmania, predicted range contractions of southern  
189 seaweed-associated species appears more cryptic and trophic consequences more uncertain.  
190 For example, sightings of red velvet fish (*Gnathanacanthus goetzei*) have declined over  
191 the past 16 years which may be a response to climate-driven decline in its primary habitat,  
192 *Macrocystis pyrifera* habitat (G. Edgar *unpub. data*).

193

#### 194 *Reduced recruitment*

195 In Western Australia (WA) there have been no explicit reports of ecological effects on  
196 temperate coasts as a result of recent climate change (Pearce and Feng, 2007). The longest  
197 biological dataset in WA concerns the distribution, abundance and recruitment of the  
198 commercially important western rock lobster (*Panulirus cygnus*). Western rock lobsters are  
199 conspicuous consumers of small invertebrates and calcareous algae, and it is possible that  
200 they influence floral and faunal assemblage structure (Edgar, 1990). Historical recruitment  
201 data for *P. cygnus* has shown a strong correlation between the strength of the Leeuwin  
202 Current and the magnitude of puerulus larval settlement. However, very low recruitment of  
203 *P. cygnus* has been recorded in the last three years, despite seemingly favourable  
204 conditions. Whether this decline is due to reduced brood stock through overharvesting or  
205 changes in physical environmental factors (i.e. ocean currents and eddies, temperature) is  
206 currently unknown, but recent analyses indicate that recruitment and migration patterns of  
207 rock lobster may have changed in response to rising temperature over the last 35 years  
208 (Caputi, *et al.*, 2010). Similarly, ocean warming in eastern Tasmania appears to be  
209 exacerbating the impacts of fishing on southern rock lobsters (*Jasus edwardsii*) by  
210 negatively influencing recruitment patterns of this species, but seemingly increasing the

211 recruitment of the con-generic eastern rock lobster (*Jasus verreauxii*) typical of waters  
212 further north (Pelc, *et al.*, 2009).

213

214 *Interactions with non-climate stressors*

215 **Fishing and harvesting.** Superimposed on the climate-driven incursion of *Centrostephanus*

216 *rodgersii* to eastern Tasmania is the heavy exploitation of marine predators. Long-term

217 changes to species inside Marine Protected Areas (MPAs) relative to adjacent fished sites

218 show that fishing has a major impact on the abundance and size structure of major target

219 species in Tasmania (Barrett *et al.* 2009). This increase in abundance includes the important

220 sea urchin predator, the spiny lobster *Jasus edwardsii*, that must reach a size of 140 mm

221 carapace length to be an effective predator of *C. rodgersii* (Ling, *et al.*, 2009a) Indeed,

222 intensive fishing for well over a century is estimated to have reduced the stock of legal-

223 sized lobsters (110 mm carapace length) on eastern Tasmanian coasts to approximately 2-8

224 % of pre-fished biomass by the 1990s (Frusher, 1997; Ling, *et al.*, 2009a).

225

226 **Introduced species.** Anthropogenic introduction of exotic species poses substantial threat to

227 patterns of global biodiversity. While increasing invasions are not directly climate related,

228 climate change has often been proposed to facilitate the establishment, further spread and

229 impact of invasive exotic species in temperate marine systems (Stachowicz, *et al.*, 2002). In

230 Australia, the introduced alga *Undaria pinnatifida* established dense mono-specific stands

231 following the temperature-related dieback of native canopy-species in eastern Tasmania in

232 2001 (Valentine and Johnson, 2004).

233

234 It has also been suggested that the spread of the European green shore crab *Carcinus*

235 *maenas* from Victoria into Tasmania has been facilitated by increasing ocean temperatures

236 in response to a strengthening of the East Australia Current (Thresher, *et al.*, 2003). *C.*  
237 *maenas* is a voracious predator in intertidal and shallow subtidal habitats where it is  
238 capable of exerting strong top-down control of marine communities (Bertness and  
239 Ewanchuk, 2002). Impacts of *C. maenas* on rocky coasts remain undocumented in eastern  
240 Tasmania, but impacts on soft sediment communities have been recorded in Tasmania  
241 (Ross *et al.* 2004).

242

### 243 **Expected impacts this century**

244 It is difficult to unambiguously attribute ecological changes to anthropogenic climate  
245 change because of the potential for other co-occurring mechanisms to explain the observed  
246 patterns. The number of cases where climate change can reasonably be linked to an impact  
247 is, however, compelling. It is clear that macroalgal-dominated coasts in southern Australia  
248 are vulnerable to the direct and indirect impacts of climate change. Interestingly, there have  
249 not been any reported changes directly or indirectly attributed to climate change factors  
250 other than increasing temperatures. This could, perhaps, reflect that little or no data is  
251 available to document changes on other environmental factors (e.g., ocean acidification).  
252 Nevertheless, warming appears to be the primary climate-related pressure of concern for  
253 the immediate future (see also discussion on ocean acidification below). It is, however,  
254 likely that the influence of additional factors will increase as the environmental changes  
255 continue to manifest.

256

#### 257 *Temperature*

258 The projected temperature increase for temperate Australian marine waters is in the order  
259 of 1-3 °C by 2030 and 2100 respectively (Lough, 2009). Existing temperature gradients of  
260 this magnitude in southern Australia (e.g., Smale and Wernberg, 2009) are associated with

261 considerable differences in physiology (Stæhr and Wernberg, 2009; Wernberg, *et al.*,  
262 2010), species distributions of algae, invertebrates and fish (O'Hara and Poore, 2000;  
263 Wernberg, *et al.*, 2003; Tuya, *et al.*, 2008a; b; Smale, *et al.*, 2010b; Wernberg, *et al.*, 2010),  
264 population structure and dynamics (Ling, 2008; Wernberg and Goldberg, 2008), and  
265 habitat structure (Connell, *et al.*, 2008) of temperate marine species. For example, along the  
266 west coast the cool-adapted and endemic canopy-forming brown alga *Scytothalia*  
267 *dorycarpa* increases in abundance with increasing latitude (Smale, *et al.*, 2010b, Wernberg  
268 *et al.* this issue). Conversely, the relative abundance of warm temperate and tropical foliose  
269 brown algae such as *Padina* spp. and *Dictyota* spp., are inversely related to latitude (Smale  
270 *et al.* 2010). It seems, therefore, very likely that the forecasted temperature increase would  
271 lead to a redistribution of flora and fauna. For most temperate species, this will imply range  
272 contractions as their northern (warm) range limits contract poleward while their southern  
273 limits can shift no farther south.

274

275 Continued ocean warming is likely to affect the successful recruitment, growth and  
276 productivity of prominent coastal organisms. For example, thermal thresholds are known  
277 for *C. rogersii* larval survival (12°C, Ling *et al.* 2008) and for growth and productivity of  
278 *E. radiata* (18.5 °C, Kirkman, 1984). A negative relationship between recruitment success  
279 and water temperature has also been shown for *E. radiata* (Wernberg, *et al.*, 2010).  
280 Similarly, the distribution of the turbinid gastropod *Turbo torquatus* show signs that  
281 elevated temperatures may limit recruitment success; populations in warmer waters at  
282 northern latitudes are strongly dominated by a single cohort which recruited during a period  
283 of relatively cool ocean conditions, whereas populations in cooler waters at southern  
284 latitudes have multiple cohorts representing continuous successful recruitment (Wernberg,

285 *et al.*, 2008). Increasing temperatures, therefore, may put marginal populations under  
286 further pressure and at risk of eventual collapse.

287

### 288 *Trophodynamics*

289 Increasing ocean temperatures are likely to affect herbivores and their foraging activities  
290 both directly and indirectly. Rates of herbivory may be enhanced as a direct result of  
291 temperature-driven increases in the metabolic rate of herbivores (Kordas *et al.*, this issue),  
292 as demonstrated in laboratory experiments for temperate sea urchins (Siikavuopio, *et al.*,  
293 2008) and amphipods (O'Connor, 2009; Sotka and Giddens, 2009). At the same time, the  
294 nutritional value of available food sources may change, either as a consequence of shifting  
295 species composition or as a consequence of altered biochemistry of existing species.  
296 Studies from Western Australia indicate that physiological adaptation and acclimatisation  
297 of *Ecklonia radiata* to warmer environments is associated with substantial changes in tissue  
298 nutrients and pigments, such that the nitrogen content (an important determinant of  
299 nutritional value) of kelp tissue decreases by  $\sim 15\% \text{ }^{\circ}\text{C}^{-1}$  temperature increase (Stæhr and  
300 Wernberg, 2009). This, in turn, can influence the ecological performance and fecundity of  
301 invertebrates that rely on kelp and other algal food sources (Foster, *et al.*, 1999; Kraufvelin,  
302 *et al.*, 2006), many of which are trophically important as herbivores or prey items for  
303 higher order consumers. Complex climate-driven interactions between key herbivores (e.g.  
304 the sea urchin *C. rodgersii*), reduced nutrient levels caused by shifting currents and strong  
305 impacts on higher trophic levels as a result of intense harvesting, will conspire to sway  
306 trophic dynamics in favour of increased herbivory in some areas (e.g., Tasmania) and thus  
307 strong impacts on ecologically important seaweed communities.

308

309 *Ocean acidification*

310 Ocean pH has dropped by 0.1 units since the industrial revolution and is predicted to drop  
311 by a further 0.3-0.4 units by 2100 (Meehl, *et al.*, 2007). Although most experimental  
312 studies on ocean acidification to date have focused on tropical assemblages, recent work  
313 has shown that effects of ocean acidification on temperate marine systems may be equally  
314 complex and deleterious (Hall-Spencer, *et al.*, 2008; Martin and Gattuso, 2009; Russell, *et*  
315 *al.*, 2009).

316

317 Calcified coralline algae occupy up to 80 % of hard substrate on the temperate coast of  
318 southern Australia , where they play an important ecological role as competitors for space  
319 and settlement cues for invertebrates (Steneck, 1986). Recent experimental work in  
320 Australia has shown that acidification associated with conservative projections of future  
321 CO<sub>2</sub> concentrations (550 ppm) are likely to have negative effects on the growth and  
322 recruitment of coralline algae, and this effect is compounded by increased temperature  
323 (Russell, *et al.*, 2009) and altered light regimes (Russell, *et al.*, 2011). In contrast to  
324 coralline algae, ocean acidification may have little negative or even positive direct effects  
325 on non-calcareous algae (Beardall, *et al.*, 1998; Russell, *et al.*, 2009; Connell and Russell,  
326 2010).

327

328 Even if changes to ocean pH may be occurring much more rapidly than originally  
329 anticipated (Wootton, *et al.*, 2008), the evidence pointing to direct effects of ocean  
330 acidification on temperate marine ecosystems in the near future is ambiguous, and it is  
331 possible that these will not be realised for the next 50-100 years. For example, recent work  
332 on early larval development suggest that impacts in the next century are unlikely for the sea  
333 urchin *Heliocidaris erythrogramma* (Byrne, *et al.*, 2009) whereas increased larval mortality

334 may be a consequence for larval abalone (Crim *et al.* this issue). Regardless, as with  
335 changes in temperature, ocean acidification is likely to initially result in increasing  
336 sublethal effects (e.g. slower growth rates, susceptibility to disease, reduced reproductive  
337 capabilities) on a wide range of processes and species and these may combine to produce  
338 unforeseen indirect effects.

339

340 It is not surprising that research into the effects of ocean acidification in marine  
341 environments has a disproportionate focus on the negative effects on organisms that form  
342 calcareous structures (i.e. coral reefs, Hoegh-Guldberg, *et al.*, 2007; Anthony, *et al.*, 2008;  
343 Dupont, *et al.*, 2008; Fabry, *et al.*, 2008; Kuffner, *et al.*, 2008; Parker, *et al.*, 2009).  
344 However, this preoccupation fails to identify the potential positive effects of increased CO<sub>2</sub>  
345 for both calcareous (e.g. echinoderm growth and feeding rates, Gooding, *et al.*, 2009;  
346 Dupont, *et al.*, 2010) and non-calcareous species (e.g. turf-forming algae, Russell, *et al.*,  
347 2009). It is important to recognise that such positive effects could act as perturbations in  
348 ecological systems. For example, filamentous turf-forming algae form a natural component  
349 of the early post-disturbance successional stages of kelp-dominated landscapes (Wernberg  
350 and Connell, 2008), yet under altered environmental conditions turfs can expand and  
351 inhibit the recruitment of kelp, potentially eroding resilience of kelp forests under future  
352 conditions (Connell and Russell, 2010).

353

#### 354 *Changes in storm tracks*

355 Recent projections suggest that long-range swell systems that originate from the Southern  
356 Ocean are likely to increase in the future. This will cause increased frequency and physical  
357 disturbance on most coasts (e.g. localised loss of seaweed canopies, Seymour, *et al.*, 1989;  
358 Thomsen, *et al.*, 2004) which could be of great ecological significance. Physical



359 disturbance regulates species richness and community structure, and disturbance regime  
360 plays an important role in maintaining diversity and driving patch dynamics in temperate  
361 marine communities in Australia (Kennelly, 1987a; Kendrick, *et al.*, 1999; Kendrick, *et al.*,  
362 2004; Toohey, *et al.*, 2007; Wernberg and Connell, 2008; Wernberg and Goldberg, 2008).  
363 Studies have shown that increased wave energy correlate well with larger gaps in (i.e.  
364 fragmentation of) the seaweed canopy (Kennelly, 1987a; Farrell, 1989; Wernberg and  
365 Connell, 2008), which has implications for local diversity, productivity and overall  
366 community structure (Kennelly, 1987b; Kendrick, *et al.*, 1999; Wernberg, 2006; Wernberg  
367 and Goldberg, 2008). Exactly how temperate marine community structure will be affected  
368 by increasing frequency and/or intensity of physical disturbance remains uncertain, but  
369 evidence from elsewhere suggests that chronically disturbed habitats generally support  
370 species poor assemblages (Sousa, 1979; Hughes and Connell, 1999; Barnes and Conlan,  
371 2007). In addition, systematic changes to weather patterns, and thus swell conditions, are  
372 likely to influence a range of ecologically important processes. For example, high wave  
373 exposure suppresses the natural post-disturbance recovery of *Ecklonia radiata* canopies  
374 (Wernberg, *et al.*, 2003). Moreover, increasing disturbance regimes will interact with, and  
375 compound, the negative effects of elevated ocean temperature on the recruitment and  
376 recruit performance of kelps, compromising the ability of kelp canopies to withstand and  
377 recover from disturbances (Wernberg, *et al.*, 2010).

378

### 379 *Rainfall, run-off and nutrients*

380 Climate change is predicted to alter rainfall patterns, but these changes will differ  
381 regionally (CSIRO, 2007); rainfall will be further reduced in regions of low rainfall, and  
382 therefore less nutrient runoff will occur, while the converse will be true in areas of higher  
383 annual rainfall. Experience from urbanised coasts shows that elevated nutrients generally

384 benefit small, more opportunistic species of algae (Pedersen and Borum, 1996; Worm, *et*  
385 *al.*, 1999; Russell and Connell, 2005), leading to shifts from canopy to turfing algal  
386 dominated systems (e.g., Worm, *et al.*, 1999; Eriksson, *et al.*, 2002; Connell, *et al.*, 2008).  
387 Therefore, increases in nutrient inputs would generally have a negative impact on algal-  
388 dominated reef assemblages. However, these effects also tend to interact in the regional  
389 biological context. For example, increasing nutrients have disproportionately large negative  
390 effects in regions of oligotrophic waters, such as those in southern Australia (Russell, *et al.*,  
391 2005). Further, eastern Australia has greater grazing pressure that may counter any  
392 negative effects of coastally derived nutrients by consuming bloom forming algae (Connell,  
393 2007; Connell and Irving, 2008). Independent of nutrient driven effects, there are also  
394 likely to be changes to inshore reefs as a result of increased frequency of extreme rainfall  
395 events. For example, hyposaline conditions have been observed to cause a major shift in  
396 reef habitat mediated by extensive mortality of *Centrostephanus rodgersii* following major  
397 flood events in 1986 and 1988 in Botany Bay (New South Wales) whereby rapid re-  
398 colonisation of seaweed habitat occurred on reefs that were previously urchin barrens  
399 (Andrew, 1991).

400

#### 401 *Disease*

402 There is considerable concern globally that predicted warming and other anthropogenic  
403 stressors may increase the spread of pathogens and enhance their virulence as well as  
404 decrease the resilience of host organisms including sea urchins (Lester, *et al.*, 2007) and  
405 macroalgae (Jackson, *et al.*, 2001; Lafferty, *et al.*, 2004). For example, massive declines  
406 (40-100%) of the kelps *Ecklonia radiata* in New Zealand (Cole and Babcock, 1996; Cole  
407 and Syms, 1999) and *Laminaria religiosa* in Japan (Vairappan, *et al.*, 2001) have been  
408 attributed to outbreaks of disease. Moreover, complex interactions between bacterial

409 pathogens, seaweed chemical defences and environmental factors, such as temperature,  
410 have been shown to be important in determining the extent to which a common red alga in  
411 southeastern Australia (*Delisea pulchra*) suffers from bacterial disease which can result in  
412 death of the alga (Case et al., unpublished data).

413

#### 414 *Expected patterns of impact*

415 Given that the impacts of climate and non-climate stressors will vary considerably among  
416 regions, ecological impacts are likely to manifest heterogeneously across temperate  
417 Australia (Figure 1). Such impacts will be greatest where large scale southward flowing  
418 currents (e.g. East Australian and Leeuwin Currents) transport additional warm water  
419 poleward, and around population centres where additional stressors are strongest, but may  
420 be delayed by local oceanic features providing refuge habitats such as zones of upwelling  
421 of relatively cool and nutrient rich water masses or deeper water refuges (e.g., Graham, *et*  
422 *al.*, 2007). Importantly, impacts may not be gradual. For example, despite evidence for  
423 concurrent warming and major ecological changes prior to their study, Stuart-Smith et al.  
424 (2009) found relatively few changes in Tasmanian coastal communities over a 10-15 year  
425 period, and suggested that this reflected a period of relative stability following major abrupt  
426 community reorganisation (see also Hsieh, *et al.*, 2005). Physiological acclimatisation may  
427 offset the immediate translation of environmental change into distributional change of  
428 temperate marine organisms (Wernberg, *et al.*, 2010). In addition, range shifts may be  
429 obscured by habitat buffering, where complex interactions between habitat-forming and  
430 modifying species, coastal topography and environmental conditions create benign micro  
431 habitats, maintaining the latitudinal extent of a species in a mosaic of micro-refugia  
432 (Helmuth, *et al.*, 2006; Hawkins, *et al.*, 2008).

433

## 434 **Management and adaptation responses**

435 Management actions focussed on reducing the risk of major shifts in ecosystems, and  
436 potential loss of high numbers of species, are particularly urgent given predictions of  
437 continued and further accelerating warming. However, a fundamental consideration in  
438 assessing and managing impacts of climate change on temperate marine communities is the  
439 broad spectrum of anthropogenic pressures operating at global (climate), regional (over-  
440 harvesting, eutrophication, non-native species) and local (coastal development, point-  
441 source pollution, aquaculture) scales that interact to drive unprecedented and complex  
442 changes in marine systems (Harley, *et al.*, 2006; Harley and Connell, 2009) (Figure 1).

443

444 Direct climate change can only be managed in a global international context and, except for  
445 supporting international initiatives, is outside the reach of national and state governments.

446 However, since reduced resilience of marine systems will be driven by interactions  
447 between global climate and regional and local scale pressures (Ling, *et al.*, 2009a; Ling, *et*  
448 *al.*, 2009b; Russell and Connell, 2009; Wernberg, *et al.*, 2010), adaptive strategies focused  
449 at these smaller scales may be better placed to ameliorate the negative impacts of an  
450 inevitably changing climate (Falkenberg, *et al.*, 2010). Recognition of this, in combination  
451 with greater attention to the anticipation and prevention of socially-undesirable regime  
452 shifts, has lead to more proactive management of local stressors in some regions. For  
453 example in South Australia, local government has encouraged research into the processes  
454 that either increase or weaken resilience, and of the socio-economic drivers and governance  
455 that regulate modification of the physical environment (e.g. water quality) and their biota  
456 (e.g. fisheries). South Australian managers now recognise global-local connections of  
457 future change, recently implementing long-term policy solutions for the sea (policy on  
458 reducing wastewater discharge) that also act as solutions for the land (policy on

459 establishing new sources of water that do not rely entirely on rainfall). Upgrades to  
460 wastewater treatment plants, to produce recycled water for residential and industrial use,  
461 not only reduces reliance on rainfall for fresh water supplies, but also reduces the nutrient  
462 rich discharge that has primarily contributed to phase shifts on metropolitan coasts from  
463 kelp to turf-dominated (Connell, *et al.*, 2008). Similarly in Tasmania, managers are  
464 recognising the need to reduce risk of climate-driven impacts of overgrazing on coastal  
465 ecosystems by supporting a program of rebuilding predator biomass to reduce the risk of  
466 overgrazing by the range-extending sea urchin *C. rodgersii* (Ling, *et al.*, 2009b). Networks  
467 of marine reserves are being established along temperate coasts Australia-wide that serve to  
468 minimise both top-down and bottom-up impacts, may increase the resilience of marine  
469 communities to climate change.

470

471 Indeed, efforts to reduce the compounding influence of multiple stressors may reduce the  
472 frequency and extent to which ecological systems change to unexpected states (Paine, *et*  
473 *al.*, 1998; Scheffer and Carpenter, 2003). If multiple perturbations reduce the resilience of a  
474 system, then local management may be effective in reducing the effects of climate change  
475 (Hughes, *et al.*, 2007; Russell and Connell, 2009). If local impacts are driving local system  
476 shifts (e.g., Gorman, *et al.*, 2009), removal of these stressors may increase the resilience of  
477 natural systems to climate change (Russell, *et al.*, 2009). Reduction of such stressors may  
478 assist restoration through actions akin to terrestrial re-forestation. For example, it may be  
479 possible to reverse observed shifts from kelp to turf dominated systems by re-seeding kelp  
480 forests with recruits from populations in cooler water.

481

482 **Future directions**

483 Improving predictions of responses to variation in biotic and abiotic variables has been a  
484 persistent challenge in ecology. Consequently, there is a considerable history on the  
485 advantages and disadvantages of alternate approaches, with general agreement centring on  
486 the need for multiple approaches combining the use of good natural history, rigorous tests  
487 of spatial and temporal patterns and experimental assessments of the combinations of  
488 factors that drive them. In this regard, it will continue to be useful to assess past changes as  
489 a function of known climate change. Whilst these assessments are necessary, their use in  
490 forecasting relies on integrating experimentally derived knowledge of the relevant  
491 combinations of processes most responsible for accelerating (e.g. synergistic processes) or  
492 resisting ecological change (e.g. counter-balancing processes).

493

494 Reconstruction of past patterns of ecosystem diversity and composition has direct relevance  
495 to predicting the consequences of climate change because it provides information about  
496 how ecosystem may respond in the future. However, it is important that such data are  
497 treated as a ‘null models’ as additional factors such as fishing and eutrophication also lead  
498 to changes in ecosystem dynamics. In the same way that climate can be related to  
499 ecological variation through time it can be related to ecological variation in space. Studies  
500 of the ways in which key species respond to various environmental and ecological  
501 conditions across existing gradients of temperature (Pennings and Silliman, 2005;  
502 Wernberg, *et al.*, 2010) and pH (Hall-Spencer, *et al.*, 2008) have provided important  
503 insights into how species or systems may respond to changing climate conditions. The  
504 gradual temperature gradients, such as those along the tropical-temperate transitions of the  
505 Australian eastern and western coastlines (Smale and Wernberg, 2009), offer strong  
506 opportunities for combining observational and experimental studies (comparative

507 experiments *sensu* Menge, *et al.*, 2002) to quantify the sublethal effects of climate on the  
508 response of systems to additional perturbations (e.g. Wernberg, *et al.*, 2010).

509

510 There are relatively few observed examples of species responding to climate change within  
511 Australian temperate waters, in part due to the paucity of large-scale long-term baseline  
512 data. It is, however, very likely that a large number of species, including conspicuous  
513 habitat formers, have experienced range shifts or changes in their population structure in  
514 response to recent warming, but these changes have gone unrecorded (Edgar, *et al.*, 2005;  
515 Richardson and Poloczanska, 2008). Therefore, there is an immediate need to initiate  
516 programs that will enable impacts on species, assemblages and ecosystem functioning to be  
517 documented, subsequently allowing appropriate management plans to be designed and  
518 implemented (Hobday, *et al.*, 2006). For some species, use of sediment cores or the fossil  
519 record as a natural baseline for species biogeographic range and turnover may be  
520 applicable (e.g., Greenstein and Pandolfi, 2008). Due to the number of biogeographical  
521 provinces in Australian temperate marine systems (Waters, *et al.*, 2010), and the high levels  
522 of biodiversity and endemism, it is not possible to monitor all species. Therefore, efforts  
523 should be made to identify climate indicator species as has been done by the MarClim  
524 project in the United Kingdom (Mieszkowska, *et al.*, 2005). Indeed, development of cost-  
525 effective indicators to detect changes in ecosystem health and ecological responses to  
526 climate change is currently underway in Western Australia, following substantial funding  
527 from the State (e.g., Smale, *et al.*, 2010a; Smale, *et al.*, 2010b).

528

529 Experiments that follow these observational assessments will need to focus on meaningful  
530 combinations of local and global stressors, ensuring that predictions of future shifts in  
531 ecological diversity are not underestimated by any false impression created by summing

532 single drivers. Such experiments may be particularly powerful for predicting context-  
533 dependencies (cf. Figure 1) associated with local needs of management. While the link  
534 between human activity and abiotic changes often appears obvious in hindsight, ecologists  
535 continue to be surprised by the ecological outcomes (Paine, *et al.*, 1998). These surprises  
536 occur as a product of synergies between abiotic and biotic drivers which cannot be  
537 predicted by simply ‘adding up’ the effects of single drivers. As progress is made in  
538 identifying the conditions leading to major biotic shifts, there will be a need to assess the  
539 parameters most responsible for ecological changes and the scales at which they operate.  
540 Experimental assessments can empower local managers because they show that policies of  
541 reducing local stressors (e.g. nutrient pollution) can reduce the effects of global stressors  
542 not under their governance (e.g. ocean acidification) (Russell, *et al.*, 2009).

543

544 Forecasts of habitat loss often centre on change to primary productivity or the strength of  
545 herbivory (Connell *et al.*, this issue). Indeed, the balance between production and  
546 consumption of species that provoke ecosystem change is often altered by local influences  
547 that are contingent on middle-scale influences (e.g. oceanography) and together are  
548 mediated by climate (Fig. 1). Regional-scale differences (e.g. Leeuwin Current versus East  
549 Australian Current) drive contrasting forecasts of loss and fragmentation of kelp forests.  
550 On coasts lacking strong herbivory (i.e. within the Leeuwin Current, Connell and Irving  
551 2008), concerns about future climate tends to focus on interactions with water quality  
552 (Russell, *et al.*, 2009; Wernberg, *et al.*, 2010). Conversely, on rocky coasts with strong  
553 consumer control (i.e. within the East Australian Current), change in consumer abundance  
554 has strong effects on kelp loss (i.e. kelps-to-barrens, Andrew, 1991; Ling and Johnson,  
555 2009) and concerns for kelp persistence focuses on recruitment and fishing of consumers  
556 and their predators (Ling, *et al.*, 2009a). Recognition of such middle-scale influences (e.g.



557 regional scales of biogeography and oceanography) may provide a framework for  
558 interpreting how local stressors (e.g. nutrient pollution and fishing) interact with global  
559 stressors to provoke change (Fig. 1).

560

## 561 **Conclusions**

562 This review recognises that the world's oceans have changed naturally at timescales  
563 ranging from days to decades to millennia, but we highlight the directional changes that  
564 overlay this natural variation as a result of human activities. A recurring theme is the  
565 context-dependency of climate change impacts that results from the mediating affects of  
566 meso-scale and local scale influences (Figure 1). Such cross-scale interactions means that  
567 the abiotic conditions at any one location will reflect the combined influence of meso-scale  
568 (e.g. oceanography and storm frequency) and local-scale interactions (e.g. catchment type ×  
569 coastal morphology). The novel environmental conditions generated by climate change  
570 (e.g. increases in temperature and CO<sub>2</sub> concentrations) are likely to drive greater change in  
571 localities that have lower resilience (e.g. nutrient pollution on oligotrophic coasts or heavily  
572 fished reefs) to combinations of global and local stressors. The largest climate driven  
573 changes are, therefore, a product of their local–regional settings.

574

575 Documented cases of climate-driven change in the temperate waters of Australia are  
576 currently limited to range shifts (both contraction and expansion) driven by increasing  
577 temperature. In combination with the climate-driven addition and loss of functionally  
578 important marine species at higher latitudes, altered rates of ecosystem processes will  
579 continue to result in major changes to the structure and function of local temperate coasts.  
580 While the only true way to mitigate climate change is to reduce the reliance on carbon-  
581 based sources of energy (Russell and Connell, 2010), research is needed to assess where it

582 may be possible to ameliorate the effects of climate through management of local stressors  
583 (e.g. reduction of nutrient pollution, MPA legislation) or biological communities (e.g.  
584 MPAs and kelp re-seeding to increase resilience).

585

586 Future patterns of diversity will include the outcome of local processes and reflect the  
587 influence of climate operating across many spatial scales. The future range shifts or  
588 changes to current mosaics will represent individual species responses to spatial  
589 heterogeneity which is continually modified by temporal change. The ecological challenge  
590 is to interface local complexity into successively larger scales. Whilst this pursuit has been  
591 a fundamental activity in ecology, the need has become more difficult to ignore if our  
592 research is to maintain its relevance as a forecasting tool. Future patterns of species  
593 diversity, and their individual functions, will be a product of the temporal modification of  
594 spatial opportunities and constraints for colonisation and persistence. Ecological research  
595 into climate change has its own opportunity to diversify its approach and integrate where  
596 previous constraints hamper a more comprehensive understanding of diversity in the past,  
597 present and future.

598

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608

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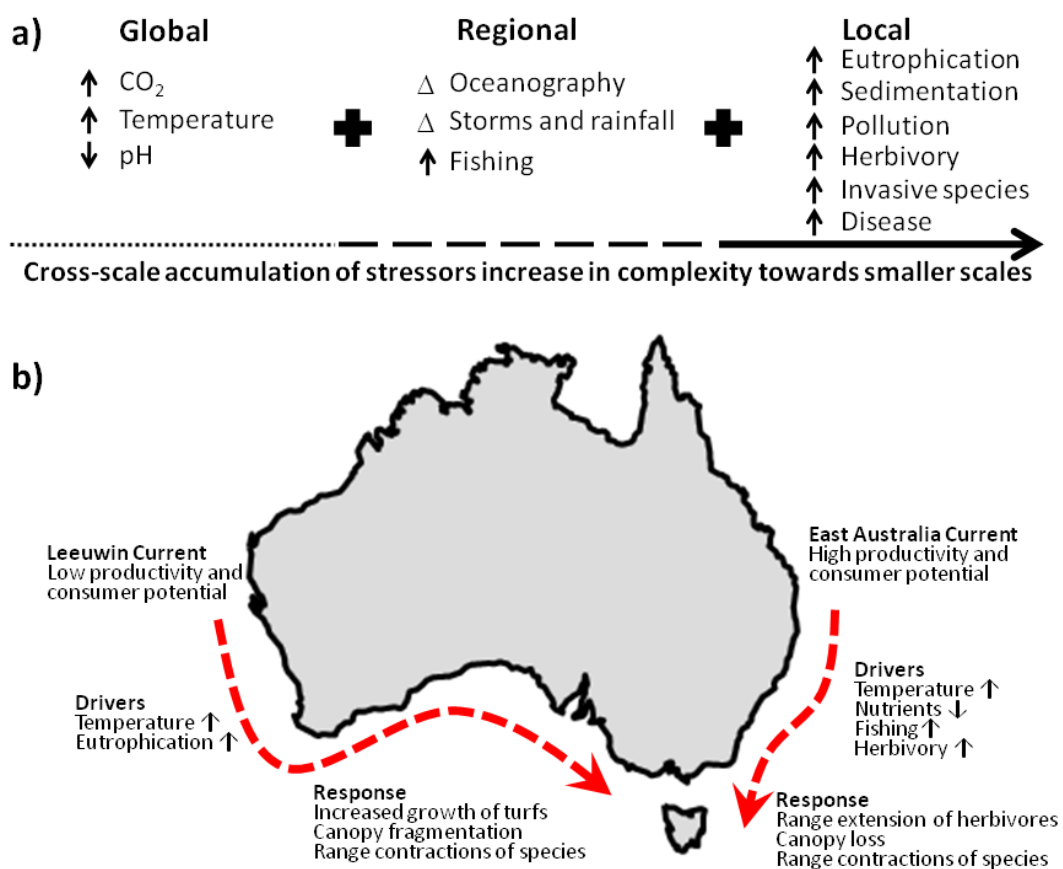
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962 **Fig. 1.** Drivers of ecological change accumulate differently across global to regional to  
 963 local scales (a). Different stressors tend to be associated with particular scales, albeit often  
 964 these are not well defined and little understanding of their explicit scales of expression  
 965 remain. Recognition of middle-scale influences (e.g. oceanography) may provide a  
 966 framework for understanding how local stressors (e.g. eutrophication and herbivory)  
 967 interact with global stressors to provoke ecological change (b). For example, responses in  
 968 coastal systems lacking strong herbivore effects have tended to focus on climate  
 969 interactions with water quality (e.g. kelp forests of the Leeuwin Current; Russell, et al.,  
 970 2009; Wernberg, et al., 2010). Conversely, on rocky coasts with strong consumer control  
 971 (i.e. East Australian Current), concerns for kelp persistence focuses on climate interactions  
 972 with recruitment and fishing of lobsters (i.e. kelp forests of the East Australian Current,  
 973 Ling, *et al.*, 2009a).



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