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Ocean acidification may slow the pace of tropicalization of temperate fish communities

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1 ***Ocean acidification may slow the pace of tropicalisation of temperate fish***
2 ***communities***

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15 **Proposed editor's summary**

16 Warming is shifting temperate zones to become more tropical. Natural warming and CO₂ vent
17 sites show that acidification buffers warming effects, reducing sea urchin numbers and
18 grazing, thus creating a turf-dominated temperate habitat which is less hospitable to tropical
19 fish than urchin barrens.

20

21 **Abstract**

22 Poleward range extensions by warm-adapted sea urchins are switching temperate marine
23 ecosystems from kelp-dominated to barren-dominated systems that favour the establishment
24 of range-extending tropical fishes. Yet, such tropicalisation may be buffered by ocean
25 acidification which reduces urchin grazing performance and the urchin barrens that tropical

26 range-extending fishes prefer. Using ecosystems experiencing natural warming and
27 acidification, we show that ocean acidification could buffer warming-facilitated
28 tropicalisation by reducing urchin populations (by 87%) and inhibiting the formation of
29 barrens. This buffering effect of CO₂ enrichment was observed at natural CO₂ vents that are
30 associated with a shift from a barren-dominated to a turf-dominated state, which we found is
31 less favourable to tropical fishes. Together, these observations suggest that ocean acidification
32 may buffer the tropicalisation effect of ocean warming against urchin-barren formation via
33 multiple processes (fewer urchins and barrens), and consequently slow the increasing rate of
34 tropicalisation of temperate fish communities.

35

36

37 The geographical ranges of species naturally ebb and flow through time¹. Nonetheless,
38 human-mediated environmental disturbances have intensified and allowed many species to
39 extend their distributions to new environments². The increase in global temperature has forced
40 many warm-adapted species (e.g., sea-urchins and tropical fishes) to expand their range
41 poleward – a process referred to as tropicalisation^{3,4}. These changing species distributions can
42 result in altered or novel biological interactions, often triggering modifications to the recipient
43 ecosystem⁵⁻⁷, such as the phase-shift from kelp-dominated to barren-dominated stage caused
44 by the poleward extension of warm-adapted temperate sea-urchin *Centrostephanus*
45 *rodgersii*^{8,9}. This shift to barren states might facilitate the presence of tropical fishes on
46 temperate reefs (native invasions) which tend to have greater associations with non-
47 macroalgae forming habitats¹⁰. Yet, the future ranges of tropical species and the consequent
48 rates of tropicalisation in temperate ecosystems remain uncertain because warming is not the
49 only global environmental driver that will alter the structure of ecological communities.

50 Ocean acidification and global warming are known to directly alter the structure of
51 marine habitats¹¹⁻¹³, and the resources that species depend on to survive^{14,15}. Warming drives
52 loss of kelp forests directly (e.g. through heatwaves¹²) and indirectly by intensifying
53 herbivory (e.g. range extensions of warm-adapted sea urchins³ and tropical herbivorous
54 fishes⁷). Yet, loss of kelp may also be driven by ocean acidification that triggers the superior
55 competition of algal turfs that benefit from CO₂^{13,16}. Whilst habitat-forming organisms, such
56 as kelps and seagrasses, can benefit directly from increased CO₂¹⁷⁻²⁰, shifts towards turf-
57 forming algae are likely to be more common because warming and acidification combine to
58 reduce the performance of habitat-creating species, but increase turf performance (e.g. in kelp
59 systems^{21,22}; coral systems^{23,24}). Yet, it is important to highlight that the majority of
60 community-level studies have focused on the single, direct and negative effects of abiotic
61 change, ignoring the fact that ocean acidification and warming can combine in synergistic and
62 antagonistic ways²⁵. In some cases, for example, change in one ‘stressor’ may act as a
63 resource to boost abundances (CO₂ can enhance algal productivity¹⁶, or fish abundances¹⁴), or
64 it may act as a stressor to suppress abundances (temperature can negatively affect secondary
65 producers²⁶).

66 Tests of the simultaneous effect of ocean acidification and warming are often easier to
67 achieve through laboratory than field experiments²⁷. However, the biological outcomes of
68 laboratory experiments may not match those of field experiments²⁸, because of the mediating
69 influence of ecological interactions²⁹ that buffer change³⁰. In addition, almost all experimental
70 studies involve the response of organisms to abrupt changes ignoring the fact that climate
71 conditions are gradually changing and the rates of the organism responses may differ from
72 abrupt to gradual changes that occur in nature³¹. Although it is not possible to study the
73 gradual effect of ocean acidification at CO₂ vents, recently many studies have highlighted the
74 benefit of natural CO₂ vents to evaluate the effect of future CO₂ conditions *in situ* on

75 organisms naturally adapted and exposed long-term to reduced pH levels. Observations from
76 natural systems, therefore, may complement and even improve laboratory experiment findings
77 because they increase the predictive value of the effects of future climate^{16,32}.

78 There has been considerable focus on how global warming enhances the poleward
79 movement of warm-adapted species^{33,34}, but there is almost nothing known on how ocean
80 acidification might accelerate or buffer these range-extensions, despite the fact that both
81 stressors will increase in strength in the near future³⁵. One key issue for marine systems is the
82 divergent forecasts of ocean warming and ocean acidification on the foraging effects of
83 ecosystem engineers such as warm-adapted sea urchins, particularly the consequences of their
84 range expansion to cooler latitudes. Whilst warming is considered a primary driver of the
85 expansion of their barrens at cooler latitudes by increasing urchin abundances leading to
86 overgrazed kelp forests³⁶, ocean acidification might inhibit the creation of barrens by reducing
87 urchin fitness and abundance, allowing the increase of non-calcified organisms. Although
88 some sea-urchin species may be able to adapt to ocean acidification³⁷, such phase-shift may
89 still occur where the CO₂-driven boost to primary productivity overwhelms the capacity of
90 urchins to compensate through herbivory¹³.

91 To investigate how these opposing effects might influence the rate of tropicalisation, we
92 assess whether ocean acidification might not only buffer the effects of ocean warming (i.e.
93 inhibit urchin barrens) but also mediate the rate of tropicalisation (i.e. accelerate or inhibit
94 recruitment of tropical fishes). Because it was not possible to investigate these two stressors
95 simultaneously *in situ* and in an orthogonal way, we present a new approach to this vexing
96 challenge using two different natural laboratories connected by a strong biological link to
97 study ocean warming (tropicalisation hotspots³⁸) and ocean acidification (natural CO₂
98 vents³⁹), both containing the range-expanding sea-urchin (*Centrostephanus rodgersii*) as an
99 important habitat engineer. Whilst warming hotspots represent ongoing warming, natural CO₂

100 vents represent pH conditions forecast for the end of the century (under various RCP
101 greenhouse gas emission scenarios). Nevertheless, our findings are important to anticipate
102 how the effects of warming on tropicalisation (i.e. at the leading edges of warm-adapted
103 species distributions where species track their native thermal niches) might be transformed by
104 acidification in the near future.

105 Here, we first observed whether moderate ocean acidification (~ RCP 4.5–6.0) might
106 reduce the densities of sea urchins and the extent of barrens (at CO₂ vents), both of which
107 would otherwise increase under ocean warming. We then propose a novel phase-shift from
108 barren to turf habitat when the effects of acidification are included (Fig. 1). Finally, we
109 consider how these shifts may also change the rate of establishment of range-extending
110 tropical fishes; i.e., we observe whether tropicalisation of fishes is facilitated by urchin
111 barrens and turf habitats. Understanding the rate of barren formation and their effect on
112 invading tropical reef fishes has direct implications for understanding tropicalisation of
113 temperate ecosystems in general.

114

115 ***Fish community composition across habitats***

116 Species richness (Fig. 2a; one-way ANOVA, $F = 28.88$; $p < 0.0001$), density (Fig. 2b; $F =$
117 18.68 ; $p < 0.0001$) and biomass (Fig. 2c; $F = 19.55$; $p < 0.0001$) of tropical fishes was highest
118 on sea urchin barrens, lowest in kelp forests, and intermediate on oyster beds and algal turf.
119 Likewise, native temperate fishes showed highest species richness (Fig. 2d; one-way
120 ANOVA, $F = 14.61$; $p < 0.0001$), total density (Fig. 2e; $F = 11.61$; $p < 0.0001$) and biomass
121 on sea urchin barrens (Fig. 2f; $F = 5.842$; $p < 0.001$). However, the three other habitats
122 showed similar richness, densities, and biomass. At the CO₂ vents, native temperate fish
123 species richness, total density and biomass were not significantly different among habitats

124 (Fig. 2h, i, j), except for a higher biomass at the vent with highest $p\text{CO}_2$ values
125 (Supplementary Fig. 1).

126 The fish community composition differed significantly among habitats for tropical
127 (Supplementary Fig. 2; ANOSIM, Global R = 0.36; $p = 0.0002$) and native temperate
128 (Supplementary Fig. 2; ANOSIM, Global R = 0.29; $p = 0.0002$) fishes in south-eastern
129 Australia, and for local species at CO_2 vents in New Zealand (Supplementary Fig. 2;
130 ANOSIM, Global R = 0.06; $p = 0.042$). For both tropical and temperate fish assemblages,
131 pairwise tests revealed that all habitats significantly differed from each other in Australia,
132 while for the fish community at the CO_2 vents, kelp forests were the most dissimilar habitat
133 (Supplementary Table 3a). The tropical fishes that contributed most to the dissimilarities
134 among habitats were the common species sergeant major *Abudefduf vaigiensis* (most
135 abundant on oyster and urchin-barren habitats) and dusky surgeonfish *Acanthurus nigrofuscus*
136 (most abundant on urchin barrens) contributing to approximately half of the dissimilarities
137 (Supplementary Table 4). For the temperate fish community, mado *Atypichthys strigatus*
138 (kelp forests) and hulafish *Trachinops taeniatus* (urchin barrens) together were responsible
139 for ~ 41–60% of the dissimilarity among habitats (Supplementary Table 5). Finally, at the
140 CO_2 vents community, ~ 56–66% of the dissimilarity among habitats was attributed to the
141 common triplefin (*Forsterygion lapillum*) (Supplementary Table 6).

142

143 ***Functional composition of fish communities across habitats***

144 The trophic functional composition of the tropical fish community (Supplementary Table 3b;
145 ANOSIM, Global R = 0.28, $p = 0.0002$) clearly differed among the four habitats in Australia,
146 except for turf and oyster habitats. For the temperate fish community, however, barrens was
147 the only habitat that significantly differed from the other habitats (Supplementary Table 3b;
148 Global R = 0.25, $p = 0.0002$). Most of the functional groups of tropical fishes were associated

149 with barrens, except for planktivores, which were also highly associated with oyster reefs
150 (Fig. 3 and Supplementary Table 7). For the temperate fish species in Australia, roving
151 grazing herbivores, territorial grazing herbivores, both browsing/grazing herbivores, and
152 planktivores were most associated with barrens, and they were the functional groups that
153 overlapped in habitat use for tropical and temperate fish assemblages (Fig. 3 and
154 Supplementary Table 7). Only temperate functional groups, particularly omnivores, kelp
155 feeders, browsing herbivores, and herbivorous/detritivores were associated with kelp habitats.
156 Turf and oyster-dominated habitats were associated with few functional groups: temperate
157 invertivores, and temperate carnivores, respectively.

158

159 ***Response of sea urchin populations to elevated CO₂***

160 Both the temperate native (Supplementary Fig. 3; one-way ANOVA, $p = 0.001$) and warm-
161 adapted (Supplementary Fig. 3; one-way ANOVA, $p = 0.021$) sea urchins occurred in greater
162 density at control sites compared to elevated CO₂ vent sites. Although the low R^2 indicates
163 high unexplained variability by the regression line (probably caused by the higher number of
164 zeros, especially for the warm-adapted sea urchins), densities of both sea urchin species still
165 showed a significant decline with reduced pH (Figs. 4a, b; linear regression – native sea
166 urchins: $R^2 = 0.22$, $p = 0.0001$, and warm-adapted sea urchins: $R^2 = 0.08$, $p = 0.019$). The
167 warm-adapted sea urchin showed higher sensitivity than the native species to reduced pH with
168 densities at $\text{pH} < 8.0$ being zero, and they were only observed at pH levels ranging between
169 8.09 and 8.30. Native urchins were found down to pH levels of 7.2, albeit at very low
170 densities.

171 Heavy metal, trace element, and sulphur concentrations in seawater sampled at the study
172 sites did not differ between controls and vents across years (Supplementary Table 2).

173 Therefore, these abiotic factors are deemed unrelated to altered sea urchin densities and

174 barren sizes between controls and vents. Only pH and $p\text{CO}_2$ differed significantly between
175 vents and controls.

176 At the control sites in New Zealand, barren size was positively related to sea urchin
177 density (Fig. 4c; both species combined: $R^2 = 0.86$, $p\text{-value} = 0.0001$) and pH (Fig. 4d; $R^2 =$
178 0.37 , $p\text{-value} = 0.036$), but not to urchin body size (Supplementary Fig. 4; both species
179 combined: $R^2 = 0.30$, $p\text{-value} = 0.101$). Native urchin species were significantly larger at
180 vents and barrens than at kelp and turf habitats (Supplementary Fig. 5; one-way ANOVA; $p =$
181 0.0001), while body size of the warm-adapted urchin species did not differ among habitats
182 (one-way ANOVA; $p = 0.461$).

183

184 These results demonstrate that ocean acidification may buffer the negative effects of
185 ocean warming by inhibiting range-extending urchins so that their abundances are sparser
186 than those required to form barren-dominated habitats in temperate ecosystems. Therefore,
187 these two divergent global forces play opposing effects on the rate of tropicalisation. Ocean
188 warming facilitates the range expansion and recruitment of tropical vagrant fishes by
189 mediating a phase-shift (through urchins) from a kelp-dominated to a barren-dominated state
190 (resulting in a 20-fold increase in densities and biomass, and a 3.5-fold increase in species
191 richness of tropical vagrant fishes at their leading edges). Ocean acidification acts as a stressor
192 on urchins so that their sparser densities are insufficient to form barrens, but also facilitates
193 the emergence of turf-dominated habitats that are directly boosted by CO_2 nutrient
194 enrichment. This individual effect of elevated CO_2 on reduced sea-urchins density and
195 barrens, and regime shifts towards turf-dominated habitats has also been observed at other
196 natural CO_2 vents⁴⁰⁻⁴². Considering the sole effect of urchin overgrazing, a reversal from
197 barrens to kelp habitat is unlikely to occur due to a hysteresis effect in which the pathway of
198 ecosystem recovery differs from the pathway of degradation⁴³ (Extended Data Fig. 1). This

199 hysteresis appears strong under future climate in which physiological performance and
200 abundance of urchins appear reduced by ocean pH so that shallow temperate ecosystems are
201 less likely to return to their previous natural state of kelp domination. Where warming,
202 acidification, and urchin grazing combine, a switch from kelp to turf-dominated habitats
203 would reduce the recruitment of tropical fishes and consequently retard the rate of
204 tropicalisation of temperate fish assemblages (see conceptual diagram in Fig. 1 and Extended
205 data Fig. 1). Yet, current models about warming alone suggest accelerated tropicalisation as
206 urchin barrens expand in distribution and extent.

207 The acidification effects we present suggest that the strength of future tropicalisation is
208 still unknown. Many tropical fishes are extending their ranges to higher latitudes under
209 warming to stay within their preferred thermal niche⁴⁴. Whilst at their leading edges these
210 species can escape the detrimental effects of warming, they are less likely to escape the
211 effects of increasing CO₂ concentrations through range extensions. By studying CO₂ vents,
212 we can disentangle the effects that future acidification might have on the establishment of
213 tropical species at their leading edges of their distribution. The mechanisms we reveal for
214 each of these stressors in natural environments appear to have strong potential to interact
215 antagonistically and create very different future ecosystems than when considered alone.

216 Our findings suggest that at temperate systems, urchin barrens sustain the highest
217 biomass and a more diverse and abundant tropical fish community than structurally more
218 complex habitats. As such, barrens are a key habitat for tropical fish to establish viable
219 populations on temperate reefs. These findings are consistent with previous observations
220 showing that most tropical species preferred non-macroalgal rocky habitats¹⁰. Urchin barrens
221 are hard substrata usually covered only with a thin layer of filamentous algae, which is a
222 principal food source for grazing herbivores and, for example, explains why the tropical
223 herbivorous dusky surgeonfish (*Acanthurus nigrofuscus*) was strongly associated with this

224 habitat^{45,46}. Although the most abundant tropical species *Abudefduf vaigiensis* was relatively
225 more abundant in oyster-dominated habitats, it also had high abundances in urchin barren-
226 dominated habitats, which may be explained by the fact that (1) *Abudefduf vaigiensis* usually
227 forages in the water column and in areas with intense water movement which may coincide
228 with the same areas where oyster reefs and urchin barrens are found and, (2) oysters and
229 urchins also create hard-substrate habitats that provide refuge for many temperate and tropical
230 fishes that prefer habitats free of algae⁴⁷⁻⁴⁹. As such, declines in oyster reefs mediated by
231 climate change^{50,51} and overfishing in Australia⁵² may further reduce the establishment of the
232 most common vagrant tropical fish in temperate ecosystems.

233 Various temperate fish species (24% of total temperate species) were observed inhabiting
234 and/or foraging in kelp-dominated habitats, suggesting that kelp forests are a key habitat for
235 the maintenance of temperate reef fish diversity and their population abundances. Besides
236 overgrazing by urchins, additional collapse of kelp forests driven by climatic disturbances
237 (e.g. marine heatwaves, ocean acidification, and range extensions of tropical herbivorous
238 fishes^{7,12,13}) may further disrupt the structure of temperate fish communities by opening up
239 more suitable habitat for range-extending coral reef fishes. Temperate fishes were similarly
240 associated with turf and kelp-dominated habitats. In contrast, vagrant tropical fishes, almost
241 completely avoided kelp habitats, while some species were associated with turf habitats. This
242 suggests that: (1) although tropical fishes are highly associated with barrens (due to increasing
243 warming), a regime shift to turf-dominated habitats (with increasing CO₂) will not completely
244 inhibit the establishment of tropical fishes in temperate ecosystems and only slow the pace of
245 tropicalisation, and (2) a regime shift from present-day kelp domination to turf-dominated
246 systems (with increasing warming and acidification combined^{12,53,54}) is more likely to have a
247 greater positive effect on vagrant tropical fishes than resident temperate fishes, facilitating the
248 creation of novel community structures under future climate.

249 Tropical and temperate trophic functional group that overlapped most in habitat use (on
250 urchin barrens) was that of the grazing herbivorous fishes. The increasing density of grazing
251 herbivorous fishes on temperate reefs may intensify the grazing pressure on kelp forests,
252 hindering their capacity to recover once they have turned into barrens^{7,55}. Alternatively, such
253 overlap in habitat use is expected to increase niche competition, which can lead to niche
254 displacement depending on which species has a higher competitive ability⁵⁶. To a lesser
255 extent planktivores also overlapped in habitat use. However, unlike grazing herbivores,
256 tropical and temperate planktivores are usually observed schooling together, allowing tropical
257 species to increase their survivorship in temperate environments⁵⁷. Thus, by adopting this
258 social behaviour, tropical and temperate planktivorous fishes might share the same habitat and
259 coexist in temperate ecosystems under climate change^{58,59}.

260 Whilst some laboratory studies have found that sea urchins might adapt to long-term
261 exposure of ocean acidification^{60,61}, species living at natural CO₂ vents showed little evidence
262 of adaptation potential to ocean acidification⁶². We showed declines in the density of both
263 native and warm-adapted temperate sea urchins and size of their barrens in natural ecosystems
264 subjected long-term to elevated CO₂. Our results suggest that the reduction in sea urchins
265 densities and the decrease in urchin feeding rates under elevated CO₂¹³ may suppress the
266 formation of urchin barrens under future ocean acidification as anticipated for species with a
267 reduced scope for adaptation.

268 Although the effects of ocean acidification on sea urchins varies with species identity⁶³
269 and laboratory designs, experimental field and laboratory suggest that our findings might be
270 quite general as sea urchins tend to be considered particularly vulnerable to lowered pH as
271 observed through a reduced performance (e.g. grazing rates, growth, reproduction) and
272 reduced density^{13, 64,65}. This is likely due to a limited extracellular acid-base regulatory ability
273 (i.e. homeostatic regulation of the pH of the body's extracellular fluid), especially when

274 exposed long-term^{66,67}. Indeed, reciprocal experiments conducted at the same vents where the
275 present study was performed (New Zealand) showed that feeding rates and densities of the
276 native urchins (*Evechinus chloroticus*) decline when translocated from control to elevated
277 CO₂ conditions at vents¹³.

278 We did not find a relationship between urchin body size and barren formation, probably
279 because of the low sample sizes or the low abundances of *C. rodgersii*, which is considered to
280 be the main sea urchin species that can enable alternative states of shallow reef communities
281 in Australasia³⁶. The increase in algal production at elevated CO₂ levels provides more food at
282 vents, which might explain the larger-sized native sea urchins at the vents compared to other
283 habitats in temperate (this study) as well as tropical regions⁶⁸. Thus, future CO₂ conditions
284 and the decreasing density and rates of urchin herbivory combined with ocean warming might
285 accelerate the expansion of turf algae cover⁵⁴. In contrast, other habitats that are sensitive to
286 one or the combination of these stressors, such as barrens (this study) and kelp^{69,70}, might be
287 rapidly overgrown by turf-forming algae which will reduce the density and diversity of range-
288 extending tropical fishes, modifying the trajectory of tropicalisation of temperate systems.
289 Despite transgenerational acclimation to reduced pH has been observed in the laboratory for
290 some sea urchins⁷¹⁻⁷³, the boosted productivity of turfs by CO₂ enrichment increases the
291 probability of turf-domination where urchin grazing rates are unable to compensate⁷⁴.

292 The limited evidence for transgenerational adaptation to climate change in fish showed
293 mixed outcomes and is likely to be species-specific⁷⁵. Whilst some studies have found
294 evidence of physiological (growth⁷⁶) and behavioural (antipredator behaviour⁷⁷) acclimation
295 through phenotypic plasticity and adaptation, others found little evidence of potential
296 adaptation of fish behaviour to elevated temperature and CO₂^{78,79}. The eutrophication effect of
297 elevated CO₂ will prompt habitat modifications through the promotion of turf algae expansion
298 in temperate systems and its effects are improbable to be altered under longer-term exposure.

299 Transgenerational alteration of tropical fish habitat choice in novel temperate habitat
300 composition (turf-dominated habitat) is therefore unlikely to occur.

301 Whilst ocean warming facilitates tropicalisation by creating barren-dominated states,
302 acidification inhibits the formation of preferred barren-habitat of tropical fish that are created
303 by urchins. We conclude that the pace of ongoing tropicalisation due to climate change may
304 be slowed by ocean acidification through its indirect (inhibiting sea-urchin abundances) and
305 direct effects (promoting the expansion of non-barren habitats).

306

307

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517

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525

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527 E.O.C.C. and C.M.F. collected the data, E.O.C.C. analysed the data. E.O.C.C, I.N., D.J.B. and
528 S.D.C. wrote the article.

529

530 **Competing interests.** The authors declare no competing interests.

531

532 **Ethics.** All experiments were performed under animal ethics approval numbers S-2015-222A
533 and S-2017-002, and according to the University's animal ethics guidelines.

534 **Methods**

535

536 **Study areas**

537 We combined observations from two subtidal volcanic CO₂ vents (New Zealand) and three
538 tropicalisation hotspots (south-eastern Australia) (Extended Data Fig. 2). We used these areas
539 as an “early warning” system to assess the combined consequences of ocean acidification and
540 ocean warming at tropicalisation hotspots across temperate coastal ecosystems. Three main
541 rocky-reef habitat types were distinguished⁸⁰: kelp forests (dominated by *Ecklonia radiata*),
542 turf-forming algae (<10 cm in height¹³) and sea urchin barrens (dominated by crustose
543 coralline algae). These barrens are created by the native temperate species (*Evechinus*
544 *chloroticus*) and warm-adapted sea urchin *Centrostephanus rodgersii*. *Centrostephanus*
545 *rodgersii* creates widespread barren habitat across ~50% of the shallow reefs in SE Australia,
546 which amounts to several thousand hectares⁸⁰. This species has been largely restricted to the
547 coast of New South Wales including Sydney, but from ~50 years ago the range of this species
548 has extended southwards to northern Tasmania⁹ and to northern New Zealand⁸¹.

549 Although the two stressors were separately evaluated, in areas with distinct
550 environmental features, the two studied regions can be compared because: (1) both are located
551 in shallow temperate rocky reef ecosystems; (2) they have similar bathymetric zones (shallow
552 reefs ranging from ~1 to 6 m); (3) the major benthic components and vegetation are similar
553 (described above); and (4) the two key ecosystem engineers (sea urchins) occur in both
554 regions. Such similarities indicate that these systems might be used to draw meaningful
555 conclusions at the leading edges of species distributions about the synergistic effect of ocean
556 warming and acidification on the tropicalisation of temperate systems.

557

558 ***Natural CO₂ vents***

559 Volcanic CO₂ vents are naturally enriched in CO₂ where the levels of ocean pH correspond to
560 predicted future levels of ocean acidification, enabling the investigation of the prolonged
561 effect of future CO₂ concentrations on marine communities *in situ*^{40,82}. The vents studied (~6–
562 8 m depth) were located on the north-eastern coast of an active volcanic island (Bay of Plenty,
563 White Island, New Zealand; 37°31.013' S, 177°11.649' E) where CO₂ bubbles are released
564 from the rocky reef substrate in a total area of ~580 m². A total of four sites were sampled:
565 two adjacent control areas located approximately 25 m from the vents, with pH levels similar
566 to normal conditions (means across years: 8.05–8.08), and two sites with locally reduced
567 seawater pH (means across years: 7.82–7.88), with values close to Representative
568 Concentration Pathway projections of 4.5 and 6.0 for the year 2100³⁵. The southern vent had
569 pH values that reflected an approximate RCP 4.5 scenario with a reduction of 0.19 pH units
570 compared to the control site, while the northern vent showed a pH reduction of 0.24 units
571 which is close to an RCP 6.0 scenario (Supplementary Table 1). The pH levels at the vents
572 were relatively stable over time and are not confounded by other physico-chemical variables
573 (Supplementary Table 2). These pH reductions represent moderate end-of-century predictions
574 rather than a more extreme RCP 8.5 scenario reflective of no greenhouse gas mitigation
575 measures⁸³.

576 At CO₂ vent sites, the benthic community is primarily composed of turfs where CO₂
577 concentrations are elevated, whereas outside this CO₂ influence kelp and barrens form
578 mosaics with turfs¹³. The fish community is composed of a few roving species, which are
579 unlikely to be continuously exposed to the low pH levels at the vents due to their high
580 mobility, but a large community (comprising >90% of the total fish density) of territorial and
581 site-attached species composed mainly of triplefins and blennies. At the CO₂ vents, we
582 defined “fish assemblage” as species with well-defined and small home range and low
583 mobility that are within the CO₂ plume and are directly affected by elevated CO₂. By using

584 only species that match these criteria (low mobility and small home range), such as triplefins
585 and blennies, we are able to draw stronger conclusions about the effects of habitat
586 modification triggered by CO₂ on a fish community. Previous studies showed that seawater
587 temperature does not differ among the four sites and the pH values show only a small
588 variation at any given site over the day^{11,13}.

589

590 *Tropicalisation hotspots*

591 Over the last two decades, Sydney's coastal areas (New South Wales, Australia) have
592 experienced arrivals of an increasing diversity and density of vagrant tropical fishes that
593 annually recruit there throughout the summer (~100 species)³⁸. There has been a gradual
594 increase in the abundance of overwintering survivors due to increasing coastal seawater
595 temperatures⁸⁴. All these factors in combination with the gradual strengthening of warmer
596 currents (e.g. East Australia Current) moving down from tropical regions to high latitudes^{85,86}
597 make the Sydney coast a tropicalisation hotspot^{4,87}. We selected the same sites where vagrant
598 tropical fish assemblages have been regularly monitored for nearly 18 years (Sydney:
599 Cabbage Tree Bay, Fairy Bower and Little Manly). These reefs are dominated by a mosaic of
600 the three main types of habitats (kelp, turf, barrens) in addition to patches of oyster reefs
601 which were also used in this study because of its importance as a habitat provider for many
602 organisms⁸⁸ including some tropical fishes that were observed using this habitat as a refuge.
603 Oyster reefs were once a common habitat of temperate coastal waters in NSW but after severe
604 overharvesting only small patches persist in the intertidal zone⁸⁹.

605

606 **Study design**

607

608 *Fish density and diversity*

609 The abundance and diversity of local (temperate) and vagrant (tropical) fishes were estimated
610 in south-eastern Australia (2017–2018), and local species in New Zealand (between February
611 and April, in years 2017 and 2018). Visual surveys estimated the density of fish within
612 sampling units that were randomly distributed among patches of the most common habitats
613 identified for each region (see *Study areas* above).

614 The specific method used to quantify fish assemblages was designed to best represent the
615 local assemblage and the size and shape of habitats. At the vents in New Zealand, only some
616 species (e.g. triplefins, blennies and scorpionfish) were considered because these species are
617 site-attached and the consequences of long-term exposure to elevated CO₂ at vents could be
618 properly investigated. The site-attached fish assemblage studied was identified to species and
619 visually quantified in replicate stationary circular census. Due to the small fish body sizes, the
620 counts were made in small cylindrical survey areas of 1 m in diameter. Fishes were counted
621 inside the cylinder for approximately 1 minute. This approach produces the best density
622 estimates for small fishes (≤ 10 cm) (methodology adapted from Minte-Vera et al.⁹⁰).

623 Individual fish body size was also estimated between two categories (< 5 and > 10 cm total
624 length). At each of the two control sites a total of ~ 15 quadrats were surveyed per habitat
625 (kelp, turf, and barrens). At the vents, the benthic cover is dominated by turf habitat and
626 therefore 27 quadrats were surveyed for this habitat at the vent sites (11 at the southern vent
627 and 16 at the northern vent).

628 In the Sydney area, belt transects were used to quantify the temperate and tropical fish
629 assemblages in each main benthic habitat type identified in this region. About 15–30 transects
630 were surveyed per habitat (kelp, turf, barren and oyster banks). The method consisted of a
631 diver swimming along a transect of 10 m length, identifying and counting all fishes including
632 their respective body length (size categories of < 5 , 5–10, 10–20, 20–30, > 30 cm total length)
633 within 2 m of each side of the transect tape (40 m² area per transect). All benthic and pelagic

634 fish species were included. First, the larger fishes were counted and then for the same transect
635 an intensive search for small and cryptic species was performed between and underneath kelp
636 leaves, rocks and inside crevices (methodology adapted from Fulton et al.⁹¹). The difference
637 in the census area and shape between the two regions (Australia vs New Zealand) corresponds
638 to the length and shape of the habitats. Larger census areas in Sydney were used because of
639 the larger and longer patches of habitats than those in New Zealand.

640 For both study regions, differences in the fish assemblage among habitats were evaluated
641 at the individual species as well as functional levels. Fishes were split into major functional
642 groups according to their diet and feeding habits: (1) planktivores; (2) omnivores; (3)
643 invertivores; (4) herbivores; and (5) carnivores (fish and invertebrate feeders). Additionally,
644 because the herbivorous fish community is not a homogeneous group we subdivided them
645 into: (6) solely epilithic algae matrix (EAM) feeders (roving-grazing herbivores, territorial-
646 grazing herbivores and herbivores/detritivores); (7) solely browsing herbivores (macroalgae
647 feeders); (8) combined browsing and grazing herbivores (EAM and macroalgae feeders); and
648 (9) kelp feeders. These categories follow Choat & Clement⁹², Clements & Choat⁹³, Ceccarelli
649 et al.⁹⁴, and Zarco-Perello et al.⁹⁵. All diet information and functional characteristics were
650 collected from FishBase⁹⁶. As the benthic fish species in New Zealand were all are part of the
651 same functional group (i.e. invertivores – following FishBase), functional group analysis was
652 not performed for the New Zealand study area.

653

654 *CO₂ effects on sea urchin populations*

655 In New Zealand, sea urchin densities were quantified inside circular quadrats of 2 m in
656 diameter at the same patches of habitats where the fishes were surveyed. A total of 15 circular
657 quadrats were performed in turf habitats at the vents and each of the three habitats at controls.
658 A maximum of 10 sea urchins within each habitat were randomly selected and their body

659 sizes (longest diameter) were measured using callipers. In total, the body size of ~400 native
660 sea urchins and 30 warm-adapted sea urchins (due to their lower abundance in comparison
661 with the natives) was measured. Finally, after each survey we measured the largest and
662 smallest dimensions of 15 patches of barrens at control sites had their largest and smallest
663 dimensions measured of each barren at control sites was measured in order to calculate the
664 area (m²) of each barren and correlate sea-urchin abundances to barren size. At the end of
665 each survey, seawater samples were collected directly above the substrate of each circular
666 transect to measure seawater pH. A diagram summarising the methodology is shown in
667 Supplementary Fig. 6.

668

669 **Statistical Analysis**

670 A canonical analysis of principal coordinates (CAP) was used to evaluate the relationship
671 between habitat type, and taxonomic and functional fish assemblages. The decision to use a
672 constrained (CAP) over an unconstrained analysis was because constrained data is normally
673 considered as the most appropriate multivariate analysis, especially when there is an *a priori*
674 assumption of how explanatory variables (in this case habitats) determine response variable
675 values (in this case species abundance) measured in the same set of objects (e.g. samples or
676 sites). In addition, constrained ordination analysis uncovers patterns that are masked in
677 unconstrained multivariate analyses (e.g. nMDS ordination), allowing us to better visualize
678 specific differences between habitat types^{97,98}.

679 As the tropical and temperate fishes do not share the same taxonomic composition,
680 comparisons between these two different communities was performed based on species
681 functionality⁹⁹. Hence, comparing the function played by vagrant tropical and temperate
682 species might reveal their potential to compete and/or share the same resources. To reduce the
683 contribution of disproportionately abundant species on the analysis, the data were square-root

684 transformed. Dissimilarities in the taxonomic and functional abundance of fish assemblages
685 (tropical, temperate and CO₂ vents fish assemblages) were calculated using one-way Analysis
686 of Similarities (ANOSIM), and ANOVAs were then used to test for univariate differences in
687 species richness, density and biomass of fish between the factors of origin (tropical vs
688 temperate) and habitat (kelp-dominated vs barren-dominated vs turf-dominated vs oyster-
689 dominated vs CO₂ vents), using habitat as a fixed factor. Biomass of each community was
690 obtained by converting fish counts to biomass using Length–Weight relationships from
691 FishBase⁹⁶. Estimates were calculated by multiplying the weight from the midpoint of each
692 size category by the number of fish per size category, and then summing size categories¹⁰⁰. A
693 similarity percentage analyses (SIMPER) was used to evaluate which species and functional
694 groups mostly contributed to dissimilarities among habitat types. Ordination and similarity
695 analyses were performed using the PRIMER 6 software. Student–Newman–Keuls (SNK)
696 multiple comparisons of means were performed as *post-hoc* tests for all ANOVAs and
697 pairwise comparisons of the mean were used in the ANOSIMs¹⁰¹.

698 To test the relationships between sea urchin density and pH, between barren size and pH,
699 urchin density, and urchin body, size simple linear regression analyses were used. Finally,
700 differences in sea urchin size across habitats were tested using a one-way ANOVA.
701 Regression and ANOVA analyses were conducted using R software version 3.4.1.

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703

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754 **Data availability**

755 The data that support the findings of this study are available from the lead contact Ivan

756 Nagelkerken (ivan.nagelkerken@adelaide.edu.au).

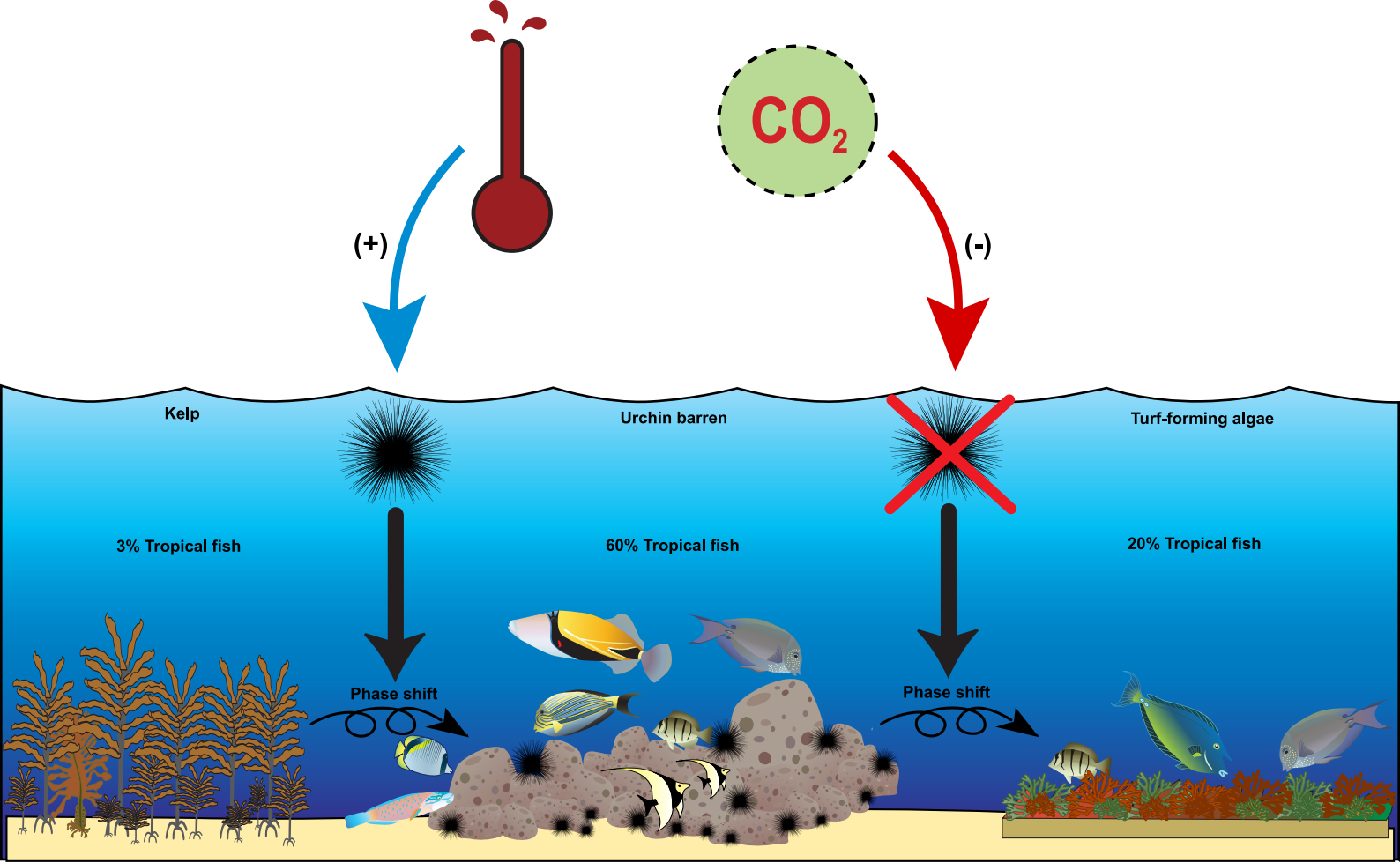
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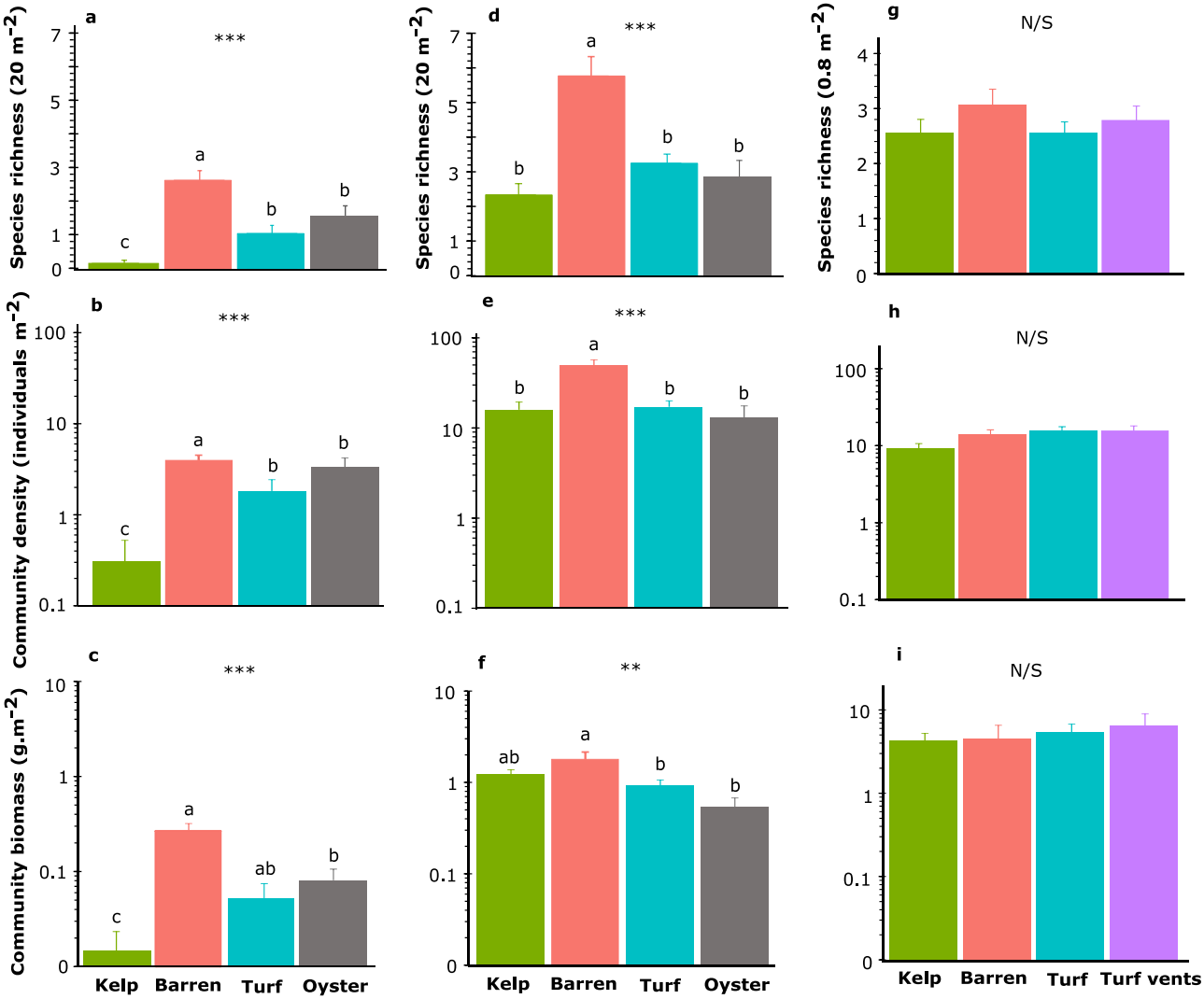
758 **Figure 1.** A conceptual diagram depicting the potential direct, indirect, negative (-) and positive (+) effects of ocean warming and ocean
759 acidification on sea urchin-induced habitat phase shifts and the cascading effects on species richness of range-extending tropical fishes in
760 temperate ecosystems (% values represents the relative fish species richness per habitat). Elevated temperature enables the range expansion of
761 sea urchins, driving a phase shift from natural kelp forests to rocky barrens. Ocean acidification, however, decreases range-extending urchin
762 densities (via negative physiological effects), and enables a phase shift from barrens to turf-dominated habitats (via CO₂ enrichment). Hence, the
763 invasion of tropical fishes in temperate waters may be slowed by ocean acidification. Symbols are courtesy of the Integration and Application
764 Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

765
766 **Figure 2.** Structure of fish assemblages across different coastal habitats showing urchin-barrens as a key habitat for tropical and temperate fish
767 assemblages while kelp-habitat is avoided by tropical fishes. Mean and standard error for a-b-c) range-extending tropical fish communities of
768 south-eastern Australia; d-e-f) local-temperate fish communities of south-eastern Australia; h-i-j) temperate fish community at CO₂ vents (turf-
769 vents) and three control habitats at White Island, New Zealand, with richness per transect (top panels), density (middle panels) and biomass
770 (bottom panels). *** p < 0.001, ** p < 0.01, N/S = not significant (tested using ANOVA); different letters above bars indicate significant
771 differences among habitats (post hoc tests). At the vents the benthic cover is dominated by turf algae, therefore it was considered as the only vent
772 habitat. The y-axes for the density and biomass graphs were all log-scaled for consistency.

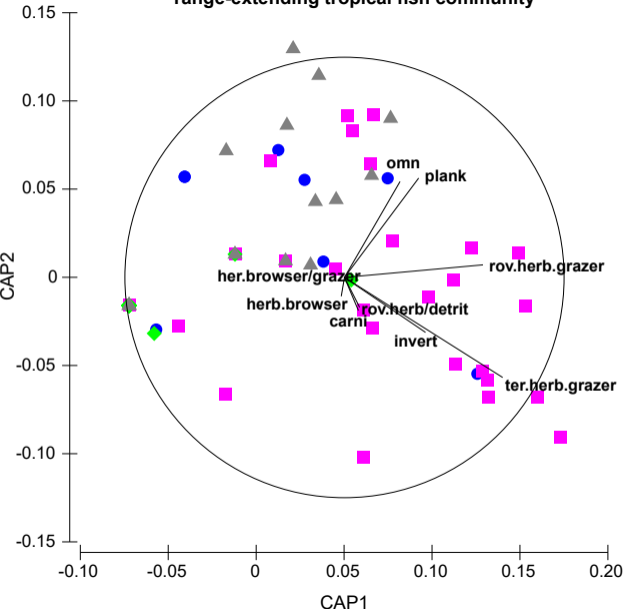
773
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775 **Figure 3.** Canonical analysis of principal coordinates (CAP) ordination based on Bray-Curtis distance showing the correlation between
776 trophic functional groups of range-extending tropical and local-temperate fish assemblages, respectively, with temperate reef habitats of
777 south-eastern Australia. The vectors (black lines) show the correlation of each functional group with each habitat and their lengths indicate
778 the magnitude of this correlation. Functional group abbreviation: omn = omnivores, plank = planktivores, rov.herb.grazer = roving grazing
779 herbivores, rov.herb/detrit = roving herbivores detritivores, invert = invertivores, ter.herb.grazer = territorial grazing herbivores, carni =
780 carnivores, herb.browser = browsing herbivores and herb.browser/grazer = browsing and grazing herbivores.

781
782
783 **Figure 4.** Linear regressions showing the relationship between seawater pH, sea-urchin densities, and barren size. a) native temperate sea
784 urchin (*Evechinus chloroticus*; R² = 0.22, p = 0.0001), and b) warm-adapted sea urchin (*Centrostephanus rodgersii*; R² = 0.08, p = 0.019),
785 respectively, across a pH gradient at CO₂ vents and controls (New Zealand). c) relationship between barren size and total sea-urchin
786 abundance (R² = 0.86, p-value = 0.0001). d) relationship between sea-urchin barren size and pH (R² = 0.37, p-value = 0.036). Sea urchin
787 density data on the y-axes of graphs a) and b) were log₁₀(x+1) transformed. Vertical dashed lines indicate the global average of present-day
788 and future seawater pH for the 21st century according to Representative Concentration Pathway scenarios by Bopp et al.³⁵.





range-extending tropical fish community



local-temperate fish community

