

Range-extending tropical herbivores increase diversity, intensity and extent of herbivory functions in temperate marine ecosystems

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AUTHORS' CONTRIBUTIONS

S.Z.-P. conceived the study; S.Z.-P and TW acquired the funding; S.Z.-P. collected the field data; S.Z.-P. and G.C. analyzed the data. S.Z.-P. wrote the paper and all authors contributed to drafting the manuscript and gave final approval for publication.

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Abstract

1. Climate change is modifying species distributions around the world, forcing some species poleward, where they can alter trophic interactions. Many tropical herbivorous fishes have successfully expanded their ranges into temperate ecosystems, and while it is clear they drive increases in herbivory rates in specific localities, little is known about how they might affect the diversity of herbivory functions across large spatial scales, considering their interaction with assemblages of native herbivores in temperate habitats.
2. We assessed the spatial overlap and habitat associations of native temperate and range-expanding tropical herbivorous fishes in six sub-regions of south-western Australia to determine how incursions of tropical species may have affected the diversity, redundancy (index of uniqueness) and the 'spatial extent' (addition of functions in new areas) and 'intensity' (increasing density of functional groups) of specific herbivory functions in recipient ecosystems.
3. Tropical herbivores had high abundances in temperate ecosystems, forming schools from 40 (parrotfish) to 200 (rabbitfish) individuals strongly associated with seagrass meadows and reefs with high cover of turf algae. Overlap with temperate herbivores was highest in the northern sub-regions, forming unique assemblages, with no apparent species displacements. The addition of tropical species increased functional diversity and uniqueness (the complement of redundancy), introducing novel herbivory functions to many locations. Seagrass browsing increased in spatial extent

32 (27%) and intensity (15 x), while seaweed browsing and grazing increased in
33 intensity by up to 2.5 x in regions with high abundances of tropical herbivores.

34 4. Our results suggest that the diversity, intensity and spatial extent of different
35 herbivory functions can change as tropical species with different habitat affinities,
36 behaviors and diets shift their distributions poleward. Changes in functional
37 redundancy are likely to be heterogeneous in space and might not increase initially
38 because the diversity of herbivory functions is relatively low in some temperate
39 marine ecosystems. However, there is the potential for greater redundancy as further
40 tropical species arrive, their abundances increase and the spatial and functional
41 overlap of communities rises.

42

43 Keywords: Climate change, tropicalization, range-shifts, herbivory, habitat
44 associations, novel interactions, spatial overlap

45 Introduction

46 Evidence is mounting about the impact of climate change on the distribution of marine and
47 terrestrial species (Pecl *et al.* 2017). While species' ranges are expanding, contracting or
48 shifting locally, overall there is a global trend for species' addition at higher latitudes (Blowes
49 *et al.* 2019). This trend has seen an increase in the proportion of species of tropical affinity in
50 temperate ecosystems, a process often referred to as 'tropicalization' (Wernberg *et al.* 2012;
51 García Molinos *et al.* 2015). Tropicalization has been particularly strong in marine ecosystems
52 (Vergés *et al.* 2014), where climate-change velocities and species range-shifts are advancing
53 at higher rates than in terrestrial environments (Sorte, Williams & Carlton 2010; Burrows *et al.*
54 2011). Range expansion of tropical species into temperate regions alters the species
55 composition of recipient ecosystems, potentially changing the diversity and intensity of
56 ecological functions, in ways that depend on the outcomes of novel species interactions and
57 the overall balance between species extirpations and additions in the ecosystem (Albouy *et*
58 *al.* 2014; Ockendon *et al.* 2014).

59 As novel species assemblages emerge, ecological processes can be modified by ecological
60 engineers (Blois *et al.* 2013). Temperate seagrass meadows and kelp forests are forecast to
61 change as the ocean warms, because top-down forces are expected to intensify with the
62 addition of tropical herbivores (Hoekman 2010; Hyndes *et al.* 2016). Herbivory is a key
63 ecological function which regulates the bottom-up energy flow between trophic levels and the
64 top-down control on habitat structure by reducing seagrass and seaweed canopy cover and

65 mediating competition for space between sessile taxa (Poore *et al.* 2012; Nowicki, Fourqurean
66 & Heithaus 2018). Consequently, the strengthening of herbivory by range-extending tropical
67 herbivores could shift temperate habitats primarily regulated by production towards states
68 regulated by consumption (Vergés *et al.* 2014), thereby accelerating the integration of biomass
69 from habitat-forming macrophytes into the food chain (Zarco-Perello *et al.* 2019) and
70 increasing the cover of turf seaweed and sessile invertebrates (Filbee-Dexter & Wernberg
71 2018; Ling, Barrett & Edgar 2018).

72 The effect of range-expanding tropical herbivores will likely depend on the magnitude of
73 functional overlap with existing temperate herbivore assemblages. Novel species associations
74 can result in competition, causing replacements of species and ecological functions (Milazzo
75 *et al.* 2013), or creating new assemblages that augment certain ecological processes (Marshak
76 & Heck 2017). Herbivorous fishes, particularly species from the family Siganidae, have been
77 some of the most successful at expanding their distributions poleward (Vergés *et al.* 2014).
78 Current evidence suggests that where they have expanded, there has not been a displacement
79 of temperate species but rather additions of new populations (Vergés *et al.* 2014; Bennett *et*
80 *al.* 2015; Zarco-Perello *et al.* 2017, 2019).

81 Herbivory is carried out by species with different feeding behaviors that are generally classified
82 into two broad functional groups: 'grazers', which bite on reef substrata and regulate
83 recruitment rates of sessile taxa by consuming turf seaweed, sediment and particulate organic
84 matter; and 'browsers', which bite at canopy-forming macrophytes, engineering the three-
85 dimensional habitat structure of the ecosystem (Bellwood *et al.* 2019). Consequently,
86 increases in the number of herbivorous species could intensify herbivory by adding to the
87 number and richness of functional groups present. However, considering that species have
88 specific habitat associations, diet preferences, consumption rates and population sizes
89 (Ruttenberg *et al.* 2019), high spatial variation in functional changes and in the degrees of
90 ecological impacts on primary producers can be expected as novel guilds of herbivores are
91 formed.

92 Knowledge of the habitat associations of range-shifting species is needed in order to evaluate
93 their interactions, identify which habitats are more likely to be affected and which ones are
94 likely to facilitate further range expansions of tropical species. However, this has rarely been
95 considered in range-shift predictions (Parravicini *et al.* 2015) and currently we lack an
96 understanding of how range-shifting tropical species can affect herbivory functions in different
97 habitats across large spatial scales (Bonebrake *et al.* 2018). The spatial overlap of temperate
98 and range-expanding tropical herbivores will determine changes in functional diversity and
99 redundancy of herbivory; however, since many species have functional plasticity (*i.e.* they can

100 graze or browse on different macrophytes) (Bennett *et al.* 2015; Zarco-Perello *et al.* 2019;
101 Ebrahim *et al.* 2020), the execution of each function also depends on the spatial overlap
102 between consumers and food resources. The concept of spatial overlap within ecological
103 communities has been applied to estimate trophic interactions between species of predators
104 and their prey (e.g. Carroll *et al.* 2019), but has not been applied to functional analyses of
105 herbivory. Here, we use this approach to assess novel species interactions between potential
106 competitors (tropical and temperate herbivores) and their associated effects on herbivory in
107 temperate marine habitats experiencing tropicalization (Wernberg *et al.* 2016). For this, we
108 evaluated (i) the habitat associations and spatial overlap of temperate and range-expanding
109 tropical herbivores, (ii) the relative effect of tropical herbivores on functional diversity and (iii)
110 changes in the spatial extent (addition of functions in new areas), and intensity (increasing
111 density of functional groups) of specific herbivory functions.

112 Methods

113 Study Location

114 The composition of fish assemblages in coastal habitats of western Australia has changed
115 following a marine heatwave that struck the region in 2011 (Wernberg *et al.* 2016). Tropical
116 rabbitfish (*Siganus fuscescens*) have since formed self-recruiting populations in temperate
117 ecosystems (Lenanton *et al.* 2017; Zarco-Perello *et al.* 2019) while parrotfish (*Scarus ghobban*
118 and *S. schlegeli*) became more abundant (Parker *et al.* 2019). To identify the effects of these
119 changes, surveys of herbivorous fish were conducted over inshore habitats along the coastline
120 of south-western Australia during summer (April-May) of 2018 and 2019, from the Perth
121 metropolitan area to Cape Naturaliste in the south of the state. The ecosystems along the
122 coast consist of carbonate reefs interspersed with boulder reefs, seagrass meadows and
123 sandy plains. Survey locations were restricted to shallow habitats (depth 1-9 m; up to 6 km
124 from the shoreline), where the abundance of herbivorous fish is highest (Hoey, Brandl &
125 Bellwood 2013).

126 Herbivorous Fish Abundance and Habitat Associations

127 The abundances of temperate (*Girella zebra*, *Olisthops cyanomelas*, *Pelates octolineatus*,
128 *Kyphosus cornelii* and *Kyphosus sydneyanus*) and tropical herbivorous fish (*Scarus* spp. and
129 *Siganus fuscescens*) were measured via a GPS-tracked roving underwater visual census with
130 15 minutes per sampling location. This method is effective to estimate the abundance of
131 schooling herbivorous fish and has proven to be efficient for range-shifting species (Fox &

132 Bellwood 2008; Beck *et al.* 2014). One roving survey was performed per site, where one
133 surveyor swam at a constant pace, registering all individuals of the species of interest in an
134 approximate area of 2000 m². A second surveyor followed the same path recording the
135 seascape with an underwater camera for subsequent assessment of habitat features. Videos
136 were analyzed with the program TransectMeasure (SeaGIS), each video transect was paused
137 at one minute intervals (n=15 per transect) to extract information on topographic complexity
138 (Wilson, Graham & Polunin 2007), substrate type, species composition, species diversity, and
139 abundance of morpho-functional groups of sessile biota based on the CATAMI classification
140 scheme (Althaus *et al.* 2015). A total of 69 sites were surveyed across six sub-regions: North
141 Perth (31.8°S, n=13), Rottnest Island (32°S, n=18), South Perth (32.2°S, n=13), Rockingham
142 (32.4°S, n=11), Bunbury (33.3°S, n=5) and Geographe Bay (33.6°S, n=9). The relationship
143 between the herbivorous fish assemblage and selected measurements of habitat was
144 assessed using a Canonical Correspondence Analysis (CCA) (Borcard, Gillet & Legendre
145 2011) with the R package Vegan (Oksanen *et al.* 2019).

146
147 Fish abundance was standardized to density (individuals 125 m⁻²); however, we also
148 considered a new metric: MaxS (maximum number of fish per school in each survey), a similar
149 approach to abundance assessments of pelagic schooling fish (*i.e.* school size; Beare 2002)
150 and abundance estimates from static video methods (*i.e.* MaxN; Cappo *et al.* 2003). In addition
151 to abundance information, MaxS can be a proxy for reproductive behaviour (Azzurro *et al.*
152 2017) and ecological impact, since certain species have positive correlations between school
153 size and *per capita* consumption rates (Michael *et al.* 2013; Basford *et al.* 2016). For simplicity,
154 we report the highest MaxS and the average MaxS (MaxSm) per subregion in the text.
155 Changes in abundance of temperate and tropical herbivorous fish across latitude were
156 evaluated in separate models with negative binomial generalized linear models using the R
157 package glmmTMB (Brooks *et al.* 2017).

158 Herbivorous Fish Spatial Overlap

159 The potential strength of ecological interactions between tropical and temperate herbivorous
160 fish species was estimated by calculating their spatial overlap with the 'local index of
161 colocation' (Pianka's *O*, Pianka 1973; Carroll *et al.* 2019). This metric assesses the correlation
162 between the proportions of the densities of two groups across sites, and can be considered a
163 proxy for their encounter rate (Pianka 1973; Carroll *et al.* 2019). For this analysis we pooled
164 the densities of all tropical herbivorous species and all temperate herbivorous species and
165 calculated the overlap between the two groups within each sub-region. A resampling jackknife
166 method was applied to estimate mean and standard errors of overlap within each sub-region,

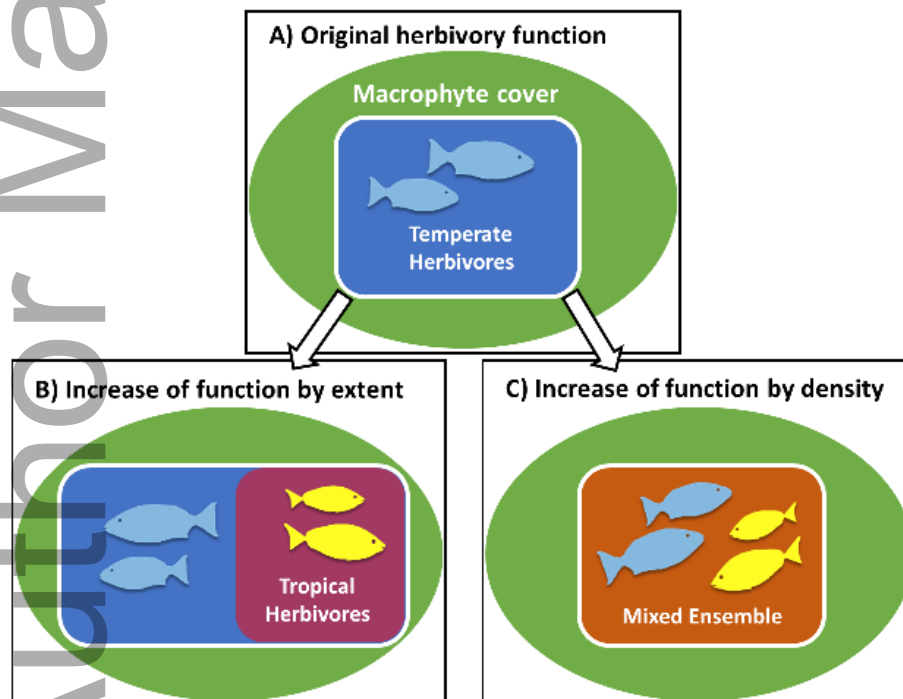
167 where we repeatedly recalculated Pianka's O , each time excluding a different site from the
168 calculations (Manly *et al.* 2007).

169 Diversity and Spatial Overlap of Herbivory Functions

170 We classified herbivory functions based on the tendency of species to feed on different groups
171 of macrophytes that affect different ecological processes: (i) grazing of turf (impacting sessile
172 taxa recruitment), (ii) browsing on seaweed canopy (impacting habitat structure) and (iii)
173 browsing of seagrass canopy (impacting nursery grounds). Because each herbivorous species
174 contributes differently to each function (Hoey & Bellwood 2009), we assigned them a species-
175 specific weight based on herbivory rates and stomach content analyses reported in the
176 scientific literature, as well as observations during our surveys in the region (Table S1 in
177 Supplementary Material). Changes in overall herbivory functions in each temperate subregion
178 were assessed by calculating functional diversity (FD) based on attribute diversity ($t = d_{\text{mean}}$
179 and $q = 1$; Chao *et al.* 2019) and functional uniqueness (U, the complement of redundancy),
180 employing the function *uniqueness* with Euclidean distance (Table S2 in Supplementary
181 Material) using the software R (R Core Team 2019): $U = Q / D$, where U is uniqueness, Q is
182 Rao quadratic entropy (an index of functional diversity) and D is the Simpson index of
183 biological diversity (Ricotta *et al.* 2016). The creators of the U index exemplify its application
184 to analyze the vulnerability of ecosystems to population declines or species extinction due to
185 disturbances, here we apply it to analyze the impact of species additions due to range shifts.
186 To assess changes in specific herbivory functions, we performed spatial overlap analyses to
187 calculate addition of functions in new areas (*i.e.* increase in spatial extent) and increase in
188 intensity of existing functions across space (*i.e.* increase in density). Functional weights were
189 not scaled for these calculations and only adult individuals were included in these analyses,
190 since herbivory rates of juveniles of most species are uncertain.

191
192 Herbivory intensity was calculated with a modified version of community weighted mean of
193 trait values (Laliberté & Legendre 2010) that incorporates spatial overlap. We refer to this as
194 the overlapped community weighted mean of trait values (oCWM), where we accounted for
195 the execution of specific herbivory functions only when there was overlap between each
196 functional group of herbivores (*e.g.* seagrass browsers) and the group of macrophytes they
197 consume (*e.g.* seagrass), similar to analyses of predator-prey interactions (Fig. 1a; Pianka
198 1973; Carroll *et al.* 2019). For each herbivory function we defined the spatial range of its
199 corresponding macrophyte type (seagrass, turf and canopy seaweed) based on whether it
200 occurred at each survey site across the region. Within the range where the macrophyte was
201 present, the densities of each temperate and tropical herbivorous species were multiplied by

202 their weight value for that function. For instance, species with a weight value of 0 for seagrass
203 browsing did not contribute to that function despite them being very abundant, whereas
204 species with values > 0 contributed only where the populations overlapped with seagrass
205 meadows. The effect of tropical herbivores for each herbivory function in each sub-region was
206 then determined as the increase in oCWM including tropical species (mixed ensemble),
207 relative to the oCWM of temperate species alone (Fig. 1). Statistical significance of observed
208 variations between temperate and mixed ensembles in all functional indices within each sub-
209 region were tested with Permutational Multivariate Analysis of Variance (PERMANOVA) using
210 the function *adonis* of the R package *vegan* (Oksanen *et al.* 2019). Herbivory extent was
211 calculated as the 'range overlap' between each macrophytes and its consumers (Carroll *et al.*
212 2019). For this, we took the spatial range for each macrophyte and then determined their
213 overlap with their corresponding herbivory function considering the presence of only a)
214 temperate consumers, b) tropical consumers and c) either temperate or tropical consumers.
215 The difference between temperate consumer overlap and the overlap between either
216 temperate or tropical consumers represented the increase in herbivory extent attributable to
217 the addition of tropical herbivores (Fig. 1).
218

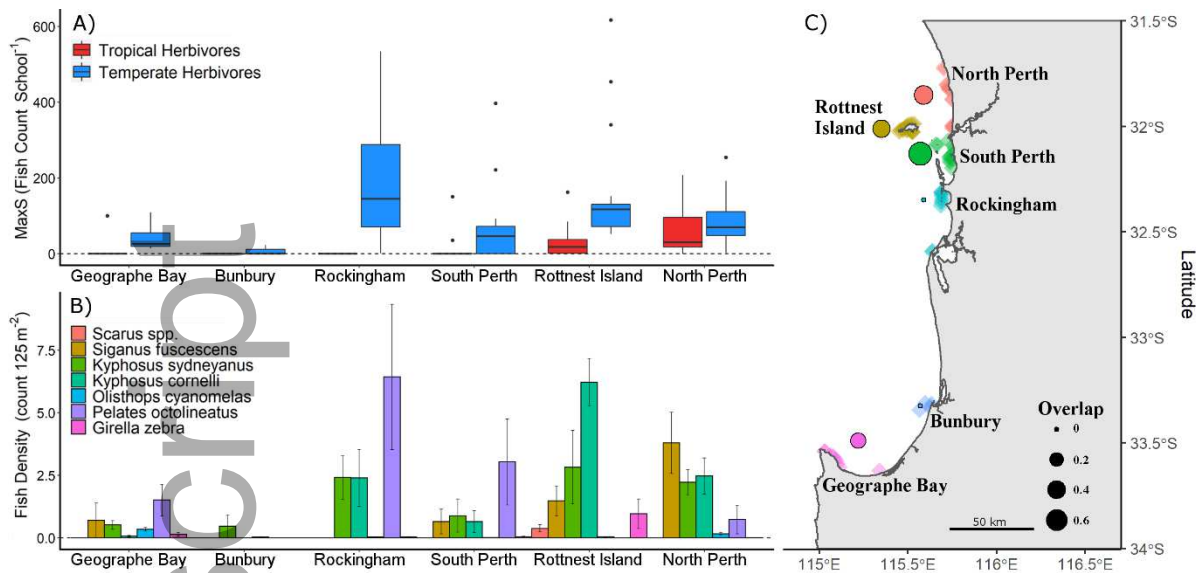


219
220 Figure 1. Conceptual diagram of the overlap analyses used to assess changes in herbivory functions
221 in temperate ecosystems due to the overlap of tropical and temperate herbivores and the
222 macrophytes they consume (A). Changes in *spatial extent*: changes in area overlap between
223 herbivory functions and corresponding macrophytes by the arrival of tropical species (B), and *intensity*
224 (*density*): calculated as overlapped weighted mean of traits of functional groups of temperate and
225 tropical herbivores (mixed ensemble) within spatial ranges of corresponding macrophytes (C).

Results

227 Spatial overlap of temperate and tropical herbivores

228 Abundance of tropical herbivores declined as latitude increased (GLM, $p < 0.01$), as did the
229 abundance of temperate herbivores (GLM, $p = 0.035$). Temperate herbivores were more
230 abundant than tropical herbivores in all subregions (Fig. 2a). Tropical rabbitfish were frequently
231 seen at North Perth (MaxSm: 60 ± 19 (mean individuals school⁻¹), MaxS: 207 (maximum
232 school size)) and around Rottnest Island (MaxSm: 24 ± 9.5 ; MaxS: 158). In South Perth
233 rabbitfish were recorded less frequently (MaxSm: 10 ± 8 ; MaxS: 100) but here we registered
234 the only school of juveniles (MaxS: 100). No rabbitfish were recorded at Rockingham or
235 Bunbury, but they were observed at Geographe Bay (MaxSm: 10.4 ± 7.9 ; MaxS: 100).
236 Parrotfish populations were only recorded at Rottnest Island, where they were generally
237 abundant (MaxSm: 6 ± 2.3 ; MaxS: 39). Temperate herbivores were recorded at all study sites
238 but with varying abundances. *Kyphosus sydneyanus* was observed across the entire latitudinal
239 gradient and was most abundant at North Perth (MaxSm: 35.4 ± 8 ; MaxS: 96), Rottnest Island
240 (MaxSm: 45.1 ± 23.5 ; MaxS: 404) and Rockingham (MaxSm: 38.5 ± 13.9 ; MaxS: 141).
241 *Kyphosus cornelii* had similar patterns, having high abundances at North Perth (MaxSm: 39.5
242 ± 11.5 ; MaxS: 130), Rottnest Island (MaxSm: 99.5 ± 15.0 ; MaxS: 290) and Rockingham
243 (MaxSm: 38 ± 18 ; MaxS: 162). *Pelates octolineatus* was most abundant at South Perth
244 (MaxSm: 48.4 ± 27.5 ; MaxS: 360), Rockingham (MaxS mean: 102.9 ± 46.5 ; MaxS: 465), and
245 Geographe Bay (MaxSm: 24.1 ± 10.2 ; MaxS: 95). *Girella zebra* was abundant at Rottnest
246 Island (MaxSm: 15.3 ± 9.3 ; MaxS: 153) and Geographe Bay (MaxSm: 2.2 ± 1.1 ; MaxS: 10).
247 *Olisthops cyanomelas* was recorded in all the regions; however, as the only non-schooling
248 herbivorous species in the study it generally had the lowest abundances, except for
249 Geographe Bay (Fig. 2b). Spatial overlap between temperate and tropical herbivores was
250 highest in the most northerly sub-regions (Pianka's O at North Perth = 0.46 ± 0.01 , Rottnest
251 Island = 0.38 ± 0.01 and South Perth = 0.73 ± 0.06), with overlap decreasing towards the south
252 (Pianka's O at Rockingham = 0, Bunbury = 0, Geographe Bay = 0.28 ± 0.01) (Fig. 2c).

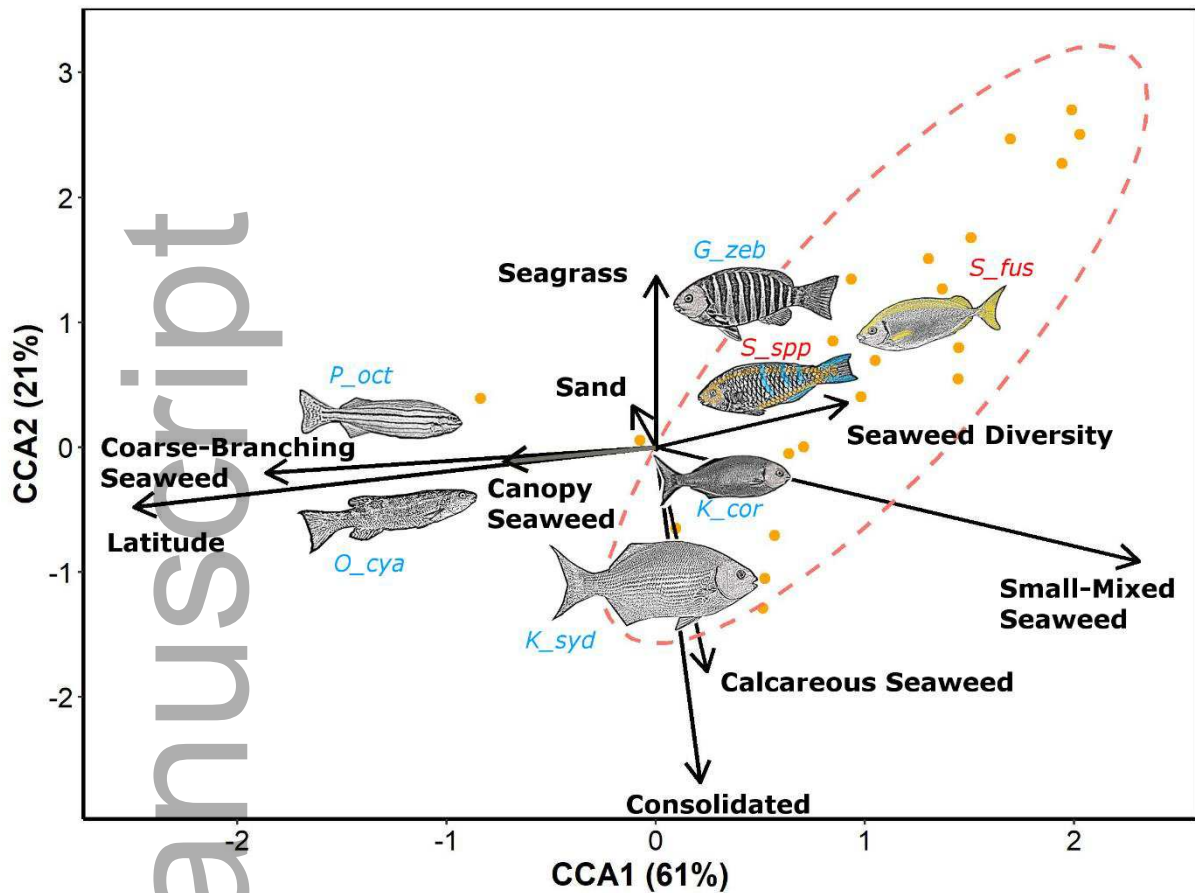


253

254 Figure 2. Abundance patterns as MaxS (school size) (A) and density (B) of herbivorous fish of tropical
 255 (*Scarus* spp. and *S. fuscescens*) and temperate climate affinity (*Kyphosus* spp., *O. cyanomelas*, *P.*
 256 *octolineatus* and *G. zebra*) and (c) their spatial overlap (Pianka's O) along the temperate sub-regions
 257 of Western Australia. Colored diamonds in map represent surveyed sites.

258 Habitat Associations

259 Canonical Correspondence Analysis of the herbivorous fish community and habitat variables
 260 accounted for 82% of the total constrained inertia in the first two axes. The first axis
 261 represented a gradient from high latitude habitats dominated by canopy-forming and coarse-
 262 branching seaweed species (*e.g. Ecklonia radiata* and *Sargassum* spp.) to lower latitude sites
 263 with higher cover of turf (small-mixed seaweed); while the second axis represented a gradient
 264 of topographic complexity, from seagrass meadows to consolidated reef substrates covered
 265 by seaweeds (Figure 3). Along these gradients, the species scores aggregated in three main
 266 groups of herbivores; (1) *P. octolineatus* and *O. cyanomelas* were more strongly associated
 267 with habitats having higher cover of large brown seaweed at higher latitudes. However, *P.*
 268 *octolineatus* associated more with seagrass, whereas *O. cyanomelas* associated more with
 269 reefs. (2) *K. cornelli* and *K. sydneyanus* were associated more with reef sites with medium
 270 canopy-cover, while (3) *G. zebra*, *Scarus* spp. and the rabbitfish *S. fuscescens* were
 271 associated more with sites with seagrass meadows and reefs with higher cover of turf
 272 seaweed. Nonetheless, schools of parrotfish and especially rabbitfish, were also found at sites
 273 with high canopy cover, over reefs associated with low seagrass density and habitats with low
 274 and high topographic complexity, co-occurring with all temperate species in several sites
 275 (Figure 3).

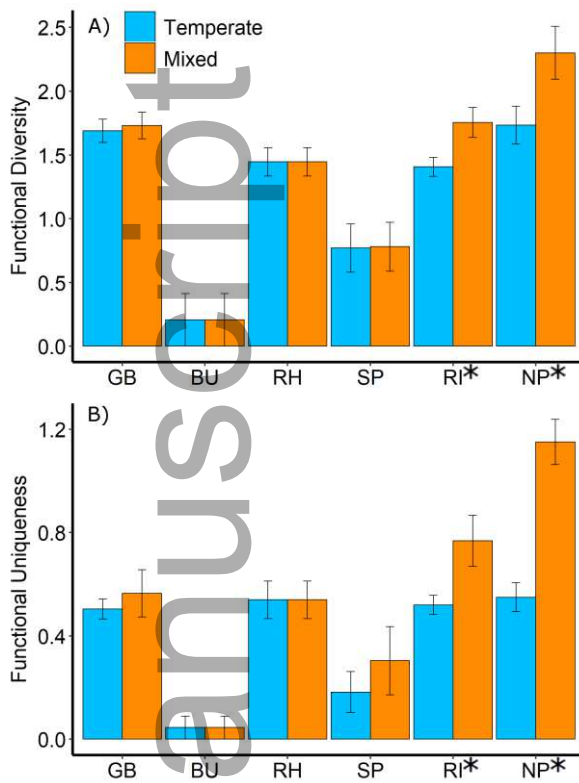


276
 277 Figure 3. Canonical correspondence analysis of herbivorous fish species and habitat variables
 278 (arrows) of temperate ecosystems in southwestern Australia. Ellipse encloses sites (dots) where
 279 rabbitfish (*S_fus*) were recorded. *P_oct* = *Pelates octolineatus*; *O_cya* = *Olisthops cyanomelas*; *K_sydneyanus*
 280 = *Kyphosus sydneyanus*; *K_cornelii* = *Kyphosus cornelii*; *G_Zebra* = *Girella zebra*; *S_spp* = *Scarus* spp. and
 281 *S_fus* = *Siganus fuscescens*.

282 Functional diversity

283 The addition of tropical species increased average functional diversity (FD) and functional
 284 uniqueness whenever they established abundant populations (Fig. 4). Considering only
 285 temperate herbivores, we found that Geographe Bay (1.68 ± 0.09) and North Perth ($1.73 \pm$
 286 0.14), the subregions at the highest and lowest latitudes respectively, had the highest FD;
 287 however, the addition of tropical species shifted the highest values towards lower latitudes,
 288 with high increases in North Perth (33% higher; 2.3 ± 0.2 ; PERMANOVA $p=0.037$) and
 289 Rottnest Island (25% higher; 1.75 ± 0.11 ; PERMANOVA $p=0.017$) with smaller or no increases
 290 in other regions with fewer or no tropical herbivores (South Perth = 1.3%, Rockingham = 0%,
 291 Bunbury = 0%, Geographe Bay = 2.5%; Fig. 4a). Average functional uniqueness values were
 292 very similar in four out of six subregions considering only temperate communities, but as with
 293 FD, the inclusion of tropical species shifted the highest values towards northern latitudes, with

294 North Perth being the highest (109% higher; PERMANOVA $p < 0.001$), followed by Rotttnest
295 Island (47% higher; PERMANOVA $p < 0.02$; Fig. 4b).
296



297
298 Figure 4. Variation (mean \pm SE) of functional diversity (A) and functional uniqueness (B) considering
299 communities of temperate herbivorous fish only, and with the addition of populations of tropical species
300 (mixed) in south western Australia (GB: Geographe Bay, BU: Bunbury: RH: Rockingham, SP: South
301 Perth, RI: Rotttnest Island, NP: North Perth). Asterisks on bar charts mark statistically significant
302 differences between temperate and mixed herbivorous communities (PERMANOVA $p < 0.05$).

303 Herbivory functions

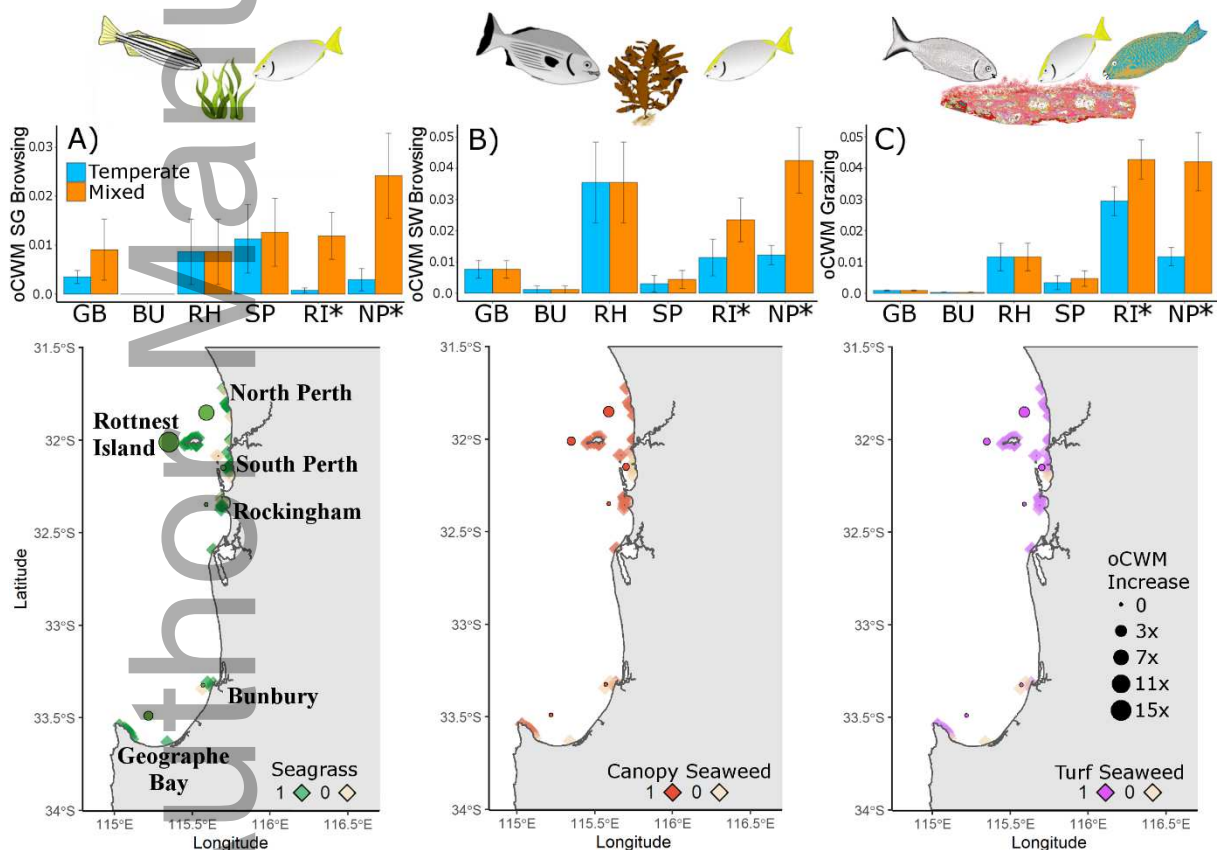
304 The addition of tropical herbivores contributed to a 27% increase in spatial extent of potential
305 seagrass browsing. Of the 157.5 km² that was surveyed during this study, 106 km² represented
306 sites where seagrass was present; of this area, 55% overlapped with temperate seagrass
307 consumers, 47% overlapped with tropical seagrass consumers, and 74% overlapped with
308 either temperate or tropical seagrass consumers. Turf seaweeds were present across 147.5
309 km²; of this area, 82% overlapped with temperate grazers, 45% with tropical grazers, and 85%
310 with either temperate or tropical grazers, thus representing an increase of 3% in spatial extent
311 of potential seaweed grazing with the addition of tropical species. Canopy seaweeds were
312 present across 129 km² of the survey area, 94% of this overlapped with temperate seaweed
313 browsers, 48% with tropical seaweed browsers, and 96% with either temperate or tropical

314 seaweed browsers, representing an increase of 2% in spatial extent of potential seaweed
 315 browsing due to tropical herbivores.

316

317 Overlapped Community Weighted Means of Traits (oCWM) for all herbivory functions
 318 increased in the northern sub-regions (Fig. 5; PERMANOVA $p < 0.02$). In the absence of
 319 tropical species, seagrass and seaweed browsing oCWM were highest at mid-latitude sub-
 320 regions, while seaweed grazing was highest at Rottnest Island. However, when tropical
 321 herbivores were mixed in the communities, Rottnest Island and North Perth had significant
 322 increases for average seagrass browsing (15x and 9x respectively; PERMANOVA $p = 0.02$),
 323 seaweed browsing (1x and 2.5x respectively; PERMANOVA $p = 0.02$) and seaweed grazing
 324 (0.4x and 2.6x respectively; PERMANOVA $p < 0.01$). Southern sub-regions had small or no
 325 changes in herbivory functions, except for Geographe Bay, which had an increase in seagrass
 326 browsing (1.6x), albeit not statistically significant (PERMANOVA $p = 0.97$).

327



328

329 Figure 5. Variation in values (bars; mean \pm SE) and relative increases (maps) of functional metrics
 330 considering communities of temperate herbivorous fish only, and with the addition of populations of
 331 tropical species (mixed). Overlapped Community Weighted Means of Traits for seagrass browsing (a),
 332 seaweed browsing (b) and seaweed grazing (c) across temperate western Australia (GB: Geographe
 333 Bay, BU: Bunbury: RH: Rockingham, SP: South Perth, RI: Rottnest Island, NP: North Perth). Asterisks
 334 on bar charts mark statistically significant differences between temperate and mixed herbivorous

335 communities (PERMANOVA $p < 0.5$). The size of the bubbles in the maps represent proportional
336 increase in herbivory functions with the addition of tropical species, colored diamonds represent
337 presence/absence of macrophytes at sampling sites.

338 Discussion

339 Our study assessed the spatial interactions between tropical and temperate herbivores and
340 evaluated their effects on herbivory functions within temperate marine habitats along a
341 latitudinal gradient. The range expansion and increase in abundance of tropical herbivores into
342 higher latitudes did not appear to modify the abundance of temperate herbivores or cause
343 species replacements. The northern sub-regions had the highest abundances and species
344 diversity of temperate herbivores, but also had the highest abundances of tropical herbivores,
345 as reflected in their high overlap values. This indicates that there is no negative relationship
346 between temperate and tropical herbivores at the densities observed.

347
348 These results align well with the resource partitioning and empty niche theories proposed to
349 explain the success of many invasive species (Lowry *et al.* 2012). This is particularly relevant
350 for herbivorous species because temperate ecosystems generally have a surplus of
351 macrophyte production and low competition (Mann 2000). For instance, the Mediterranean
352 Sea has extensive and productive seagrass and seaweed habitats (Sales & Ballesteros 2012),
353 yet hosts only two native herbivorous fish species (*Sarpa salpa* and *Sparisoma cretense*),
354 which likely has eased the expansion of tropical herbivores in the region. *Scarus ghobban*
355 remains uncommon in the Mediterranean Sea, but the occurrence of this species has extended
356 from Israel to Greece (Erguden *et al.* 2018), while the rabbitfish *Siganus luridus* and *Siganus*
357 *rivulatus* have become abundant in many locations, attaining MaxS of ~100 individuals at the
358 edge of their expansion in Linoza, Italy (Azzurro *et al.* 2017). The region of our study has a
359 higher diversity, with five dominant species, but still lags far behind herbivore assemblages in
360 the tropics with 30 to 100 species (Steneck, Bellwood & Hay 2017).

361
362 Our results on habitat associations also indicate that the different behaviors and diet of each
363 species can facilitate coexistence of competitors. Some species were associated with reefs
364 with different cover of canopy-forming and turf seaweed, and some were also more strongly
365 associated with seagrass. Thus, although tropical and temperate species inhabit the same
366 location, their overlap decreases at finer spatial scales (Streit, Cumming & Bellwood 2019).
367 Moreover, specific feeding behaviors can also increase niche dissimilarity among species; for
368 instance, species that tend to feed on drifting macrophytes, such as *S. fuscescens*, reduce
369 resource competition in the benthic space (Zarco-Perello *et al.* 2019). Hence, there seem to

370 be ample niche spaces available in temperate ecosystems for range-shifting tropical
371 herbivores to occupy, without directly competing against their temperate counterparts (Vergés
372 *et al.* 2019).

373

374 The addition of tropical herbivorous fish to temperate ecosystems changed the spatial patterns
375 of functional diversity, functional uniqueness and the intensity of specific herbivory functions
376 in our study. Changes in species richness caused by climate change have been forecast and
377 described by multiple studies, with tropical regions expected to suffer losses in biodiversity,
378 while temperate regions are likely to experience increases in species richness that could
379 modify ecological processes (Blowes *et al.* 2019). Our results expanded on this from a
380 functional perspective, showing that the expansion of tropical species to temperate
381 ecosystems could initially lead to general increases in functional diversity (FD) at sites where
382 they establish permanent and abundant populations. This can lead to increases in functional
383 redundancy but also to the introduction of new herbivory functions. The low number of
384 temperate species per herbivory function implies that some functions are not performed at
385 many sites, and that the arrival of tropical species could fill these empty functional niches. This
386 explains the increase in functional uniqueness (U) that we observed in sub-regions where
387 tropical herbivores had established. However, increments were heterogeneous in space
388 depending on how functionally redundant tropical ensembles were in relation to the temperate
389 communities they overlapped with.

390 While increments in FD were similar between Rottnest Island and North Perth (24% and 33%),
391 the increment in U was double in the latter (47% vs 109%). This shows that there was a higher
392 redundancy of functions at Rottnest Island, and conversely that there were more sites in North
393 Perth where rabbitfish brought new functions (Ricotta *et al.* 2016). Among these, seagrass
394 browsing seemed to be the main driver of change, since it was the only function that increased
395 significantly in spatial extent and up to 3x and 32x more in intensity than seaweed grazing and
396 browsing in North Perth and Rottnest Island respectively. This is understandable since only
397 the trumpeter *Pelates octolineatus* has been identified as an important temperate seagrass
398 consumer (Bessey & Heithaus 2015), reflecting historically low rates of herbivory in seagrass
399 meadows of the region (White, Westera & Kendrick 2011).

400 Knowledge of the baseline abundance and functional role of herbivorous species in recipient
401 ecosystems is crucial to accurately assess and forecast changes in functional processes under
402 tropicalization. While tropical species drove increases in all functions, the total intensity was
403 strongly determined by the native temperate assemblages. From a species diversity
404 perspective, Rottnest Island is the most tropicalized sub-region of south-western Australia,
405 being the only one hosting both rabbitfish and parrotfish. Nonetheless, from a functional

406 perspective it had similar diversity to Geographe Bay, and substantially lower functional
407 diversity than North Perth, owing to the more diverse temperate communities in those regions
408 prior to the addition of tropical rabbitfish. Likewise, Rottnest Island experienced by far the
409 highest increase in seagrass browsing intensity but maintained similar overall mean values to
410 other sub-regions not hosting tropical species. Additionally, seaweed browsing and grazing
411 increased the most in North Perth, but overall Rockingham had similar levels for the former
412 and Rottnest Island for the latter, since both had strong temperate communities in these
413 functions.

414 The fact that the average intensities of seaweed browsing were similar between some
415 tropicalized and non-tropicalized areas indicates that consumption rates in the region have not
416 yet reached levels that pose a significant risk of regime-change at extensive spatial scales.
417 However, shifts could occur in the future as tropical herbivores further expand their distribution
418 and abundance in temperate ecosystems. High densities of tropical herbivores at local spatial
419 scales have been correlated with increases in herbivory, declines in biomass of kelp (Zarco-
420 Perello *et al.* 2017) and the maintenance of canopy-free states and high turf cover following
421 environmental disturbances, resulting in a positive feedback loop that favors the persistence
422 of tropical herbivores and decreases the seascape resilience of temperate ecosystems
423 (Bennett *et al.* 2015). This is consistent with ecological theories indicating that ecosystem
424 processes are strongly determined by the abundance of species with high importance in
425 certain ecological functions (Mokany, Ash & Roxburgh 2008). Species composition and
426 dominance within ecosystems are therefore likely to be highly significant, and the impact of
427 the tropicalization of herbivorous communities could be driven in great part by the expansion
428 of keystone species of tropical herbivores (Hoey & Bellwood 2009), in combination with the
429 establishment of abundant populations of other species with lower impact *per capita*
430 (Ruttenberg *et al.* 2019).

431 Our study shows empirically how range-shifting tropical species can affect herbivory in
432 temperate habitats across large spatial extents. The high overlap with temperate species that
433 we observed is not surprising considering that tropical coral reefs have fewer macrophyte
434 resources shared among a higher number of species and populations than temperate
435 ecosystems do. Consequently, we can expect that resource limitation in the form of space and
436 food will not constrain further tropicalization of temperate ecosystems under climate change,
437 with reefs with high turf cover and seagrass meadows facilitating the range-expansion and
438 persistence of tropical fish in temperate regions. By assessing novel species interactions in
439 three levels of overlap between temperate herbivores, tropical herbivores and temperate
440 macrophytes, we found that in a first stage of tropicalization, temperate marine ecosystems
441 will experience increases in the diversity, intensity and spatial extent of different herbivory

442 functions as tropical species with different habitat affinities, feeding behaviors and diets shift
443 their distribution poleward. Functional redundancy will be heterogeneous and might not
444 necessarily increase initially in many sites due to the low abundance and diversity of herbivory
445 functions in some temperate ecosystems, but it will likely do so more broadly as further tropical
446 species arrive, their abundance increase and both the spatial and functional overlap of the
447 communities rise.

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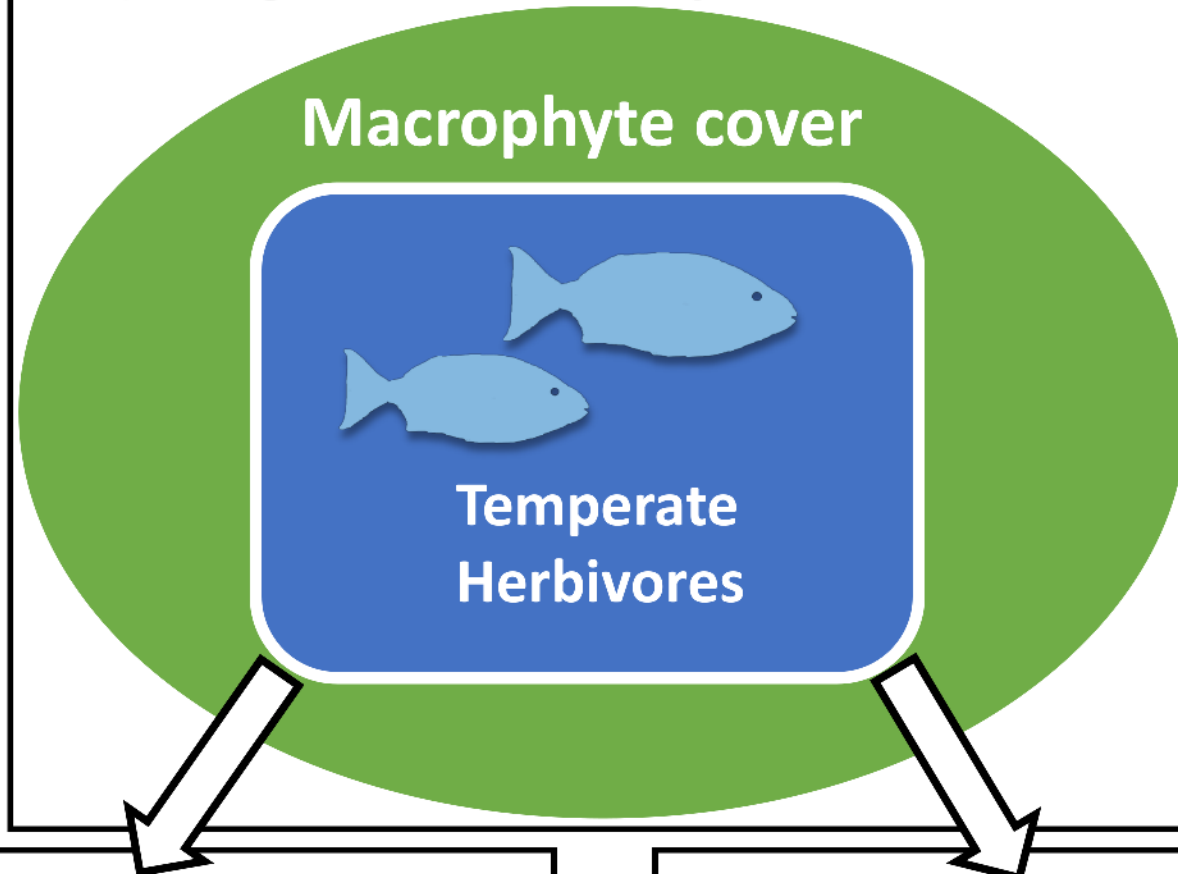
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- 655 Zarco-Perello, S., Wernberg, T., Langlois, T.J. & Vanderklift, M.A. (2017) Tropicalization
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657 820.

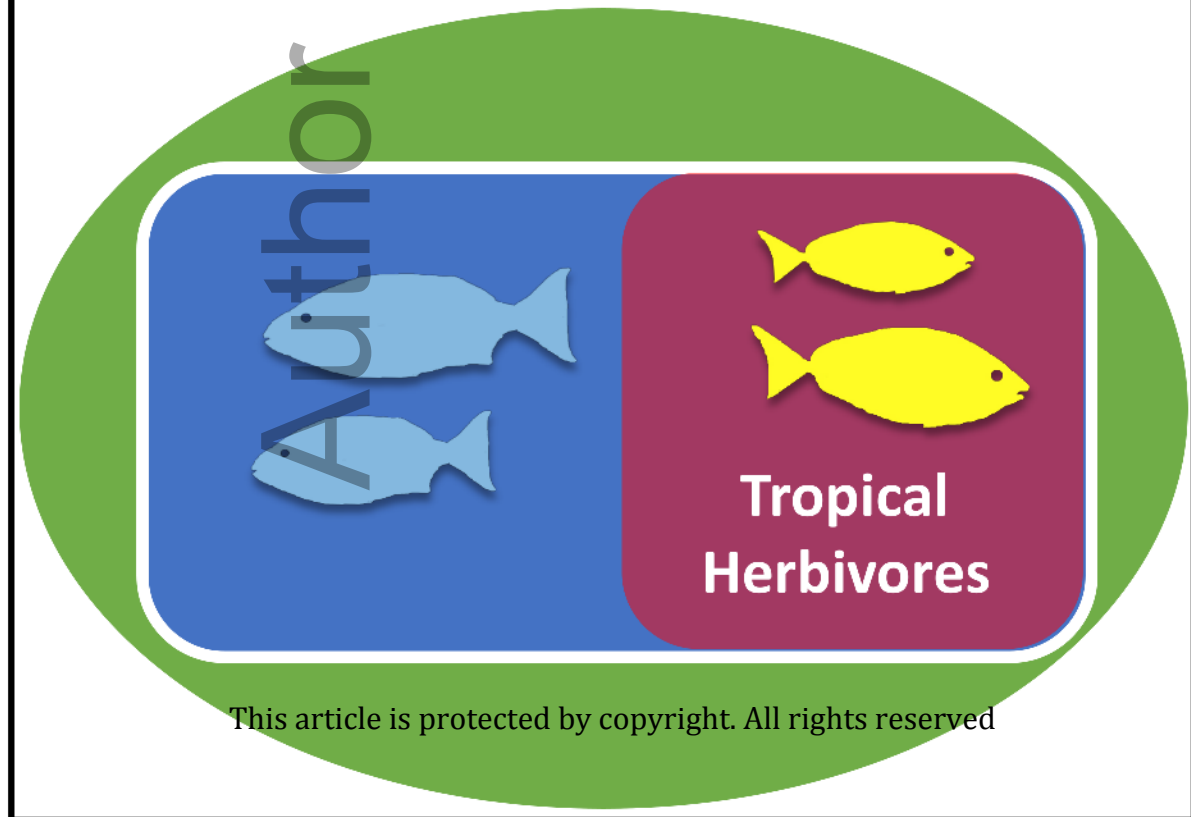
658 Zarco-Perello, S., Wernberg, T (2020) Data from: range-extending tropical herbivores
659 increase diversity, intensity and extent of herbivory functions in temperate marine
660 ecosystems. Dryad Digital Repository: <https://doi.org/10.5061/dryad.8w9ghx3hx>

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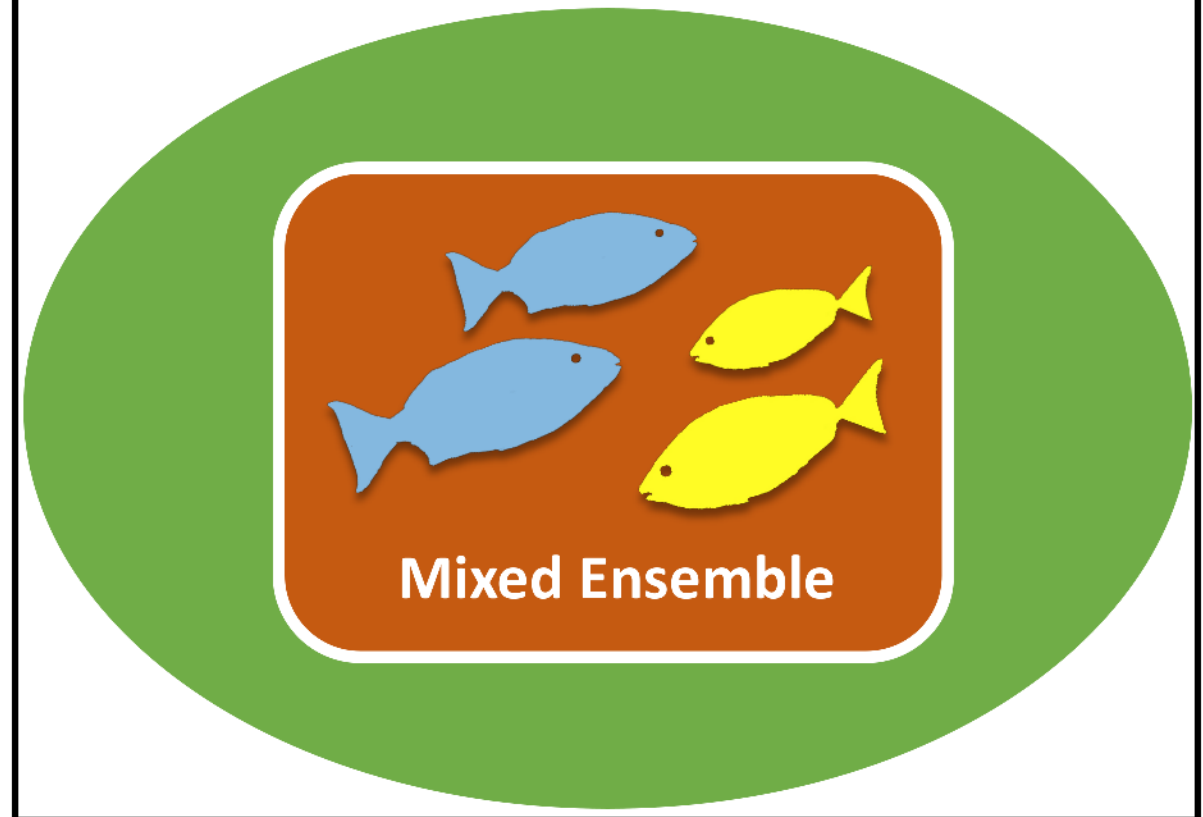
A) Original herbivory function



B) Increase of function by extent

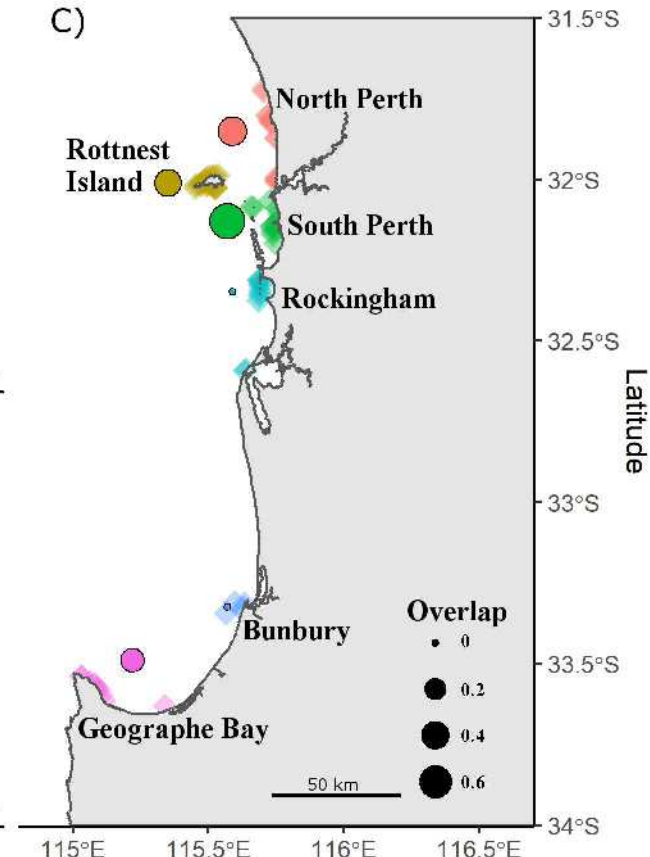
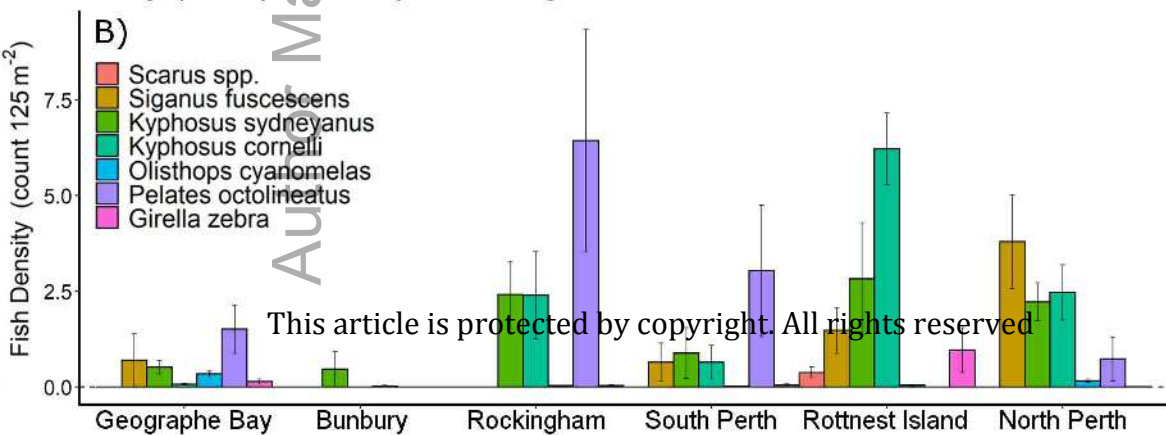
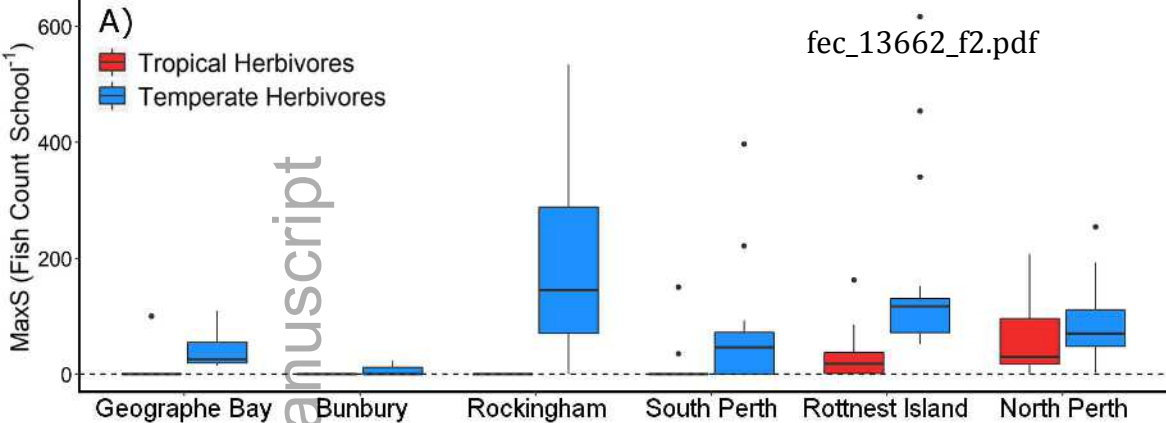


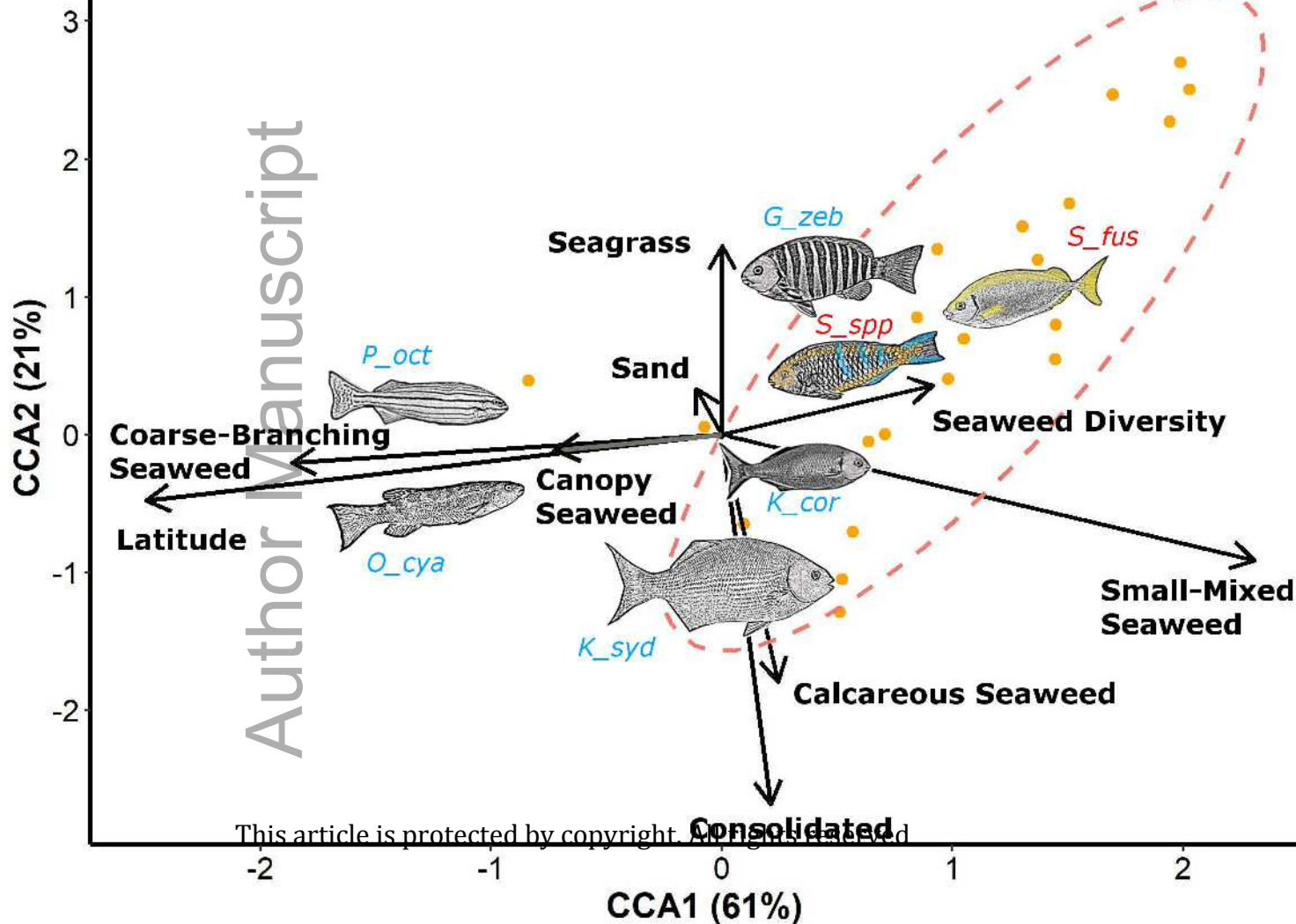
C) Increase of function by density

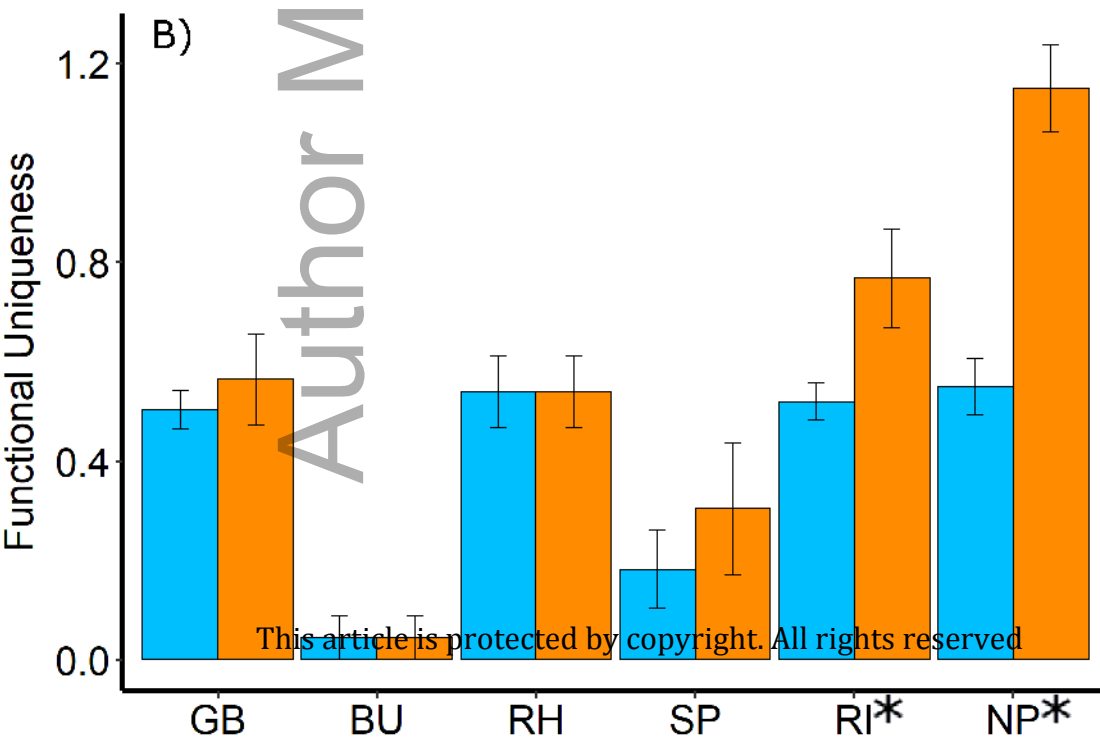
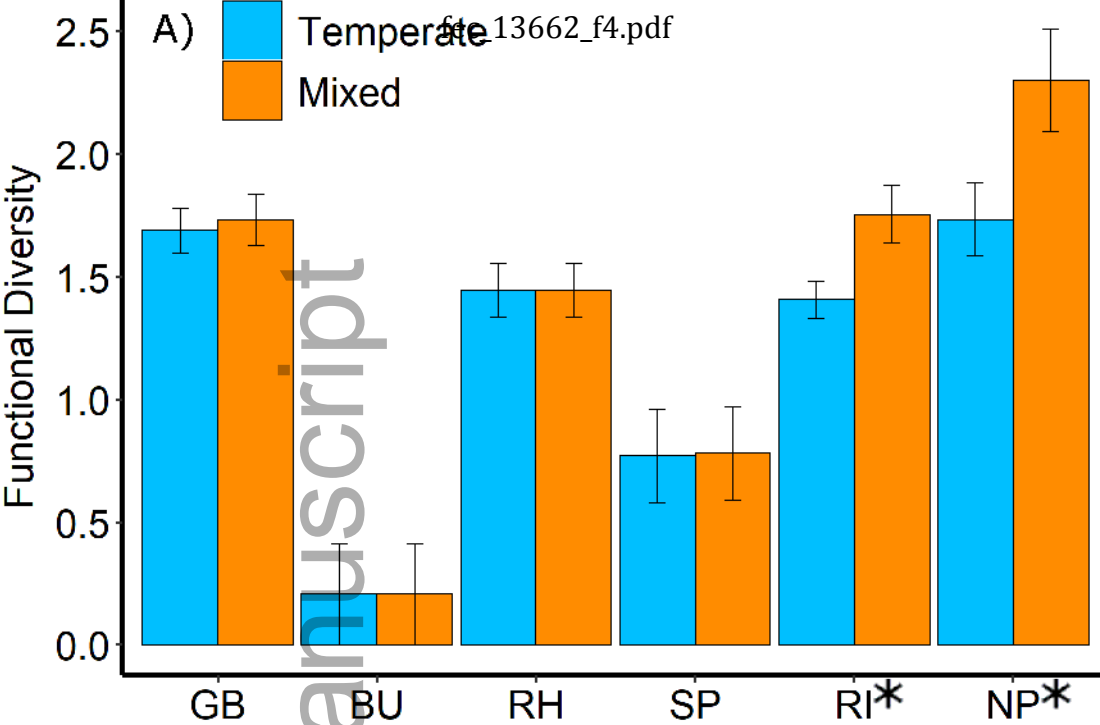


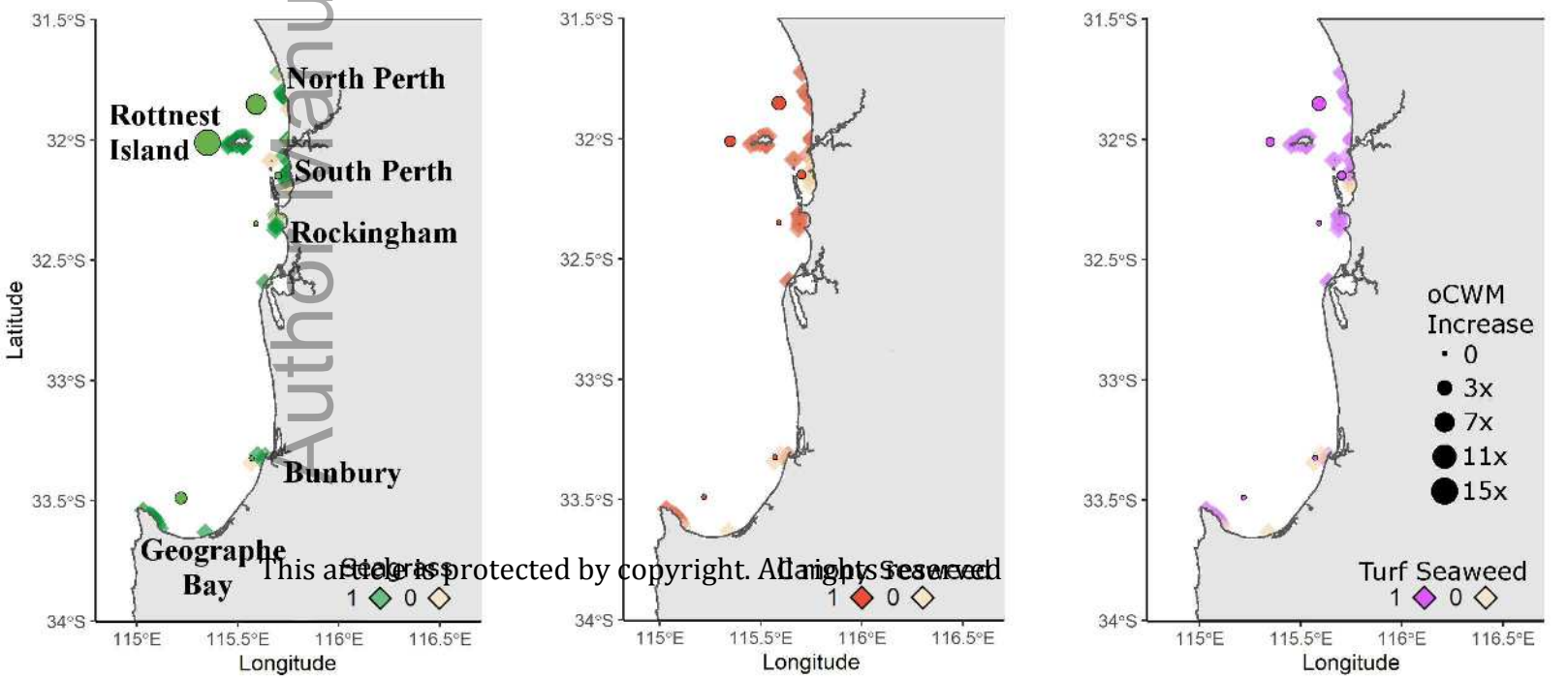
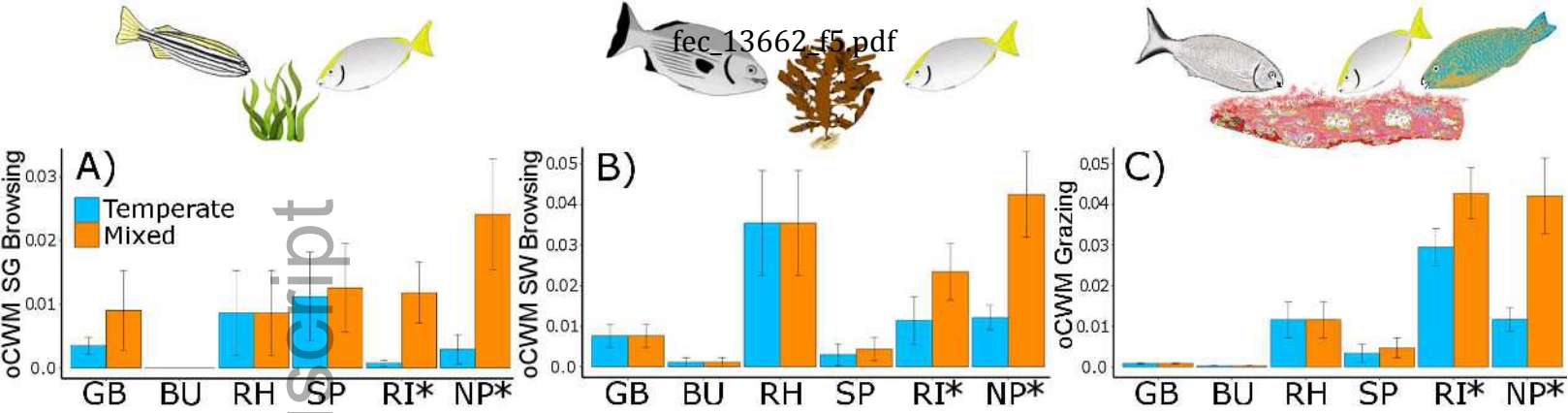
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