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3   **Wave-sheltered embayments are recruitment hotspots for tropical fishes on temperate**
4   **reefs**

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28 **ABSTRACT**

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30   Poleward range shifts of species, facilitated by global warming, will be compromised if

31   habitats at higher latitudes do not support early life success. For tropical reef fishes, reef

32   structure may mediate colonisation of low-latitude temperate regions, however an

33   understanding of key habitat requirements for colonisation is currently lacking. We show that

34   density, diversity (taxonomic and trophic) and species richness of newly-recruited tropical

35   reef fishes were greater in embayed than exposed reefs in two low-latitude temperate zones,

36   where coastal waters are rapidly warming; southeastern Australia and western Japan. Dietary

37   generalists (e.g. planktivores and herbivores) and specialists (corallivores) associated more

38   commonly with embayed reef. DistLM revealed wave exposure of temperate reefs was a

39   stronger predictor of the density and richness of dietary generalists than water temperature,

40   latitude, predatory fish densities, reef rugosities, distance to river mouths and benthos .

41   Corallivores were strongly associated with branching corals, which were exclusive to wave-

42   protected reefs. We also explored habitat-associations of seven focal species within a coral

43   reef, One Tree Island (OIT), Great Barrier Reef. Four species associated with wave-sheltered

44   over exposed reef on OTI and temperate Australian reef. However, *Abudefduf vaigiensis*,

45   *Pomacentrus coelestis* and *Acanthurus triostegus* associated more with wave-sheltered reef in

46   temperate regions. We hypothesise that cooler temperate waters promotes greater sheltering

47   of some warm-adapted, tropical fishes by impacting their swimming/physiological

48   performance. Results suggest availability of sheltered reefs may impact tropical fish

49   recruitment at temperate latitudes, suggesting that wave exposure of reefs needs consideration

50   when predicting geographic responses of many tropical fishes to climate change.

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52   **KEYWORDS:** Climate change, range shift, novel habitat, temperate rocky reef, wave

53   exposure

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INTRODUCTION

Anthropogenic warming of terrestrial and aquatic environments threatens the existence of species globally (Chen et al. 2011; Poloczanska et al. 2013). If species fail to acclimate or adapt to rising environmental temperatures (Bradshaw and Holzapfel 2006), they may shift elevation (altitude/depth) (Dulvy et al. 2008; Lenoir et al. 2008) or poleward to more suitable climates to avoid extinction (Walther et al. 2002; Parmesan & Yohe 2003; Parmesan 2006). Hence, accurate predictions of where and when species may colonise are required to guide species conservation, as well as management of adverse impacts to receiving ecosystems that result from this redistribution (Gilman et al. 2010). However, many factors controlling geographical responses of species to climate change are poorly understood, so that species' range expansions are still difficult to accurately predict (HilleRisLambers et al. 2013; Bates et al. 2014). There is mounting evidence that propagule pressure and physiological tolerance of species to environmental temperatures may organise species redistribution (Sorte 2013; Burrows et al. 2014). However, availability of suitable habitat, encapsulating the full suite of biological and physical factors required to support survival of a species, including all life stages, may ultimately determine if species redistribute poleward with shifting isotherms (Opdam & Wascher 2004; Bennie et al. 2013). For instance, early life (post-recruitment) success of a species within a new range may be highly influenced by spatial heterogeneity in abiotic stressors (Helmuth et al. 2006; Lenoir et al. 2010), resource availability (Hill et al. 2001; Schweiger et al. 2008) and/or interactions with resident fauna (HilleRisLambers et al. 2013).

For tropical marine organisms expanding into temperate latitudes, the abiotic and biotic environment structuring habitats within destination latitudes may largely constrain colonisation (Cheung et al. 2010; Sommer et al. 2014). Many tropical reef fishes are expected to shift their range in response to increased poleward supply of tropical and subtropical water to temperate regions, associated with strengthening of western boundary currents (Figueira & Booth 2010; Wernberg et al. 2013; Feary et al. 2014; Vergés et al. 2014). This influx of tropical fish into temperate bioregions may impact the structure and function of some temperate communities through novel interactions and processes (Vergés et al. 2014). For example, tropical herbivorous fish may decimate kelp forests (or suppress their recovery

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90 following warming-induced mortality), leading to stable canopy-free stable states (e.g.,

91 Vergés et al. 2014; Basford et al. 2015; Bennett et al. 2015). However, despite strong

92 evidence that many tropical fishes could physiologically tolerate some temperate waters

93 (Figueira et al. 2009), and that larval supply could be sufficient to support colonisation of

94 many species (Figueira & Booth 2010), some temperate reef habitats may not support the

95 successful settlement and recruitment of tropical fishes (Feary et al. 2014). For example, the

96 absence of coral habitats within some temperate reefs may strongly limit recruitment of

97 obligate coral-feeding fishes (i.e. corallivores, hereafter termed 'trophic specialists'), which

98 depend on live corymbose corals for food and shelter (Feary et al. 2014). But in temperate

99 regions where corals are colonising with warming coastal waters, such as western (W)

100 Japanese coast of Shikoku (Nakamura et al. 2013; Verges et al. 2014), these habitat-forming

101 corals may strongly influence where and when corallivores may recruit and survive

102 (Soeparno et al. 2013). In contrast, absence of coral resources may not restrict recruitment of

103 trophic generalists, such as those that graze on algae, or prey upon benthic invertebrates

104 and/or fishes in temperate reefs (Nakamura et al. 2013; Feary et al. 2014). However, even for

105 dietary generalists, fine-scale variance in the structure of temperate reefs arising from

106 macroalgal cover may influence recruitment, at least on fine-spatial scales (Feary et al. 2014).

107

108 Within coastal reef systems, differences in habitat characteristics between exposed and

109 sheltered reef environments may strongly influence where tropical fishes colonise temperate

110 latitudes on broad spatial scales. The strength of ocean waves may structure the diversity and

111 composition of marine communities by interacting with an organisms' physiological

112 tolerance and morphology (McQuaid & Branch 1985; Friedlander et al. 2003; Fulton &

113 Bellwood 2004; Munks et al. 2015). For instance, swimming performance varies

114 considerably amongst tropical reef fishes during their early life stages, due to interspecific

115 variance in body/fin shape and size (Fisher et al. 2005), which may influence habitat choice

116 and survival following settlement through interacting with wave action (Fulton & Bellwood

117 2004). Wave energy influences the diversity and abundance of reef fishes across a range of

118 tropical and temperate biomes, with fish assemblages in shallow waters (where wave action is

119 strongest), often greater in wave-sheltered than -exposed reef aspects (Friedlander et al. 2003;

120 Fulton & Bellwood 2004; Depczynski & Bellwood 2005). Wave action may also influences

121 recruitment of some tropical fishes by determining habitat distribution and composition

122 (Floeter et al. 2007; Santin & Willis 2007). For instance, waves shape the structure and

123   composition of corymbose corals and/or macroalgae (Fowler-Walker et al. 2006; Madin et al.

124   2014), which may influence distribution of fishes that depend on these habitat formers for

125   resources (Jones 1992; Feary et al. 2007a). Nevertheless, recruitment success of tropical reef

126   fishes within temperate regions may be organised by a range of abiotic and biotic factors,

127   which covary with the degree of wave action. Embayed temperate reefs in coastal temperate

128   regions may be substantially influenced by freshwater runoff and/or tides, which can restrict

129   recruitment of some tropical fishes where water parameters, such as turbidity, oxygen and

130   temperature, exceed their physiological tolerance (Figueira et al. 2009; Wenger et al. 2012).

131   Near-shore embayed reefs also often contain high piscivore densities, leading to high

132   mortality of tropical fishes during recruitment (Baker & Sheaves 2005). Hence, a range of

133   biotic and abiotic factors may differ between embayed and exposed temperate reef habitats,

134   posing potential constraints to tropical fish recruitment, and ultimately, impact their

135   distributional response to sea surface warming.

136

137   The influence of embayed and exposed shallow temperate reefs, and the abiotic and biotic

138   factors differing between them, on recruitment success of tropical reef fishes was explored by

139   underwater visual surveys within SE Australia and W Japan. Since both regions are at the

140   forefront of the range expansion of many tropical fishes (Feary et al. 2014), they provide a

141   unique opportunity to explore how temperate reef habitats structure their recruitment success.

142   Each summer, expatriating tropical reef fish larvae (hereafter termed 'vagrants') are

143   transported 100s to 1000s of km into these temperate regions by poleward flowing boundary

144   currents [East Australian Current (EAC) in Australia, and the Kuroshio Current in Japan],

145   where they recruit to coastal reef habitats (Booth et al. 2007; Feary et al. 2014). Although

146   coastal waters in SE Australia and W Japan are warming at over twice the global average

147   (Wu et al. 2012), and may facilitate colonisation of tropical fishes by reducing severity of

148   winter water temperatures (Figueira & Booth 2010), variability in physical and abiotic

149   stressors associated with embayed and exposed temperate reefs may essentially limit

150   recruitment. Due to variance in the biophysical nature between embayed and exposed

151   temperate reefs, we predicted differences in the density, richness, diversity and composition

152   of vagrant fish assemblages between these habitats. For corallivores, reliant on coral for

153   food/shelter, we also expected their recruitment success to be strongly associated with the

154   presence, distribution and structure of live coral communities. We also explored if exposure

155   of reefs influences tropical recruits similarly in tropical and temperate regions, by surveying

156 focal species on exposed and protected aspects of a coral reef [i.e. One Tree Island (OTI),

157 Great Barrier Reef].

158

159 **MATERIALS AND METHODS**

160

161 **Study locations**

162

163 To explore how tropical fish recruitment varies between embayed and exposed shallow

164 temperate reefs, new recruit and early juvenile tropical fishes were surveyed at four locations

165 in SE Australia separated by 100s km; Nambucca (NB), Camden (CA), Forster (FO) and

166 Swansea (SW) (Fig. 1). Within W Japan, vagrant fishes were surveyed in Otsuki (OT),

167 Yokonami (YO), Tei (TE) and Nahari (NA), separated by 10s - 100s of km (Fig. 1). Within

168 each location, vagrant fishes were surveyed within two or three embayed and exposed rocky

169 reef sites, separated by > 100 m. Exceptions were OT, where all sites were embayed, and TE,

170 where there was only one embayed site. Embayed reefs in SE Australia were positioned

171 within estuary mouths (predominantly formed by artificial rockwalls) and on lee-sides of

172 headlands, while embayed reefs surveyed in W Japan were all naturally formed, with little

173 freshwater influence. Exposed reefs in both regions were exposed or partially-exposed to

174 ocean swell (i.e. > 15º of exposure to the open ocean; see Supplementary Material, Fig. S1).

175 In total, 42 and 21 thirty-minute visual surveys were undertaken in SE Australia and W

176 Japan, respectively.

177

178 **Density and distribution of tropical fishes in temperate reefs**

179

180 Underwater visual surveys were conducted to examine the richness, diversity and density of

181 new recruit and juvenile vagrant tropical fishes in exposed and embayed temperate reef

182 habitats of SE Australia and W Japan (Fig. 1). Both regions hold sub-tidal coastal reefs prone

183 to moderate to high wave energy (Young et al. 2011). Surveys were conducted during

184 recruitment of tropical fishes in both 2011 and 2012 in SE Australia (i.e. March to May) and

185 2013 in W Japan (i.e. June to November) (Booth et al. 2007; Figueira et al. 2009; Nakamura

186 et al. 2013). Vagrant fishes were surveyed during 30-minute timed swims in 0-4 m water

187 depth whilst snorkelling. To standardise survey effort and calculate fish densities, paths swam

188 were measured at five-second intervals by towing a GPS (Garmin^{TM} GPS 60; accuracy 3 m)

189 at a fixed-distance (3 m), following Beck et al. (2014). This survey method allows greater

190 detection of sparsely-distributed vagrant fishes than traditional belt transects since it is more

191 time-efficient and provides reliable density estimates (Beck et al. 2014). Starting positions

192 and swim patterns were haphazardly determined prior to surveys. All tropical fishes observed

193 within 1 m either side and in front of the observer were recorded by hand. Individuals were

194 identified as recruits of the present season (i.e. year-of-the-year) and juvenile based on family

195 specific length-age criteria established by Booth et al. (2007), while trophic groupings were

196 determined according to Froese and Pauly (2015), IUCN red list of threatened species

197 (V2015.2) and a review of scientific literature (See Supplementary Material, Table S1). We

198 assigned trophic grouping based on diets of juveniles where possible. Where known, we

199 assigned trophic groups based on feeding preferences during early life stages and/or within

200 temperate reef habitats (e.g. Beck et al. 2014; Basford et al. 2015; Luiz et al. *in press*).

201 Tropical "vagrant" species were defined by the latitudinal range of a species; only found as

202 breeding-aged adults between the Tropics of Cancer and Capricorn; 23°27' N and S,

203 respectively [distribution data from Kuiter 1993; Froese and Pauly 2015 and and IUCN red

204 list maps (V2015.2); See Supplementary Material, Table S1].

205

206 **Influence of exposure on distribution of tropical fishes on a coral reef**

207

208 To test if reef exposure influences tropical fish recruitment similarly in both temperate and

209 tropical reefs, tropical fish assemblages were also surveyed on the coral reef, OTI, Great

210 Barrier Reef, Australia (Fig. 1). Replicate half-hour roaming surveys (using same method

211 described above) were conducted in exposed (reef flats exposed to >15° to open ocean) and

212 protected reef habitats (wave-oblique reef flats with <15° exposure to open ocean) during

213 summer recruitment seasons (March-June) of both 2011 and 2012 (see Supplementary

214 Material, Fig. S1), counting new recruit and juveniles of species observed within temperate

215 SE Australian reefs during the above surveys. Nine and 23 surveys were conducted in

216 exposed and protected reef aspects, respectively.

217

218 All surveys were conducted by HJB at a constant speed between 09:00 and 17:00 when water

219 visibility was > 5 m and swell was < 1 m. These conditions were chosen to minimise any

220 potential bias to visual surveys associated with inherent differences in wave action and

221 visibility between exposed and embayed reefs.

222

223 **Temperate reef habitat variables**

224

225 To assess roles of biophysical factors in determining the composition and density of vagrant

226 fishes amongst locations and reef habitats in temperate regions, *in situ* density of temperate

227 predatory fishes (identified according to Froese & Pauly 2015) were surveyed within each

228 site using timed swim surveys (as above; Beck et al. 2014), water temperature (measured at

229 half-hour to hourly intervals by permanent loggers installed at ~2.5 m below MSL; SE

230 Australia only), topographic complexity (using the ratio of surface distance to linear distance

231 of a five metre chain within ten haphazardly selected areas within each site), and substrate

232 composition (within 30 haphazardly selected $0.25m^2$ quadrats, with benthic habitats

233 quantified using Underwood 1991 and Bradbury & Young 1981 were recorded). Wave-

234 exposure for each site was calculated using a fetch-based index (Hill et al. 2010) with

235 MicroStation^{TM} GIS. Fetch lines were constructed with 7.5° spacing around the midpoint of

236 survey sites to a maximum of 650 km (i.e. minimum fetch distance for fully developed seas

237 to form) and divided by the sum of fetch distances by the maximum possible total; index

238 units are dimensionless, with exposure increasing from 0 to a maximum exposure value of

239 one (Hill et al. 2010). In addition, as a proxy for water parameters subjected to fishes within

240 estuaries (e.g. nutrients, turbidity, oxygen etc), Google Earth^{TM} was used to calculate the

241 distance of each site from the mouth of nearest estuary (i.e. minimum manhattan distance).

242

243 **Statistical analyses**

244

245   Overall assemblage densities (i.e. individuals per 1000 m^2) and species richness (i.e. total

246   number of species per 1000 m^2) for vagrant fish assemblages were compared between

247   habitats (exposed, embayed: fixed), recruitment years (2011, 2012: random; Australia only),

248   between countries (Japan and Australia; random) and among locations (locations nested

249   within respective country: random) using univariate permutational analysis of variance (based

250   on Euclidean distances between untransformed data; Type III Sums of Squares; 9999

251   permutations under the reduced model; Anderson 2001). Density and species richness were

252   calculated as the total number of individuals and species divided by the area searched within

253   each replicate survey, respectively (see Supplementary material, Table S2; both metrics were

254   expressed per 1000m^2 due to rarity of many species). OT was excluded from analyses of

255   population richness, diversity and densities since no exposed sites were surveyed there, but

256   vagrant/environmental data from OT were included when exploring environmental influences

257   on vagrant recruitment.

258

259

260   *K*-dominance plots were used to test whether species and trophic group diversity of vagrant

261   fish assemblages differed between embayed and exposed reef habitats, years (SE Australia

262   only), and locations (Clarke & Gorley 2006). As a diversity measure, *K*-dominance plots

263   better account for species and trophic group evenness than single value diversity indexes

264   (Lambshead et al. 1983). *K*-dominance plots were constructed individually for survey

265   replicates by cumulatively ranking fourth-root transformed species and trophic group

266   densities, expressed as a percentage of all species density, in decreasing order of their

267   density. Fourth root transformations were used since there were many low and some high fish

268   counts within survey replicates; as recommended by Quinn and Keough (2002). Pairwise

269   distances between values in *K*-dominance plots were calculated using DOMDIS (PRIMER

270   v6) (Clarke 1990; Clarke & Gorley 2006). *K*-dominance curves, both for species and trophic

271   diversity, were compared between years (SE Australia only), habitats and amongst locations

272   by permutational multivariate analysis of variance (PERMANOVA; same design as above).

273   Trophic groups that were important contributors to dissimilarity of fish assemblages between

274   habitats were identified using the similarity percentages routine (SIMPER; Clark 1993) then

275   graphically explored by PCO using Spearman's rank correlation. *A priori*, we considered

276   species and trophic groups with $\bar{\delta}_i /SD(\bar{\delta}) > 1$, and % $\bar{\delta}_i > 4\%$ and 10%, respectively, as

277 important contributors to overall dissimilarity between habitats; where $\bar{\delta}_i$ is the average

278 contribution of the ith trophic group to the overall dissimilarity [$\bar{\delta}$] between the two groups

279 and SD is the standard deviation. Densities of these species and trophic groups, found by

280 SIMPER as important contributors to variance in fish assemblages, were then compared

281 between years (SE Australia only), countries, habitats and locations using PERMANOVA (as

282 above).

283

284 Species found to be important (by SIMPER) in distinguishing assemblages between exposed

285 and embayed temperate reefs were compared between wave-shelter and exposed habitats of a

286 coral reef, OTI. Densities of these species were compared between these reef habitats by

287 permutational univariate anlaysis of variance, with factors including year (random), exposure

288 (protected and exposed reef aspects; fixed) and site (nested within exposure; random).

289

290 All survey data were inspected for homogeneity of variance using the PERMDISP procedure

291 (PRIMER^{TM}), with data ln(X+1), square-root or forth-root transformed where required. Data

292 was converted to presence/absence prior to analysis where variances were still non-

293 homogenous following these transformations. PERMANOVA was used as it is more robust

294 to heterogeneity of variances and assumptions of data normality than parametric analyses

295 (Underwood 1997; Anderson & Walsh 2013). For all univariate analyses, factors were pooled

296 with the residual, pertaining to the rule of pooling when $p > 0.25$ (Underwood 1997). *Post*

297 *hoc* pair-wise PERMANOVA tests were performed to identify differences in assemblage

298 densities, richness and diversity amongst locations.

299

300 To determine the combination of environmental variables (i.e. minimum, maximum and

301 mean water temperature, habitat rugosity, predator density, distance from estuary mouth, and

302 latitude), that best predicted variance in trophic generalist and specialist fish assemblages

303 between embayed and exposed temperate reef habitats, the best-fit DistLM procedure

304 (PERMANOVA^{TM}; 9999 permutations pertaining to the Akaike information criterion with a

305 correction for finite sample sizes - AIC_c; maximum of 10 variables) was conducted using

306 Bray-Curtis similarity measures on fourth-root transformed fish abundance data for all

307 countries, years, locations, habitats and species (Clarke & Gorley 2006); trophic specialists

308　(corallivores) were analysed separately, expecting coral habitats to be more important for

309　their recruitment. Biophysical factors driving variance in vagrant assemblages were also

310　analysed separately between SE Australia and W Japan, since water temperature was only

311　measured in SE Australia. Moreover, W Japanese reefs are at a later stage of tropicalization

312　than SE Australia (Nakamura et al. 2013; Vergés et al. 2014), so factors impacting

313　recruitment success may differ between these regions. We considered the most parsimonious

314　model as the combination of environmental variables with an AICc value within 2 units of

315　the overall best solution with the least number of variables, as suggested by Anderson et al.

316　(2008). Environmental data were checked for multicollinearity and dispersion using

317　draftsmen plots, $\ln(X+1)$ or square-root transformed where required, then normalised prior to

318　analysis (PRIMER v6). Relationships amongst environmental data (post-transformation)

319　were also checked for linearity prior to analysis. *A priori*, $p < 0.05$ was the set level of

320　significance for all analyses.

321

322　**RESULTS**

323

324　A total of 4854 vagrant tropical fishes were surveyed within SE Australia and W Japan,

325　encompassing 13 families and 69 species (See Supplementary Material, Table S1). There was

326　a 26.1 % overlap in species between countries, with six families (i.e. Acanthuridae,

327　Chaetodontidae, Labridae, Ostraciidae, Pomacentridae and Zanclidae) encompassing 18

328　species observed in both countries.

329

330　**Association of vagrant assemblage with embayed and exposed temperate reefs**

331

332　Overall density (total individuals), species and trophic diversity (*K*-dominance) and species

333　richness (total species) of vagrant fishes were significantly greater in embayed then exposed

334　reefs (PERMANOVA, $p < 0.05$ for these four metrics, Table 1, Fig. 2). Density and richness

335　of vagrants was over 4.9 and 2.4 times greater, respectively, within embayed than exposed

336　reefs for SE Australia and W Japan, after pooling data at the year (SE Australia only),

337　location and site level (Fig. 2). Years surveyed were pooled prior to analysis for SE Australia

338 since the factor 'year' did not significantly explain patterns of vagrant density, richness nor

339 diversity (PERMANOVA, $p > 0.3$ for these metrics). All other interactions between factors

340 within models were not significant ($p > 0.05$; Table 1).

341

342 **Species and trophic composition of assemblages in embayed and exposed temperate**

343 **reefs**

344

345 Vagrant species assemblages differed between exposed and protected habitats in SE Australia

346 (PERMANOVA; $p = 0.03$; Table 1) and (but not quite significant) W Japan (PERMANOVA,

347 $p = 0.08$; Table 1). There was clear separation of species composition of assemblages

348 between embayed and exposed habitats along PCO Axis 1, whilst species assemblages were

349 separated between countries along PCO axis 2, explaining 29.1 and 21% of variance,

350 respectively (Fig. 3a). In reducing order, *Abudefuf vaigiensis*, *Pomacentrus coelestes*,

351 *Acanthurus dussumieri*, *Chaetodon Auriga*, *Acanthurus nigrofuscus*, *Abudefduf bengalensis*,

352 *Labroides dimidiatus*, *Abudefduf sexfasciatus* and *Acanthurus triostegus* primarily accounted

353 for division of assemblages between habitats (SIMPER; % $\overline{\delta}_i > 4\%$, $\overline{\delta}_i /SD(\overline{\delta}_i) > 1$) and were

354 positively associated with PCO axis 1 (Spearman's rank correlation, $r_s > 0.28$, $p < 0.05$ for

355 these species; Fig. 3a). All nine species were in significantly greater densities or more

356 frequently observed in embayed than exposed reefs (see Supplementary Material, Table S3).

357

358

359 Trophic generalists comprised the entire vagrant assemblage in SE Australia and 98% of

360 assemblages in W Japan. Planktivores were the most common generalist trophic guild in both

361 SE Australia (55.7%) and W Japan (86.9%), followed by herbivores (23.5% Australia; 4.7%

362 Japan), benthivores (12% Australia; 4.3% Japan), omnivores (4.8% Australia; 1.6% Japan),

363 parasite cleaners (1.5% Australia; 0.3% Japan) and piscivores (1.2% Australia; 0.03% Japan).

364 Corallivores made up the remaining ~2% of vagrant assemblages in W Japan, but were never

365 found within SE Australia.

366

367   Vagrant dietary preferences differed significantly between embayed and exposed reefs

368   (PERMANOVA, $p = 0.006$; Table 1). Trophic composition of assemblages was separated

369   between embayed and exposed habitats along PCO Axis 1, explaining 50.3% of variance in

370   assemblages (Fig. 3b), whilst dietary composition of assemblages were separated between

371   countries along axis 2, explaining 21.5% of data variance (Fig. 3b). Of the habitat generalists,

372   planktivores, herbivores, benthivores and omnivores primarily accounted for division of

373   assemblages between habitats (SIMPER; % $\bar{\delta}_i > 10\%$, $\bar{\delta}_i /SD(\bar{\delta}_i) > 1$) and were positively

374   associated with PCO axis 1 (Spearman's rank correlation, $r_s > 0.57$, $p \leq 0.01$ for each trophic

375   group; Fig. 3b).

376

377   Embayed reefs supported greater densities of planktivores ($F_{1, 42} = 45.5$, $p = 0.001$) and

378   benthivores ($F_{1, 42} = 53.6$, $p = 0.001$) than exposed reefs, with this consistent in both SE

379   Australia and W Japan (see Supplementary Material, Table S3). Herbivores were in greater

380   densities in both SE Australian and W Japanese embayed reefs (t = 7.05, p = 0.01 and t = 8.8,

381   p = 0.03, respectively), but omnivores were in greater densities in embayed than exposed

382   reefs in SE Australia (t = 7.36, $p = 0.001$) not W Japan (t = 0.93, $p = 0.37$). For herbivores

383   and omnivores, there was a significant interaction between exposure and country ($F_{1, 42} =$

384   4.09, $p = 0.02$ and $F_{1, 42} = 8.52$, $p = 0.04$, respectively). Dietary specialists (corallivores),

385   were in significantly greater densities in embayed than exposed Japanese reefs ($F_{1, 14} = 5.02$,

386    $p = 0.006$).

387

388   Interactions of the factor 'habitat' with other terms in models were non-significant for all

389   trophic groups and species reported here [i.e. $p > 0.05$ for all interactions between 'habitat'

390   and 'location' and 'year' (SE Australia only)]. Densities of planktivores, herbivores,

391   benthivores and omnivores did not significantly differ between survey years in SE Australia

392   ($p > 0.34$ for these trophic groups), allowing abundance data to be pooled for the above

393   trophic analyses.

394

395   **Influence of exposure on distribution of species on a coral reef**

396

397   Of species that explained considerable variance in assemblages between embayed and

398   exposed temperate reefs (SIMPER; result above), *A. sexfasciatus* and *L. dimidiatus* were in

399   significantly greater densities in protected than exposed aspects of OTI; $F_{1, 29} = 9.16$, $p =$

400   0.015 and $F_{1, 30} = 4.69$, $p = 0.04$, respectively. *A. nigrofuscus* and *C. auriga* were only found

401   in wave-protected reef (n = six and 47 individuals, respectively). There was no difference in

402   densities of *P. coelestis* and *A. triostegus* between exposed and protected reefs; $F_{1, 28} = 0.3$, p

403     $= 0.84$ and $F_{1, 28} = 0.7$, $p = 0.67$, respectively. *A. vaigiensis* was in significantly greater

404   densities in exposed than protected reef aspects in 2011 ($t = 2.43$, $p = 0.012$), but not in 2012

405   ($t = 1.02$, p = 0.36); influence of exposure on *A. vaigiensis* densities depended on year ($F_{1, 28}$

406     $= 5.25$, $p = 0.03$). *A. bengalensis* and *A. dussumeiri* were not detected. All interaction terms

407   including the term 'exposure' not reported were non-significant (i.e. $p > 0.1$).

408

409   **Environmental correlates and recruitment of tropical fishes to temperate reefs**

410

411   Wave exposure best predicted variance in trophic generalist fish composition between

412   embayed and exposed reefs within both SE Australia (30.17%; $AIC_c = 297.53$) and W Japan

413   (16.44%; $AIC_c = 157.24$). The richness and density of generalist assemblages in both

414   countries increased monotically as the exposure of reefs reduced (Fig. 4). In W Japan, wave

415   exposure, independent of any other measured factor, best explained variance in the

416   composition of trophic generalists (See Supplementary Material, Table S4). In SE Australia,

417   the overall best combination of factors explaining variance in vagrant assemblage also

418   included predator density (22%) and latitude (7.5%) ($AIC_c = 294.06$; (See Supplementary

419   Material, Table S4). Richness and density of SE Australian generalist assemblages was

420   significantly and positively correlated with predator density (density: $r_s = 0.64$, $p = 0.001$,

421   richness: $r_s = 61$, $p = 0.001$, See Supplementary Material, Tables S5), but there was no

422   significant correlation with latitude (density: $r_s = -0.15$, $p = 0.35$; richness: $r_s = -0.09$, $p =$

423   0.59).

424

425   Presence of branching coral cover in W Japan best explained differences in densities of

426   corallivore fishes amongst sites (39.9%; $AIC_c = 131.53$), independent of any other factor

427   measured (See Supplementary Material, Table S4). Richness and densities of corallivores

428   were significantly and positively correlated with branching coral cover (density: $r_s = 0.74$, $p <$

429   0.001; richness: $r_s = 0.72$, $p < 0.001$; Fig. 5a). Branching corals were almost exclusively

430   found within highly embayed reefs; sites with branching corals showing a fetch-based wave

431   exposure index values < 0.1 (Fig. 5b; Hill et al. 2010).

432

433   **DISCUSSION**

434

435   To range-expand poleward with warming waters, some tropical fishes require reefs at

436   temperate latitudes that support their recruitment (Figueira & Booth 2010). We show that

437   availability of wave-sheltered temperate reefs may strongly organise recruitment of many

438   tropical reef fishes. Specifically, we found that density, species richness, and species and

439   trophic diversity of newly recruited tropical fish communities was substantially higher on

440   embayed than exposed temperate reefs. This result was consistent within SE Australia (across

441   2 years) and W Japan (during 1 year). Prior to this study, larval supply (Booth et al. 2007;

442   Soeparno et al. 2012), water temperatures (Figueira et al. 2009; Figueira & Booth 2010) and

443   species traits (e.g. life history and diet: Luiz et al. 2013; Feary et al. 2014) were considered

444   the major factors influencing range expansions of tropical fishes into temperate regions.

445   However, our results suggest that even if tropical fishes are readily supplied as larvae to low-

446   latitude temperate regions where they may physiologically tolerate local water temperatures

447   (Figueira et al. 2009) and access necessary resources (Feary et al. 2014), recruitment success

448   (an important step to colonisation; Bates et al. 2014) may depend on the availability of

449   moderately to highly embayed temperate reefs.

450

451   Of the environmental variables measured, wave exposure (estimated by a fetch-based index)

452   was the primary factor organising tropical fish recruitment between embayed and exposed

453   temperate reefs in our study, since the density and richness of tropical fish assemblages was

454   positively correlated with the degree of protection from wave action. This influence of

455   estimated wave exposure on tropical fish recruitment among temperate reefs appeared to

456   outweigh other measured abiotic and biotic factors that have been shown to strongly organise

457   reef fish recruitment elsewhere. For example, habitat complexity, which may influence

458   survival of reef fish recruits by determining refuge from predators, competition strength

459   and/or environmental stress (Almany 2004; Johansen et al. 2008), did not explain differences

460   in tropical fishes assemblages among sites in the present study. Water temperatures (at least

461   in SE Australia) and distance from river mouth (i.e. estuarine influence) also did not explain

462   such strong association with embayed reefs, despite the greater potential for physiological

463   stress associated with high fluxes in salinity, oxygen, thermal and nutrients associated with

464   low flushing and rainfall influences that occur within these habitats (Figueira & Booth 2010;

465   Wenger et al. 2012). Furthermore, although there is evidence that native predators may

466   constrain colonisation of range-expanding marine fishes (Bates et al. 2013; Luiz et al. 2013),

467   our results showed that the diversity and density of temperate predators also appeared here to

468   have little influence on tropical fish recruitment to embayed reefs, as densities of tropical fish

469   recruits were positively correlated with predators in SE Australia, whilst vagrant assemblage

470   composition did not vary with predator densities in W Japan (See Supplementary Material,

471   Table S5). Moreover, negative influences of wave exposure on tropical fish recruitment may

472   have been underestimated here because surveys were conducted during periods of low swell

473   (i.e. < 1 m). Hence, we did not consider periods of high wave energy, which can occur during

474   summer recruitment of tropical fishes in both SE Australia (Short & Trenaman 1992) and W

475   Japan (Sasaki et al. 2005), and may intermittently constrain reef fish populations from

476   establishing in wave-exposed reefs (e.g. Friedlander & Parrish 1998).

477

478   Wave exposure appeared to have a stronger influence on tropical fish recruitment than

479   latitude, suggesting habitat composition of temperate reefs may strongly influence

480   colonisation, regardless of larval supply rates. Although larval supply may be spatially patchy

481   throughout the W Japanese coast due to the almost perpendicular orientation of this coastline

482   to the Kuroshio current and chaotic nearshore flow (Waseda & Mitsudera 2002), the East

483   Australian Current (EAC) typically flows along the SE Australian coast (Fig. 1), leading to

484   reducing vagrant diversity and density from north to south (Booth et al. 2007). Nevertheless,

485   wave exposure of temperate reefs in SE Australia better explained spatial variation in vagrant

486   assemblages among sites than did latitude, at least on spatial scales of 100s m to kms -

487   studied here. It is possible that latitudinal trends in larval supply may be masked by sporadic,

488   but reoccurring eddies in SE Australia (Matis et al. 2014), which form where the EAC

489   encounters particular topographic features of the continental shelf and coastline in this region

490   (Ridgway & Dunn 2003). However, patchiness of embayed and exposed reefs is at a much

491   smaller scale than eddies (kms vs 100s of kms; Ridgway & Dunn 2003), so eddy effects did

492   not confound our results. Hence, although larval supply is an important precursor/prerequisite

493   to range expansions of tropical fishes, influence of temperate reef habitats on recruitment

494   success, such as exposed and embayed reefs, may ultimately control/limit colonisation at

495   local scales.

496

497   The effects of wave exposure on temperate establishment of tropical reef fishes may be

498   mediated through wave motion effect on fish swimming ability. Many recruiting tropical

499   fishes seek shelter from hydrodynamic stress to reduce energetic demand (Johansen et al.

500   2008) and/or to feed more efficiently (MacKenzie & Kiørboe 2000). Although there is

501   considerable variance in swimming performance within and among tropical fish families

502   (Fulton & Bellwood 2004; 2005; Fulton et al. 2005), the majority of tropical fishes,

503   independent of their potential swimming performance, may be forced into sheltered aspects

504   of shallow reefs during periods of high swell activity (Friedlander et al. 2003; Fulton &

505   Bellwood 2004). Alternatively, fishes may avoid hydrodynamic stress associated with wave

506   action by moving to deeper reefs (Fulton & Bellwood 2004). However, a depth response to

507   wave action by these range-expanding fishes was unlikely, at least at the forefront of their

508   redistribution, since isotherms are typically warmer toward the surface, which best supports

509   colonisation success of such warm-adapted, range-expanding species (Bates et al. 2014). This

510   hypothesis was supported by a pilot study, which found tropical fishes assemblages were

511   richer and more diverse in shallow ($< 4m$) than adjacent deeper reef ($> 4m$) in at least one SE

512   Australian site (HJ Beck 2015, unpublished data). Hence, the high wave energy of SE

513   Australian and W Japanese reefs in this study may have been sufficient to force the majority

514   of tropical fish recruits into highly wave sheltered regions, and exclude them from using

515   exposed sites due to the wave action exceeding these fishes' physiological tolerance for water

516   movement, while also limiting their access to suitable resources. Nevertheless, many tropical

517   fishes are highly-mobile during their early life stages (Fisher et al. 2005), so some species

518   may recruit to exposed reefs during calm conditions, moving to more sheltered reefs when

519   ocean swells increased. For instance, sheltering of reef fishes in response to high wave action

520   was recently recorded by Munks et al. (2015), with the diversity and abundance of many reef

521   fishes reducing on temperate reefs during periods of high swell activity.

522

523   One salient result was a difference in habitat association of some damselfishes and
524   surgeonfishes between their natal, tropical range and expanding, temperate range. Although
525   *A. sexfasciatus*, *L. dimidiatus*, *A. nigrofuscus* and *C. auriga* associated with embayed reef on
526   coral and temperate reefs, *A. vaigiensis*, *P. coelestis* and *A. triostegus* had a similar or greater
527   association with exposed reef in the tropical than temperate reef. Such a difference in habitat
528   association of fishes between latitudes may be due to differences in hydrodynamic forcing
529   between coral and temperate-rocky reef. For example, at least within shallow waters, wave
530   energy may dissipate rapidly across a coral reef flat, as opposed to a temperate reef, where
531   the surf zone is typically shorter, and hence potentially prone to higher wave energy on
532   average (HJ Beck, personal observation). However, physiological responses of tropical fishes
533   to cool water temperatures may also account for differences in habitat use between latitudes.
534   For example, *A. vaigiensis* swimming performance may be substantially reduced at temperate
535   latitudes by sub-optimal water temperatures (Figuiera et al. 2009), which may have led to
536   greater sheltering from swell at temperate latitudes. This is highly possible since sheltering
537   responses to cool waters are apparent even for some temperate fishes, which are more
538   thermally tolerant to temperate waters than tropical species. For instance, although capable of
539   high-swimming performance due to their body morphology and fin shape, many temperate
540   Labrids still opt for more sheltered temperate reefs, which is thought to result from a
541   physiological response to cool waters (Fulton & Bellwood 2004). Further work is required to
542   better understand how swimming performance, thermal thresholds and other intrinsic
543   characteristics of tropical fishes shape inter-specific patterns of recruitment at temperate
544   latitudes. This work should involve using empirically tested wave energy models, and
545   consider seasonal and inter-annual fluxes in wave energy and water temperatures.

546

547   As well as directly structuring tropical fish recruitment, wave action also appeared to further
548   organise colonisation success by determining the distribution and morphology of coral
549   habitats at temperate latitudes. At least in W Japan, densities and richness of corallivore
550   fishes were positively associated with branching corals. In SE Australia, corallivores were not
551   detected, likely due to an absence of hard tropical corals in this region (Feary et al. 2014).
552   This was consistent with our expectation, since corallivores typically depend on hard
553   branching corals for food, but also living space and refuge (Syms & Jones 2000; Feary et al.
554   2007b). However, branching corals were exclusive to highly-embayed W Japanese reefs (i.e.
555   wave exposure index < 0.1; Fig. 5). Although branching coral cover increased monotonically

556 with reducing wave action, so the positive response of tropical fishes to embayments may

557 have been driven by hydrodynamic stress rather than coral habitats, we are confident that

558 coral structure was important since all observed individual corallivores were found amongst

559 branching corals (HJ Beck 2015, unpublished data). Factors organising the range expansions

560 of corals and their morphology are largely untested, however we may expect that low wave

561 action in these embayed Japanese reefs was important for the establishment of branching

562 coral habitats. Complex growth forms of corals, such as fine branching, are often preferred by

563 fishes but are highly prone to hydrodynamic stress (Madin et al. 2014), so that at least in

564 shallow coastal waters prone to moderate to high wave energy, they often best establish in

565 reef aspects protected from wave action (e.g. Sommer et al. 2014). Hence, by supporting the

566 establishment of structurally suitable corals, embayed temperate reefs may indirectly assist

567 the colonisation of tropical fishes that depend on these corals for resources.

568

569 This study identified the importance of reef exposure in organising tropical fish colonisation

570 in temperate regions with moderate to high wave energy, yet these habitat influences will

571 likely be weaker where regional and/or seasonal (i.e. through summer recruitment) wave

572 action is lower (Santin & Willis 2007). However, while progressive warming of oceans may

573 eventually lead to poleward expansions in temperate regions globally, where shifts have so

574 far been documented, wave action should be sufficient to limit recruitment success since

575 many regions prone to tropical fish range expansions often have considerable wave energy.

576 For example, the eastern continental boundaries of South America, Africa and USA, as well

577 as the Western Australian coast, where poleward expansions of many tropical fishes are most

578 rapid, all receive moderate to high wave energy (Young et al. 2011; Vergés et al. 2014),

579 which are similar to that of the SE Australian and W Japanese coasts studied here.

580 Nevertheless, even in presence of moderate to high swell, recruiting tropical fishes may

581 establish where they can access natural shelter from wave action, such as where headlands

582 and offshore reefs block swell. Anthropogenic disturbance associated with the development

583 of rocky sea walls and other wave barriers may also increase the availability of embayed reef

584 in temperate regions, and hence assist tropical fish recruitment. For instance, in W Japan,

585 ~70% of shallow, embayed reefs are afforded by artificial wave barriers, which include

586 harbours, jetties, seawalls and detached breakwaters (Walker & Mossa 1986). Protection of

587 reefs from wave action, afforded by such constructions, may also promote recruitment

588 success of coral-associated fishes because these relatively calm environments facilitate
589 establishment of branching coral habitats (Iwas 2004).

590

591 We predict that embayed reef habitats will substantially constrain colonisation of some
592 tropical fishes into SE Australia and W Japan since the availability of embayed reefs, which
593 promote recruitment of many species, appears to be greater in the source tropical range for
594 tropical fishes in these regions (c.f. Bates et al. 2014). Along eastern Australia, embayed
595 habitats are most abundant throughout the Great Barrier Reef (GBR), a vast habitat for Indo-
596 Pacific tropical fishes and the primary larval source of tropical fishes for vagrant fishes in this
597 region (Allen et al. 2003). Within the GBR, mid- and inner-shelf reefs are largely protected
598 from ocean swells by the outer reef. For example, between from ~16º to ~9ºS, the outer reef
599 runs almost continuously north, blocking ~80% of reefs leeward from the outer edge from
600 direct exposure to regular ocean swells (Lewis 2001). Similarly, an island chain that extends
601 from the Philippines to the Ryukyu Islands, which composes the primary historic range for
602 tropical fishes colonising W Japan (Soeparno et al. 2012), provides substantial protection
603 from wave action since reefs bordering western shores are considerably sheltered from the
604 dominant, east swell; wave energy is on average at least half that on the westward than
605 eastward sides of these islands (Barstow et al. 2009). Hence, the general incidence of
606 embayed reefs reduces approaching the poles in both eastern Australian and W Japan, with
607 high potential to impact capacities of tropical fish populations to shift poleward with sea
608 surface warming.

609

610 Resource requirements and physiological performance of tropical fishes may change between
611 their early and later life stages, potentially leading to ontogenetic shifts in association with
612 and impacts on temperate reef habitats. For example, individuals may shift from sheltered
613 estuarine and back-reef nursery habitats to more exposed, offshore reefs in response to
614 dietary changes, reduced predation risk, and greater physiological performance (Nagelkerken
615 et al. 2000; Adams et al. 2006). Nevertheless, at least for some species of tropical fishes, their
616 habitat requirements in thermally marginal temperate reefs may be consistent between
617 recruit/early juvenile and later life-stages. For example, although rarely observed in surveys
618 of temperate reefs in the current study, mature-sized individuals of 26 species, belonging to
619 Chaetodontidae, Labridae, Lutjanidae, Ostraciidae, Pomacentridae and Tetradonitidae, were

620   only observed in embayed reefs of W Japan and SE Australia (See Supplementary material,

621   Table S6). Analysis of the entire adult assemblage also revealed greater densities and richness

622   of adult tropical fishes in embayed than exposed temperate reefs, when data was pooled

623   across countries, locations and survey years (See Supplementary material, Table S6). Such

624   concentration of tropical fishes, particularly for those associating with embayed reefs from

625   settlement through to adulthood, may substantially impact communities native to sheltered

626   temperate reefs. Such impacts may include competition for food and shelter, added predation

627   pressure and decimation of habitat forming species, including kelp. Determining temperate

628   species associated with sheltered reefs will be important in predicting impacts of colonising

629   tropical fishes.

630

631   **CONCLUSION**

632

633   Accurate predictions of species range expansions are required for effective management of

634   climate change impacts in natural ecosystems, but reliable projections of species' geographic

635   responses to climate change are currently elusive (HilleRisLambers et al. 2013). Although

636   propagule supply and species thermal requirements are important considerations (Sorte 2013;

637   Burrows et al. 2014), the timing and location of species range expansions may be more

638   accurately predicted by determining habitat requirements of species at higher latitudes

639   (Cheung et al. 2010), yet field-based studies that test this are largely lacking (Wernberg et al.

640   2012). This study highlights the importance of understanding habitat constraints to

641   recruitment of tropical species, such as wave action, not only larval supply and local

642   environmental temperatures, when predicting where and when they may colonise with

643   ongoing climate change. We show here that for many tropical fishes, failure to consider wave

644   exposure of low-latitude temperate reefs when predicting their future distribution may lead to

645   vast over-estimates of range expansion success. Further studies of physiological performance

646   of tropical fishes in temperate waters, combined with empirically tested wave modelling,

647   should better inform predictions of tropical reef fish distribution under climate change

648   scenarios.

649

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21

659

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TABLES

Table 1. Permutation Analysis of Variances testing for differences in total vagrant tropical fish assemblage density, richness and diversity (i.e. K-dominance) between embayed and exposed temperate reefs (Habitat), locations and years (Australia only), and interactions amongst these factors, within SE Australia and W Japan. Bold p - values denote a significant difference of $p < 0.05$. Where variable was $p > 0.25$, it was pooled with the residual.

| | Effects of variable | | | | | | |
| | Habitat (H) | | | Other variable's p-values | | | |
| | | | | | | C x | H x |
Parameter	*Pseudo-F*	d.f.	*p*	C	L(C)	H	L(C)
Density	33.57	1, 42	**0.005**	0.09	0.90	0.58	0.22
Species richness	40.32	1, 42	**0.003**	0.08	0.29	0.19	0.43
Species composition	7.61	1, 42	**0.006**	**0.03**	**0.0004**	**0.04**	**0.01**
Species diversity	43.05	1, 42	**0.001**	0.54	0.69	0.08	0.64
Trophic composition	11.76	1, 42	**0.005**	0.09	**0.006**	0.05	0.09
Trophic diversity	22.14	1, 41	**0.006**	0.08	0.67	0.25	0.15

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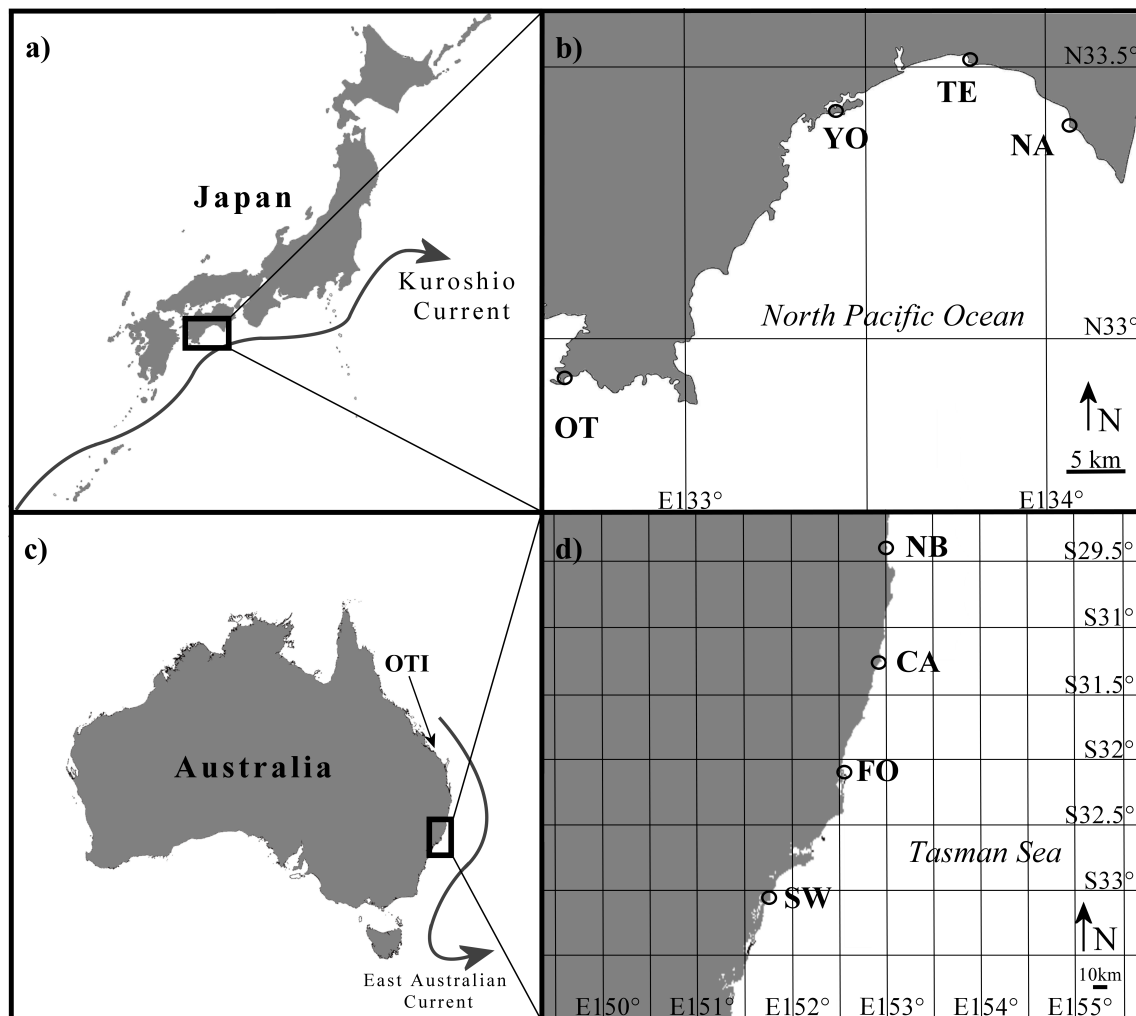
932 **Fig. 1** Location of survey locations within western (W) Japan [insets a) and b)] and

933 southeastern (SE) Australia [insets c) and d)]. Within each location, two to three 30-minute

934 underwater visual surveys of tropical vagrant were conducted in both embayed and exposed

935 temperate reefs. Vagrant tropical fishes are supplied through summer from tropical fishes to

936 temperate reefs by the poleward flowing a) Kuroshio and c) East Australian Currents within

937 SE Japan and Australia, respectively [flow path and direction illustrated by arrows, insets a)

938 and b)]. Surveys conducted for two recruitment seasons in SE Australia and one in W Japan.

939 CA = Camden Haven, FO = Forster, NA = Nahara, NB = Nambucca, OT = Otsuki, SWA =

940 Swansea, TE = Tei, YO = Yokonami. Tropical fish recruitment was also studied on exposed

941 and sheltered aspects of a coral reef - One Tree Island [OTI; inset c)], Great Barrier Reef (see
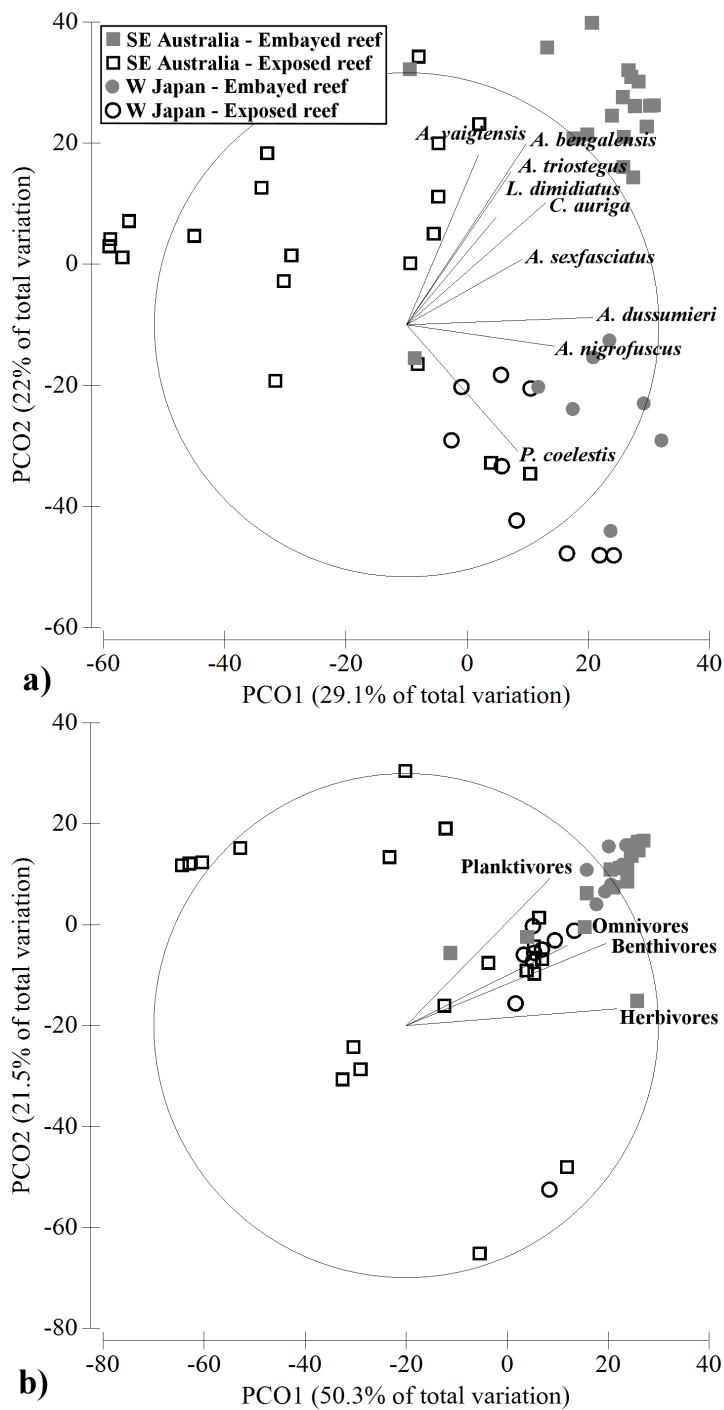
942 Supplementary Material, Fig. S2).

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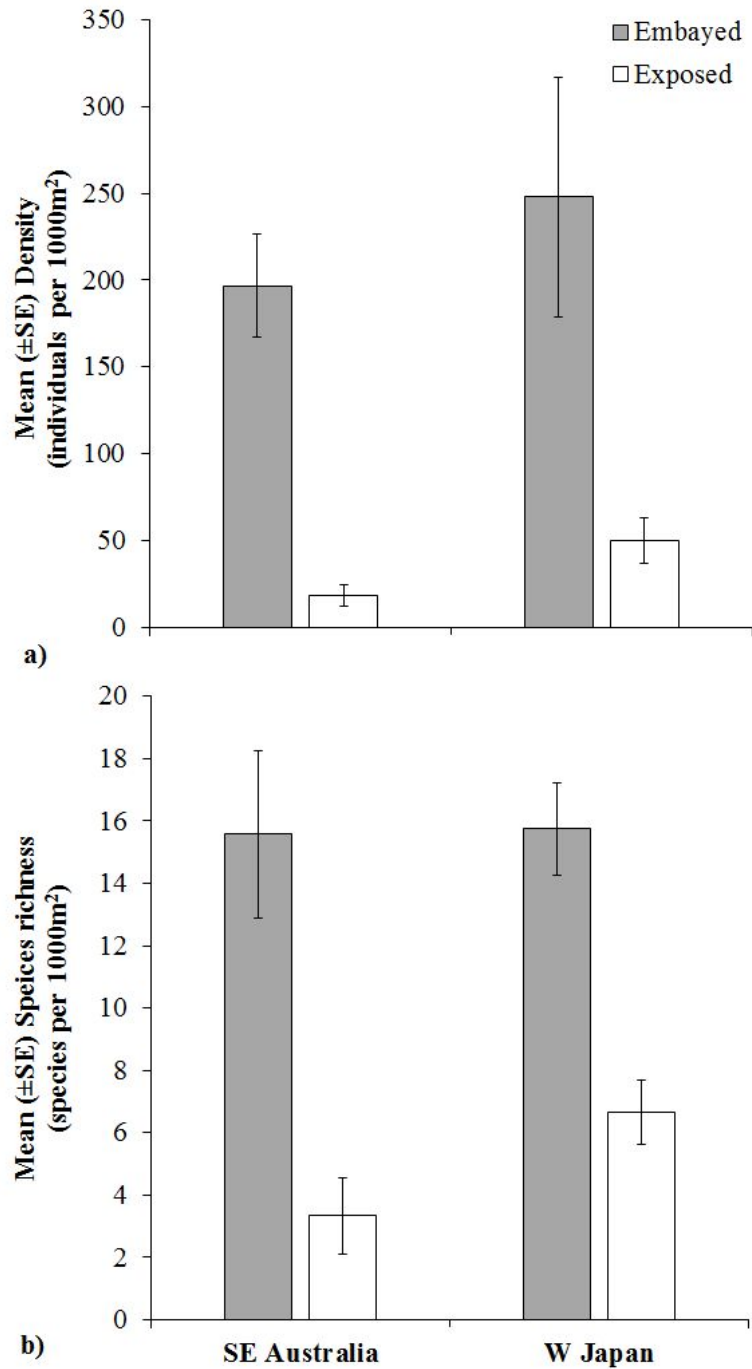
Fig. 2 Mean (±SE) a) density and b) species richness of vagrant tropical fishes within
embayed (grey bars) and exposed (white bars) reef habitats of southeastern (SE) Australia
and western (W) Japan.

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**Fig. 3** Principal co-ordinate analysis of tropical vagrant fish a) species and b) trophic groups within embayed (grey markers) and exposed reefs (open markers) of southeastern (SE) Australia (squares) and western (W) Japan (circles). Vectors overlaid display the primary a) species and b) diet groups responsible for division of sites along PCO axis 1, determined by SIMPER analysis (result reported in text). N = 40 and 21 replicate 30 minute-timed swims within SE Australia and W Japan, respectively.

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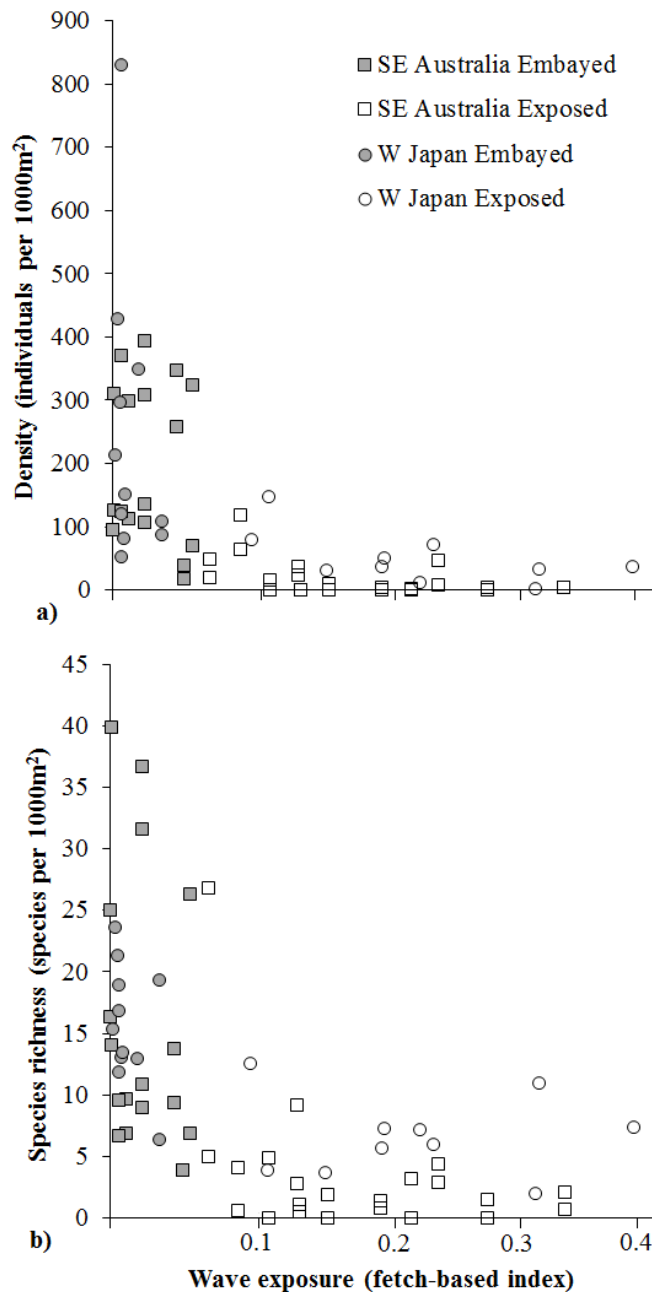
Fig. 4 Correlation of a) densities and b) species richness of tropical vagrant fish assemblages against wave exposure of sites within southeastern (SE) Australia (squares) and western (W) Japan. Grey markers = embayed sites, Open markers = exposed sites. Fetch-based wave exposure indices calculated according to Hill et al (2010). N = 40 and 21 replicate 30 minute-timed swims within SE Australia and W Japan, respectively. Density and richness of vagrant assemblages were significantly correlated with wave exposure within both countries; spearman's rank correlation statistic (r_s) was significant ($p < 0.001$), ranging between -0.74 and -0.76 for both metrics.

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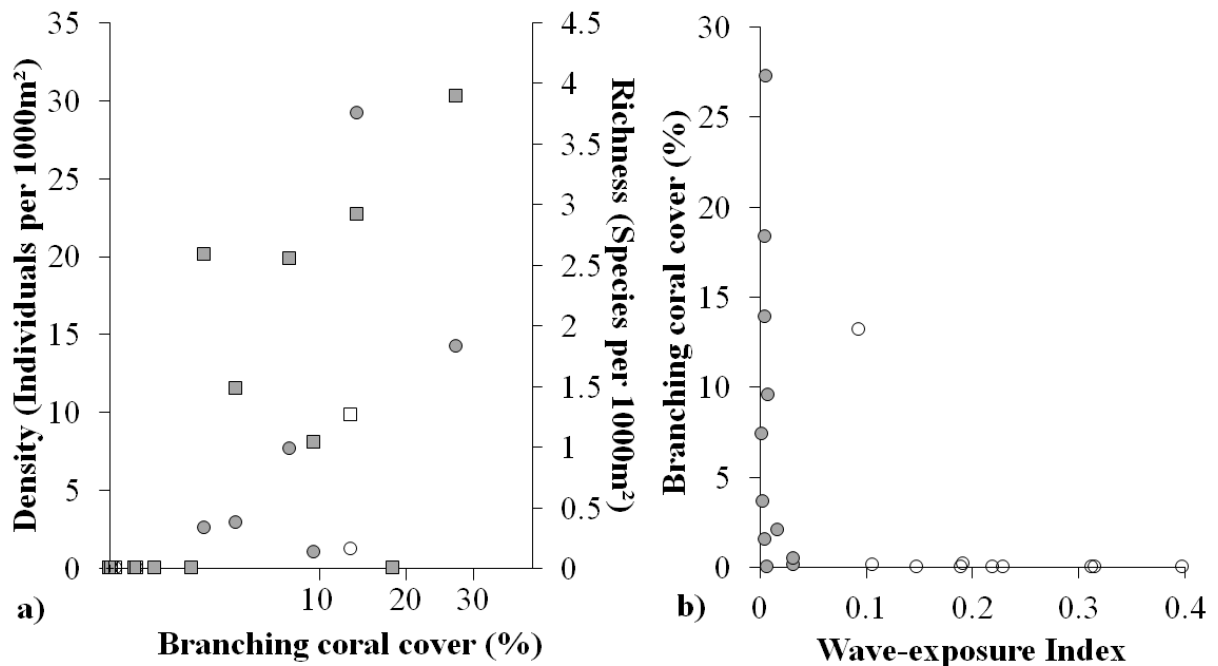
Fig. 5 Regression of (a) densities (circles, axis 1) and species richness (squares, axis 2) of corallivores with mean branching coral cover of reefs in embayed (grey markers) and exposed reef (open markers) of western (W) Japan, and (b) branching coral cover with wave exposure of embayed (grey markers) and exposed (open markers) sites within W Japan. N = 21 sites; within each site, fishes quantified by one 30 minute-timed swim survey and coral cover was quantified 20 haphazardly arranged 0.5 m^2 quadrates. Spearman's rank correlation statistic (r_s) was significant ($p < 0.001$) for regression of density and richness of corallivores with branching coral cover; r_s was 0.74 and 0.72 for these regressions, respectively).
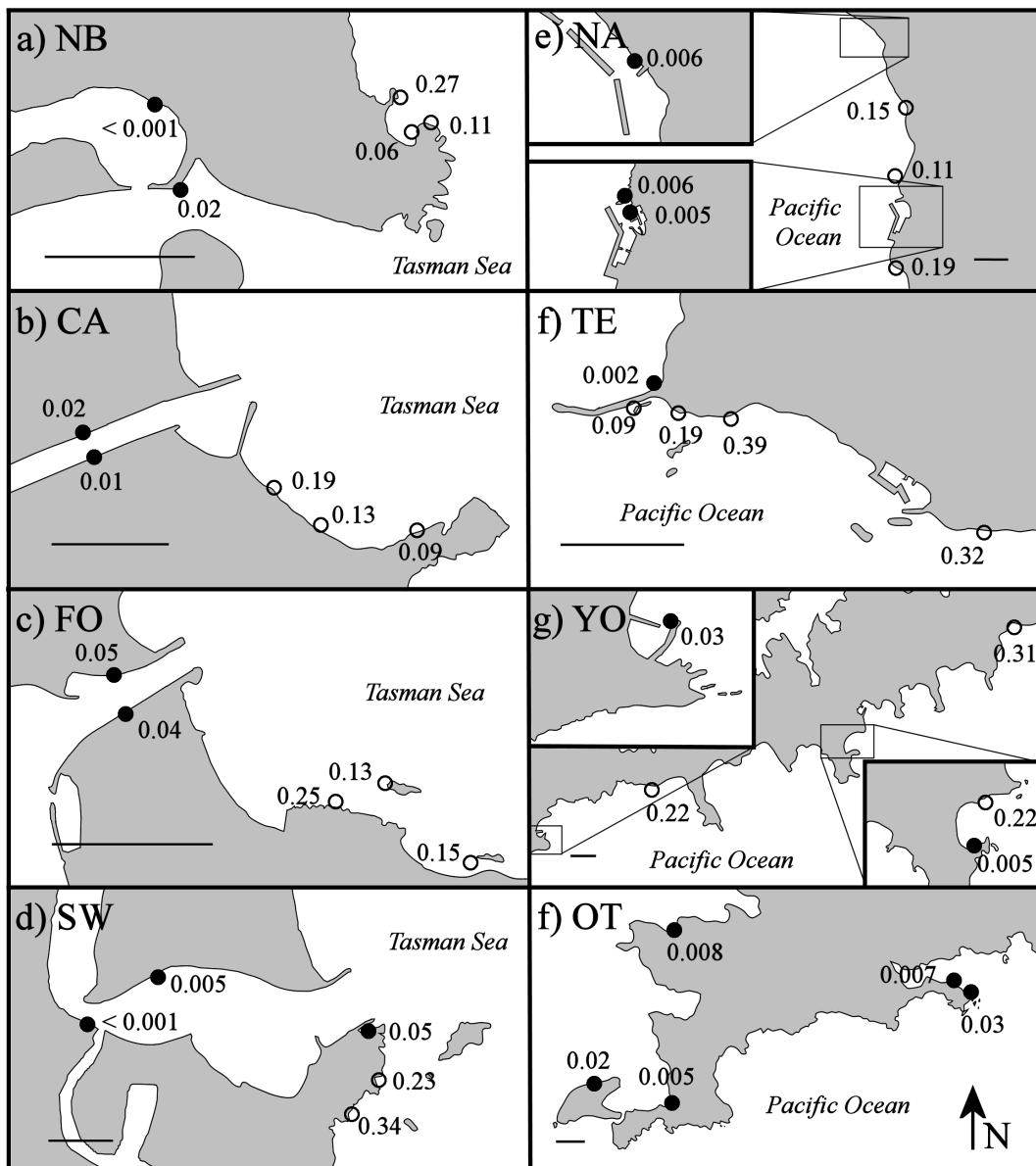
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ELECTRONIC SUPPLEMENTS

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987   **Figure S1.** Wave-exposure index values for embayed (closed circles) and exposed (open

988   circles) reefs surveyed within southeastern Australia [a)-d)] and western Japan [e)-f)]. Wave

989   exposure indices out of a maximum exposure value of 1, respectively. Embayed and exposed

990   sites had index values < and > 0.4 (i.e. 15 of exposure), respectively. Index values were

991   constructed with 7.5° spacing around the midpoint of survey sites to a maximum of 650 km,

992   the minimum fetch distance for fully developed seas to form. CA = Camden Haven, FO =

993   Forster, NA = Nahara, NB = Nambucca, OT = Otsuki, SWA = Swansea, TE = Tei, YO =

994   Yokonami. Scale bar = 500m.

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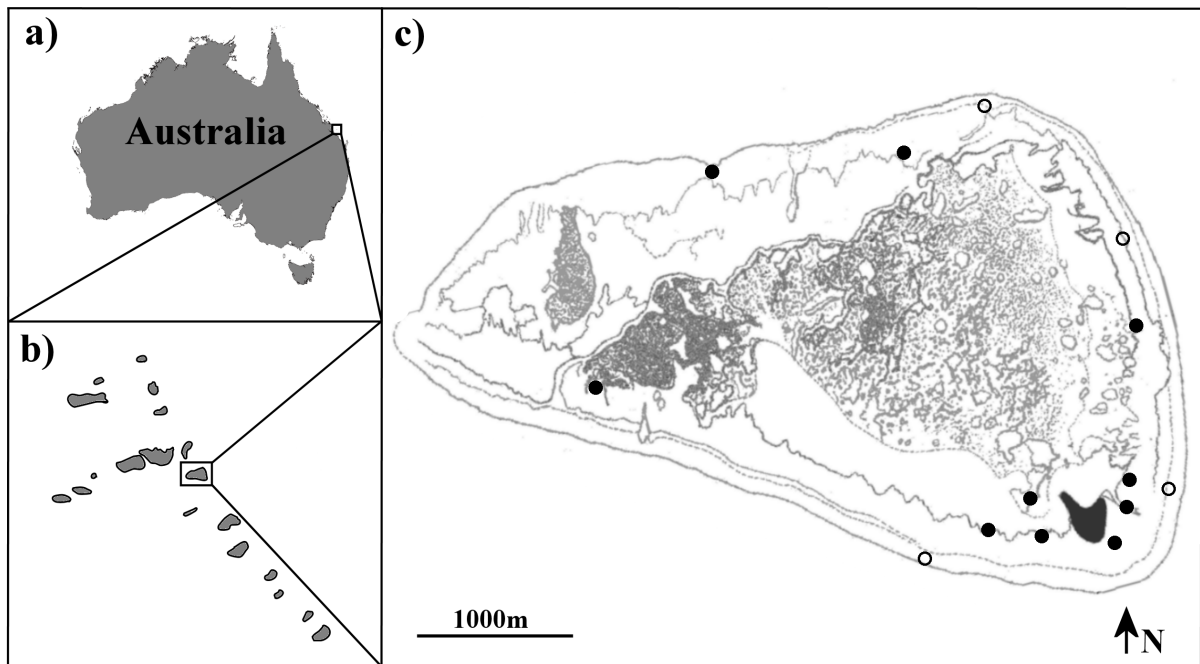
Figure S2. Location of survey sites in One Tree Island (OTI), Great Barrier Reef. OTI is located off the coast of Queensland, Australia in the southern Capricorn-Bunker Group of the Great Barrier Reef [insets a) and b)]. To determine habitat associations within their natal, historic range, recruit and early juvenile tropical fishes were surveyed in sheltered (closed circles) and exposed (open circles) reef sites of OTI. Exposed sites were those on the windward side of the island, positioned on the reef flat and reef edge (i.e. spur-and-groove); sites were on the eastern and southern aspects of the reef, which are exposed to the predominant southerly swell direction. Sheltered sites were those on the reef flat and reef edge on the leeward side of the island, as well as back reef sites protected from swell by the reef crest. In total, nine and 23 half-hour GPS-tracked roaming surveys were conducted in exposed and sheltered reef sites. Note: Surveys were conducted at the same site during 2011 and 2012. In some cases replicate surveys were conducted ~100m of each other, so not all survey sites were marked here.

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1013 **Table S1.** Species, primary trophic guild and country tropical reef fishes were detected.

1014 Species classified as tropical according to IUCN Red List, Froese and Pauly (2015) and/or

1015 Kuiter 2003. Trophic guilds allocated from references below. A = Southeastern Australia; J =

1016 Western Japan. Where known, dietary preferences were assigned for recruits/juveniles (R), as

1017 well as for vagrant fishes (V).

Tropical Fishes detected	Primary dietary classification	Region	Do
F. Acanthuridae			
Acanthurus dussumieri	Herbivore	A, J	Grazer/detritivore, algae in temp
Acanthurus lineatus	Herbivore	A, J	Algal turfs[3,4]
Acanthurus mata	Herbivore	A	Juveniles feed on benthic algae,
Acanthurus nigrofuscus	Herbivore	A, J	Algal turfs[1,4]
Acanthurus olivaceus	Detritivore	A, J	Organic detritivore with some al
Acanthurus triostegus	Herbivore	A, J	Algal turfs (R; V)[4]
Ctenochaetus binotatus	Detritivore	A, J	Organic detritivore with some al
Ctenochaetus striatus	Detritivore	J	Organic detritivore with some al
Naso unicornis	Herbivore	A, J	Macroscopic algae, mainly large
F. Balistidae			
Sufflamen chrysopterus	Benthivore	A	Benthic invertebrates[7]
F. Chaetodontidae			
Chaetodon auriga	Benthivore	A, J	Benthic invertbrates, including p
Chaetodon auripes	Benthivore	J	Benthic invertebrates[9]
Chaetodon citrinellus	Benthivore	A	Facultative corallivore, algae, po
Chaetodon flavirostris	Benthivore	A	Facultative coralivore, benthic in
Chaetodon guentheri	Omnivore	A	Omnivore (occasionally zooplan
Chaetodon kleinii	Benthivore	A	Facultative corallivore and hydro
Chaetodon melannotus	Corallivore	J	Obligate corallivore (hard and so
Chaetodon plebeius	Corallivore	J	Obligate corallivore (mostly on l
Chaetodon selene	Omnivore	J	Omnivore[13]
Chaetodon speculum	Corallivore	J	Obligate corallivore (wide range
Chaetodon trifasciatus	Corallivore	J	Obligate corallivore (wide range
Chaetodon vagabundus	Omnivore	A, J	Anemones, coral polyps, polycha
Heniochus acuminatus	Planktivore	A	zooplankton, supplemented with

F. Gobiesocidae

Species	Feeding	Stage	Diet
Diademichthys lineatus	Benthivore	J	Pedicellariae and sphaeridia of h
F. Labridae			
Anampses caeruleopunctatus	Benthivore	A, J	Small benthic crustaceans and p(
Anampses melanurus	Benthivore	J	Small crustaceans, molluscs and
Anampses meleagrides	Benthivore	J	Benthic invertebrates[23]
Cirrhilabrus temminckii	Planktivore	J	Zooplankton[24]
Coris gaimard	Benthivore	J	Benthic molluscs, crabs, tunicate
Gomphosus varius	Benthivore	J	Benthic crustaceans, sometimes
Halichoeres margaritaceus	Benthivore	J	Benthic crustaceans, molluscs, p
Hologymnosus annulatus	Benthivore	J	Crustaceans (R)[26]
Labroides dimidiatus	Parasite cleaner	A, J	Ectoparasites and fish mucus (V
Pseudocheilinus hexataenia	Benthivore	J	Crustaceans[8]
Stethojulis bandanensis	Benthivore	A, J	Crustaceans and benthic inverteb
Stethojulis strigiventer	Benthivore	J	Benthic invertebrates, including
Thalassoma hardwicke	Benthivore	J	Benthic and planktonic crustace; foraminiferans[30,31]
Thalassoma jansenii	Benthivore	A	Benthic invertebrates[30]
F. Lutjanidae			
Lutjanus argentimaculatus	Piscivore	A	Fish and pelagic invertebrates, s(
Lutjanus russellii	Piscivore	A	Fish and pelagic invertebrates, s(
F. Ostraciidae			
Ostracion cubicus	Benthivore	A, J	Benthic invertebrates, including crustaceans[34]
F. Pomacentridae			
Abudefduf bengalensis	Omnivore	A	Crabs, gastropods, benthic algae
Abudefduf sexfasciatus	Plankivore	A, J	Zooplankton and algae[34]
Abudefduf sordidus	Omnivore	A	Algae, crustaceans and other ber
Abudefduf vaigiensis	Planktivore	A, J	Zooplankon (R; V), supplemente
Abudefduf whitleyi	Planktivore	A	Zooplankton[34]
Amphiprion clarkii	Planktivore	J	Zooplankton[34]
Chromis fumea	Planktivore	A	Zooplankton[34]
Chromis margaritifer	Planktivore	A, J	Zooplankton[34]

Chromis weberi	Planktivore	J	Zooplankton[34]
Chrysiptera starcki	Omnivore	J	Zooplankton and algae[34]
Chrysiptera unimaculata	Herbivore	J	Algae[30]
Dascyllus reticulatus	Omnivore	J	Zooplankton and algae[34]
Dascyllus trimaculatus	Omnivore	J	Zooplankton, copepods and alga
Plectroglyphidodon leucozonus	Herbivore	A, J	Benthic algae[30]
Pomacentrus coelestis	Planktivore	A, J	Primarily zooplankon, sometime
Pomacentrus nagasakiensis	Planktivore	A, J	Primarily zooplankon, sometime
Pomachromis richardsoni	Benthivore	J	Zoobenthos[30]
F. Scaridae			
Scarus forsteni	Herbivore	J	Benthic algae[38]
F. Scorpaenidae			
Pterois volitans	Piscivore	J	Small fishes, shrimps and crabs[3]
F. Serranidae			
Cephalopholis argus	Piscivore	A	Fishes[39]
Diploprion bifasciatum	Piscivore	A	Fishes[34]
Grammistes sexlineatus	Piscivore	A	Fishes[34]
Pseudanthias squamipinnis	Planktivore	J	Zooplankton[40]
F. Tetraodontidae			
Canthigaster rivulata	Omnivore	J	Uncertain - assumed similar to C
Canthigaster valentini	Omnivore	J	Benthic algae, bryozoans, polycl
F. Zanclidae			
Zanclus cornutus	Benthivore	A, J	Benthic invertebrates, including

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1113 **Table S2.** Mean (SD) areas (m^2) surveyed during replicate surveys of embayed and exposed
1114 habitats of a) southeastern (SE) Australia and b) western (W) Japan. n = number of replicate
1115 half-hour timed swim surveys, following Beck et al. (2014). Note: replicate surveys averaged
1116 across two years in SE Australia and one year in W Japan.

Location	Habitat	n	Mean (SE) area m^2
a) SE Australia			
Nambucca	Embayed	5	505.33 (100.08)
	Exposed	6	925.38 (666.75)
Camden Haven	Embayed	4	1714 (596.04)
	Exposed	6	1378.03 (482.69)
Forster	Embayed	4	1190.25 (446.26)
	Exposed	6	1428.59 (504.71)
Swansea	Embayed	4	1008.21 (491.67)
	Exposed	6	1208.03 (220.96)
b) W Japan			
Nahara	Embayed	3	707.64 (55.61)
	Exposed	3	1170.54 (182.72)
Tei	Embayed	2	778.88 (7.34)
	Exposed	3	915.14 (32.07)
Otsuki	Embayed	2	719.25 (223.12)
	Exposed	3	778.65 (6.02)
Yokonami	Embayed	3	629.98 (84.13)
	Exposed	2	1044.32 (67.38)

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1119 **Table S3.** PERMANOVA comparison of trophic guilds and species of importance between

1120 habitats (H; embayed and exposed), countries (C; Australia and Japan) and locations (L; n =

1121 4 in SE Australia, n = 3 in W Japan). Bold denotes a significant result (i.e. $p < 0.05$). *

1122 indicates species converted to presence/absence prior to analysis due to non-homogenous

1123 density data (i.e. PERMDISP, $p < 0.05$). Data for all trophic groups and species pooled across

1124 survey years in SE Australia ($p > 0.25$ for all listed trophic groups and species). A = Australia

1125 only, as was only observed there.

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| | Effects of variable | | | | | | |
| | Habitat (H) | | | Other variable's *p*-values | | | |
Parameter	*Pseudo-F*	d.f.	*p*	C	L(C)	C x H	H x L(C)
Trophic guilds							
Planktivores	11.55	1, 42	**0.02**	0.12	0.20	0.63	0.09
Herbivores	38.99	1, 42	**0.002**	0.77	**0.01**	**0.02**	0.41
Benthivores	53.59	1, 42	**0.001**	1.28	0.05	0.05	0.54
Omnivores	16.16	1, 42	**0.01**	0.94	0.26	**0.04**	0.26
Species							
A. vaigiensis	8.49	1, 42	**0.03**	0.15	0.15	0.32	0.06
A. bengalensis[*][A]	22.22	1,32	**0.02**	-	0.47	-	0.22
A. sexfasciatus[*]	18.17	1, 42	**0.008**	1	0.10	0.98	0.09
P. coelestis	10.08	1, 42	**0.03**	**0.03**	0.43	0.08	0.07
A. dussumieri[*]	7.66	1, 42	**0.04**	0.09	0.001	0.12	0.05
A. nigrofuscus[*]	10.50	1, 42	**0.002**	0.09	0.17	0.83	0.36
A. triostegus[A]	16.76	1, 32	**0.02**	-	**0.02**	-	0.29
L. dimidiatus[*]	8.43	1, 42	**0.04**	0.28	0.36	0.74	0.11
C. auriga[*]	41.40	1, 42	**0.002**	0.09	0.44	0.09	0.45

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1131 **Table S4.** Results of Distance Based Linear Modelling of biophysical variables within
1132 temperate reefs on assemblages of dietary generalist [a) Southeastern Australia and b)
1133 western Japan] and specialist [a) W Japan only] tropical fishes.

Factor	Pseudo-F	*P*	Proportion (%)
a) SE Australia - Trophic generalists			
Wave exposure	16.41	0.001	30.17
Predator density	10.63	0.001	21.86
Distance from river mouth	9.12	0.002	19.35
Invertebrate cover (other than coral)	5.18	0.002	12.00
Folios algal cover	4.94	0.003	11.51
Latitude	3.07	0.02	7.47
SD water temperature	3.02	0.04	7.35
Sand	2.59	0.04	6.37
Encrusting algal cover	2.15	0.07	5.35
Average water temperature	2.06	0.08	5.14
Minimum water temperature	1.73	0.13	4.35
Reef rugosity	1.10	0.31	2.83
Bare rock	1.00	0.38	2.57
Rubble	0.84	0.49	2.16
Turfing algal cover	0.58	0.73	1.51
b) W Japan - Trophic generalists			
Wave exposure	3.74	0.0002	16.44
Latitude	3.01	0.001	13.67
Branching coral cover	2.52	0.005	11.71
Sand	1.93	0.03	9.23
Encrusting algal cover	1.37	0.18	6.71
Live coral cover	1.36	0.19	6.69
Plate coral cover	1.22	0.27	6.02
Invertebrate cover (other than coral)	1.18	0.29	5.83
Coral rubble	1.15	0.32	5.71
Reef rugosity	1.08	0.39	5.38
Distance from river mouth	0.94	0.51	4.72
Encrusting coral cover	0.92	0.51	4.60

Bare rock	0.75	0.68	3.31
Folios algae cover	0.62	0.83	3.16
Predator density	0.62	0.83	3.16
Turfing algae cover	0.48	0.92	2.49
c) W Japan - Trophic specialists			
Branching coral cover	12.63	0.001	39.93
Live coral cover	6.83	0.01	26.44
Plate coral cover	5.48	0.01	22.38
Encrusting algal cover	5.36	0.01	22.02
Wave exposure	3.73	0.04	16.41
Turfing algae cover	3.04	0.05	13.80
Invertebrate cover (other than coral)	1.54	0.22	7.52
Latitude	1.04	0.38	5.17
Encrusting coral cover	0.71	0.49	3.60
Folios algae cover	0.65	0.53	3.30
Reef rugosity	0.45	0.63	2.33
Bare rock	0.43	0.93	2.21
Predator density	0.39	0.71	2.01
Sand	0.34	0.71	1.74
Distance from river mouth	0.14	0.88	0.73
Coral rubble	0.14	0.88	0.72

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Table S5. Mean (SE) piscivore densities within embayed and protected reef habitats within a)

SE Australia and b) W Japan. * denotes significant difference in densities between habitats

(PERMANOVA; $p < 0.05$).

Species	Common name	Embayed reef Mean (SE)	Exposed reef Mean (SE)
a) SE Australia			
Acanthopagrus australis	Yellowfin Bream	45.64 (7.82)*	4.91 (1.65)
Argyrosomus japonicas	Jewfish	0.32 (0.33)	0.00
Brachaelurus waddi	Blind shark	0.00	0.03 (0.03)
Dinolestes lewini	Longfin Pike	2.12 (1.55)	1.20 (0.60)
Epinephelus coioides	Estuary cod	0.24 (0.14)	0.00
Epinephelus daemelii	Black cod	0.16 (0.17)	0.03 (0.03)
Gymnothorax prasinus	Green Moray	0.23 (0.24)	0.00
Lutjanus argentimaculatus	Mangrove Jack	0.12 (0.13)	0.00
Lutjanus russellii	Moses' snapper	4.88 (2.11)	1.71 (1.71)
Platycephalus bassensis	Sand flathead	2.67 (2.37)	0.03 (0.03)
Platycephalus fuscus	Dusky flathead	0.80 (0.53)	0.09 (0.09)
Sepia plangon	Mourning cuttlefish	0.20 (0.21)	0.00
Sepia sp.	Unidentified cuttlefish	0.00	0.09 (0.09)
	Total	57.54 (8.69)*	8.09 (2.28)
b) **W Japan**			
Acanthopagrus schlegelii	Japanese black porgy	0.13 (0.13)	0.44 (0.25)
Apagon sp.	Unidentified cardinal fish	19.29 (9.88)	4.16 (4.16)
Gymnothorax sp.	Unidentified morey eel	0.13 (0.13)	0.00
Lethrinus genivattatus	Thread-finned emporer	0.15 (0.15)	0.00
Lethrinus nebulosus	Spangled emperor	0.12 (0.12)	0.56 (0.56)
Lutjanus russelli	Moses' snapper	0.13 (0.13)	0.00
Lutjanus stellatus	Star snapper	0.23 (0.15)	0.10 (0.10)
Plectropomus leopardus	Coral trout	0.10 (0.10)	0.00
Pterois volitans	Red lionfish	0.10 (0.10)	0.00
Scolopsis affinis	Monocole bream	0.15 (0.15)	0.35 (0.35)
Sphyraena japonica	Japanese barracuda	2.52 (2.52)	1.76 (1.76)
Synodus ulae	Red lizard fish	0.61 (0.47)	0.07 (0.07)

	Total	25.49 (9.10)	5.63 (3.13)

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1143 **Table S6.** Mean (SE) densities, overall densities and species richness of adult tropical fishes
1144 in embayed and exposed temperate reefs of SE Australia (A) and W Japan (J). Data combined
1145 amongst countries (for species observed in both), survey years (SE Australia only) and
1146 locations. Adults identified by length categories provided by Booth et al. (2010). Bold species
1147 denote those only found in embayed reefs. * Indicates a significant difference in densities
1148 between exposed and embayed habitats (i.e. $p < 0.05$), as determined by T-test.

Species	Exposed	Protected
F. Acathuridae		
Acanthurus dussumieri[A, J]	0.67(0.30)	1.38(0.39)
Acanthurus nigrofuscus[A, J]	0.0(0.0)	0.46(0.24)*
Ctenochaetus striatus[J]	0.0(0.0)	0.11(0.11)
Naso unicornis[J]	0.11(0.11)	0.0(0.0)
F. Blenniidae		
Meiacanthus kamoharai[J]	0.0(0.0)	1.26(0.52)*
F. Centropyge		
Centropyge tibicen[J]	0.0(0.0)	0.89(0.55)
Centropyge vrolikii[J]	0.0(0.0)	0.38(0.38)
F. Chaetodontidae		
Chaetodon auriga[A, J]	0.0(0.0)	0.33(0.31)
Chaetodon auripes[A, J]	11.93(1.73)	21.88(4.73)*
Chaetodon flavirostris[A]	0.0(0.0)	0.27(0.18)
Chaetodon melannotus[J]	0.0(0.0)	0.13(0.13)
Chaetodon septentrionalis[J]	0.0(0.0)	0.11(0.11)
Chaetodon speculum[J]	0.0(0.0)	0.11(0.11)
Chaetodon vagabundus[J]	0.0(0.0)	0.12(0.12)
F. Cheilodactylidae		
Goniistius zonatus[J]	1.04(0.35)	1.11(0.49)
F. Diagramma		
Diagramma pictum pictum[J]	0.32(0.23)	0.11(0.11)
F. Diodontidae		

***Diodon holocanthus*[J]**	0.0(0.0)	0.11(0.11)
F. Gobiesocidae		
***Diademichthys lineatus*[J]**	0.0(0.0)	0.09(0.09)
F. Labridae		
Anampses caeruleopunctatus[A, J]	0.03(0.03)	0.09(0.09)
Anampses melanochir[J]	0.11(0.11)	0.00(0.00)
***Anampses melanurus*[J]**	0.0(0.0)	0.25(0.17)
***Anampses meleagrides*[J]**	0.0(0.0)	0.21(0.21)
***Cirrhilabrus cyanopleura*[J]**	0.0(0.0)	0.13(0.13)
***Cirrhilabrus temminckii*[J]**	0.0(0.0)	0.25(0.25)
Gomphogus varius[J]	1.58(0.81)	0.97(0.38)
Halichoeres melanochir[J]	0.11(0.11)	0.12(0.12)
Labroides dimidiatus[J]	0.41(0.22)	0.08(0.05)
F. Lethrinidae		
***Lethrinus genivatatus*[J]**	0.0(0.0)	0.13(0.13)
Lethrinus nebulosus[J]	0.08(0.08)	0.57(0.47)
F. Lutjanidae		
***Lutjanus argentimaculatus*[A]**	0.0(0.0)	0.33(0.19)
Lutjanus russeli[A, J]	0.09(0.05)	0.59(0.29)*
Lutjanus stellatus[J]	0.23(0.15)	0.11(0.11)
F. Ostraciidae		
***Lactoria fornasini*[J]**	0.0(0.0)	0.11(0.11)
F. Pomacanthidae		
***Chaetodontoplus septentrionalis*[J]**	0.0(0.0)	0.19(0.13)
F. Pomacentridae		
Abudefduf bengalensis[A, J]	0.18(0.13)	3.07(0.73)*
***Abudefduf sexfasciatus*[J]**	0.0(0.0)	2.82(2.53)
Abudefduf vaigiensis[A, J]	3.84(1.60)	4.68(1.30)
Abudefduf whitleyi[A]	0.1(0.1)	0.0(0.0)
Amphiprion clarkii[J]	0.80(0.35)	2.47(0.94)
***Chromis weberi*[J]**	0.0(0.0)	0.29(0.29)
***Chromis leucura*[J]**	0.0(0.0)	0.66(0.52)
***Chrysiptera unimaculata*[J]**	0.0(0.0)	0.53(0.30)*

Dascyllus trimaculatus[J]	0.0(0.0)	2.53(1.94)
Plectroglyphidodon leaucozonus[A]	1.16(0.9)	0.0(0.0)
F. Serranidae		
Plectropomus leopardus[J]	0.0(0.0)	0.09(0.09)
F. Tetraodontiform		
Canthigaster rivulata[J]	0.21(0.14)	0.00(0.00)
Mean overall density (individuals/1000m²)	15.00(4.06)	27.19(5.28)*
Mean overall richness (species/1000m²)	1.95(0.49)	4.46(0.71)*

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