

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

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ABSTRACT: Poleward redistribution of species, facilitated by global warming, will be compromised if habitats at higher latitudes do not support the species' early life stages. For tropical reef fishes, reef structure may mediate colonisation of temperate regions; however, an understanding of key habitat requirements for colonisation is currently lacking. We show that density, diversity (taxonomic and trophic) and species richness of newly recruited tropical reef fishes were greater in embayed than exposed reefs in 2 mid-latitude temperate zones, where coastal waters are rapidly warming: southeastern Australia (30.5–33° S) and western Japan (32–33.5° N). Dietary generalists (e.g. planktivores and herbivores) and specialists (corallivores) associated more commonly with embayed reefs. Wave exposure was a stronger predictor of the density and richness of dietary generalists than water temperature, latitude, predatory fish densities, reef rugosities, benthos and distance to river mouths. Corallivores were strongly associated with branching corals, which were exclusive to highly sheltered reefs. We also explored habitat associations of 7 focal species within a coral reef, One Tree Island (OTI), Great Barrier Reef. Four species associated with wave-sheltered over exposed reef on OTI and temperate Australian reef. However, *Abudefduf vaigiensis*, *Pomacentrus coelestis* and *Acanthurus triostegus* associated more with wave-sheltered reef in temperate regions. We hypothesise that cool temperate waters promote greater sheltering of some warm-adapted, tropical fishes by impacting their swimming/physiological performance. Results suggest availability of embayed temperate reefs may influence where some tropical fishes colonise with warming waters, through impacting recruitment. Wave exposure of reefs should be considered when predicting geographic responses of tropical fishes to climate change.

KEY WORDS: Climate change · Range shift · Novel habitat · Temperate rocky reef · Wave 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 & Holzapfel 2006), they may shift in elevation (altitude or 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, Polo-

czanska et al. 2013). 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). Propagule pressure and physiological tolerance of species to environmental

temperatures may determine species redistribution (Sorte 2013, Burrows et al. 2014). However, abilities of species to redistribute poleward with shifting isotherms may ultimately be determined by availability of suitable habitat at higher latitude, encapsulating the biological and physical factors required for species to survive through all their life stages (Opdam & Wascher 2004, Bennie et al. 2013). In particular, due to their high vulnerability, species during their early life stages may be strongly impacted in a new range 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 (HilleRis-Lambers et al. 2013).

For tropical marine organisms, expanding their range into temperate latitudes, the abiotic and biotic environment structuring habitats within destination latitudes may constrain colonisation (Cheung et al. 2010, Sommer et al. 2014). Many tropical reef fishes are expected to expand 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, Luiz et al. 2016). Notably, tropical herbivorous fish may decimate kelp forests (or suppress their recovery following warming-induced mortality), leading to stable canopy-free stable states (e.g. Vergés et al. 2014, Bennett et al. 2015, Basford et al. 2016). Tropical fishes may also impact temperate reef fish communities, through predator–prey interactions and competition (Beck et al. 2014, 2016, Feary et al. 2014). However, despite strong evidence that many tropical fishes could physiologically tolerate some temperate waters (Figueira et al. 2009), and that larval supply may support colonisation of many species (Figueira & Booth 2010), some temperate reef habitats may limit settlement and recruitment of tropical fishes (Feary et al. 2014). One of the most obvious impacts of temperate reef habitats on tropical fish range-expansions is the absence of coral habitat there, which may strongly restrict recruitment of obligate coral-feeding fishes (i.e. corallivores, hereinafter termed ‘trophic specialists’), which depend on live corymbose corals for food and shelter (Feary et al. 2014). But in temperate regions where corals are colonising with warming coastal waters, such as the western Japanese coast of Shikoku (Nakamura et al.

2013, Vergés et al. 2014), habitat-forming corals may strongly influence where and when corallivores recruit and survive (Soeparno et al. 2013). In contrast, absence of coral resources may not restrict recruitment of trophic generalists, such as those that graze on algae or prey upon benthic invertebrates or fishes in temperate reefs (Nakamura et al. 2013, Feary et al. 2014). However, even for dietary generalists, fine-scale variance in the structure of temperate reefs arising from macroalgal cover may influence recruitment, at least on fine spatial scales (Beck 2014, Feary et al. 2014).

Within coastal reef systems, differences in habitat characteristics between exposed and sheltered reef environments may strongly influence where tropical fishes colonise temperate latitudes. Ocean waves may structure the diversity and composition of marine communities by interacting with an organism’s physiological tolerance and morphology (McQuaid & Branch 1985, Friedlander et al. 2003, Fulton & Bellwood 2004, Munks et al. 2015). This is shown within tropical reef fishes, where swimming performance often varies considerably amongst families during their early life stages, resulting from interspecific variance in body/fin shape and size (Fisher et al. 2005), which may influence habitat choice and survival after settlement by interacting with wave action (Fulton & Bellwood 2004). Wave energy influences the diversity and abundance of reef fishes across a range of tropical and temperate biomes, with fish assemblages in shallow waters (where wave action is strongest) often more abundant and diverse in wave-sheltered than in wave-exposed reef aspects (Friedlander et al. 2003, Fulton & Bellwood 2004, Depczynski & Bellwood 2005). Wave action may also influence recruitment of some tropical fishes by determining habitat distribution and composition (Floeter et al. 2007, Santin & Willis 2007). Certainly, wave action strongly shapes the structure and composition of many corymbose coral and macroalgal communities (Fowler-Walker et al. 2006, Madin et al. 2014), which likely influences the distribution of fishes that depend on these habitat-formers for resources (Jones 1992, Feary et al. 2007a). Nevertheless, recruitment success of tropical reef fishes within temperate regions may be organised by a range of abiotic and biotic factors that covary with the degree of wave action. Embayed temperate reefs in coastal temperate regions may be substantially influenced by freshwater runoff and/or tides, which may restrict recruitment of some tropical fishes where water parameters, such as turbidity, oxygen and temperature, exceed their physiological tolerance (Figueira

et al. 2009, Wenger et al. 2012). Near-shore embayed reefs also often contain high piscivore densities, leading to high mortality of tropical fishes during recruitment (Baker & Sheaves 2005). Hence, many biotic and abiotic factors may differ between embayed and exposed temperate reef habitats, posing potential constraints to tropical fish recruitment, and ultimately, impact their distributional response to sea surface warming.

The influence of embayed and exposed shallow temperate reefs, and the abiotic and biotic factors differing between them, on recruitment success of tropical reef fishes was explored by underwater visual surveys within southeastern (SE) Australia and western (W) Japan. Since both regions are forefronts of range expansion for many tropical fishes (Feary et al. 2014), they provide a unique opportunity to explore how temperate reef habitats structure their recruitment success. Each summer, expatriating tropical reef fish larvae (hereafter termed 'vagrants') are transported 100s to 1000s of km into these temperate regions by poleward-flowing boundary currents (East Australian Current [EAC] in Australia, and the Kuroshio Current in Japan), where they recruit to coastal reef habitats (Booth et al. 2007, Feary et al. 2014). Although coastal waters in SE Australia and W Japan are warming at over twice the global average (Wu et al. 2012), and may facilitate colonisation of tropical fishes by reducing severity of winter water temperatures (Figueira & Booth 2010), variability in physical and abiotic stressors associated with embayed and exposed temperate reefs may limit recruitment. Due to variance in the biophysical nature between embayed and exposed temperate reefs, we predicted differences in the density, richness, diversity and composition of vagrant fish assemblages between these habitats. For corallivores, reliant on corals for food, we expected recruitment success to be also strongly associated with the presence, distribution and structure of live coral communities. We then explored whether wave exposure of reefs influences tropical fish recruitment similarly in tropical and temperate regions, by surveying focal tropical fishes on exposed and protected aspects of the coral reef One Tree Island (OTI), Great Barrier Reef.

MATERIALS AND METHODS

Study locations

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

reefs, new recruit and early juvenile tropical fishes were surveyed at 4 locations in SE Australia separated by 100s of km: Nambucca (NB), Camden (CA), Forster (FO) and Swansea (SW) (Fig. 1). Individuals were identified as recruits of the present season (i.e. young-of-the-year) and juveniles based on family-specific length-age criteria established by Booth et al. (2007). Within W Japan, vagrant fishes were surveyed in Otsuki (OT), Yokonami (YO), Tei (TE) and Nahari (NA), separated by 10s to 100s of km (Fig. 1). Within each location, vagrant fishes were surveyed within 2 or 3 embayed and exposed rocky reef sites, separated by >100 m (the maximum distance between an embayed and exposed site was approx. 5 km). Exceptions were OT, where all sites were embayed, and TE, where there was only 1 embayed site. Embayed reefs in SE Australia were positioned within estuary mouths (predominantly formed by artificial rockwalls) and on lee-sides of headlands, while embayed reefs surveyed in W Japan were all naturally formed, with little freshwater influence. Exposed reefs in both regions were exposed or partially exposed to ocean swell (i.e. >15° of exposure to the open ocean; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m546p197_supp.pdf). In total, 42 and 21 visual surveys (30 min each) were undertaken in SE Australia and W Japan, respectively.

Density and distribution of tropical fishes in temperate reefs

Underwater visual surveys were conducted to examine the richness, diversity and density of new recruit and juvenile vagrant tropical fishes on exposed and embayed temperate reef habitats of SE Australia and W Japan (Fig. 1). Both regions hold subtidal coastal reefs prone to moderate to high wave energy (Young et al. 2011). Surveys were conducted during recruitment of tropical fishes in both 2011 and 2012 in SE Australia (i.e. March to May) and 2013 in W Japan (i.e. June to November) (Booth et al. 2007, Figueira et al. 2009, Nakamura et al. 2013). Vagrant fishes were surveyed by snorkelling during 30 min timed swims in 0–4 m water depth. To standardise survey effort and calculate fish densities, paths swam were measured at 5 s intervals by towing a GPS (Garmin™ GPS 60; accuracy: 3 m) at a fixed distance (3 m), following Beck et al. (2014). This survey method allows greater detection of sparsely distributed vagrant fishes than traditional belt transects since it is more time-efficient and pro-

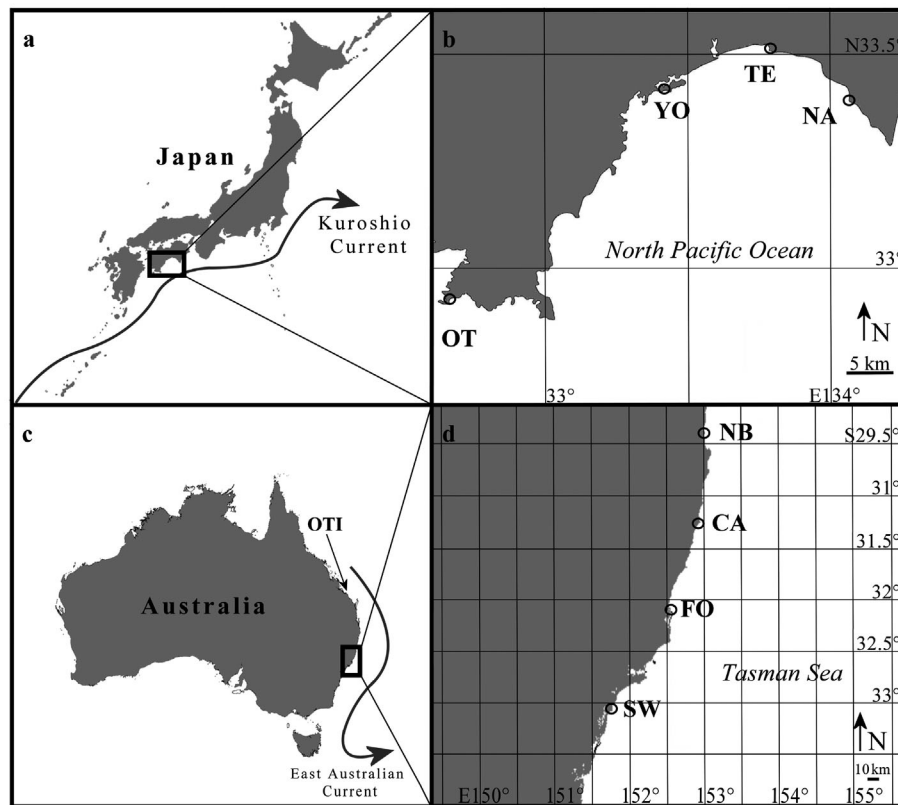


Fig. 1. Survey locations within (a,b) western (W) Japan and (c,d) southeastern (SE) Australia. Within each location, 2–3 underwater visual surveys (30 min each) of vagrant tropical fishes were conducted in both embayed and exposed temperate reefs. Vagrant tropical fishes are supplied through summer to temperate reefs by the poleward-flowing (a) Kuroshio and (c) East Australian Currents around Japan and Australia, respectively (flow path and direction illustrated by arrows). Surveys conducted for 2 recruitment seasons in SE Australia and 1 in W Japan. CA = Camden Haven, FO = Forster, NA = Nahari, NB = Nambucca, OT = Otsuki, SW = Swansea, TE = Tei, YO = Yokonami. Tropical fish recruitment was also studied on exposed and sheltered aspects of (c) a coral reef, One Tree Island (OTI), Great Barrier Reef (see Fig. S2 in the Supplement)

vides reliable density estimates (Beck et al. 2014). Starting positions and swim patterns were haphazardly determined prior to surveys. All tropical fishes observed within 1 m either side and in front of the observer were recorded by hand. Trophic groupings were determined according to Froese & Pauly (2015), the IUCN Red List of Threatened Species (v.2015.2, www.iucnredlist.org) and a review of the scientific literature (see Table S1 in the Supplement). Where known, we assigned trophic groups based on feeding preferences during early life stages and/or within temperate reef habitats. Tropical 'vagrant' species were defined by the latitudinal range of a species: only found as breeding-aged adults between the Tropics of Cancer and Capricorn, as per Feary et al. (2014), 23° 27' N and S, respectively (distribution data from Kuitert 1993, Froese & Pauly 2015, IUCN Red List maps v.2015.2; see Table S1 in the Supplement).

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

To test whether wave exposure influences tropical fish recruitment similarly in temperate and tropical reefs, tropical fish assemblages were also surveyed on the coral reef OTI, Great Barrier Reef, Australia (Fig. 1). Replicate half-hour roaming surveys (using the same method described in the previous subsection) were conducted in exposed (reef flats exposed >15° to the open ocean) and protected reef habitats (wave-oblique reef flats with <15° exposure to open ocean) during summer recruitment seasons (March–June) of both 2011 and 2012 (see Fig. S1 in the Supplement), counting new recruits and juveniles of species observed within temperate SE Australian reefs during the above surveys. Nine and 23 surveys were conducted in exposed and protected reef aspects, respectively.

All surveys were conducted by H.J.B. at a constant speed between 09:00 and 17:00 h when water visibility was >5 m and swell was <1 m. These conditions were chosen to minimise any potential bias to visual surveys associated with inherent differences in wave action and visibility between exposed and embayed reefs.

Temperate reef habitat variables

To assess the roles of biophysical factors in determining the composition and density of vagrant fishes amongst locations and reef habitats in temperate regions, we recorded *in situ* density of temperate predatory fishes (identified according to Froese & Pauly 2015) within each site using timed swim surveys (as above; Beck et al. 2014), water temperature (measured at half-hour to hourly intervals by permanent loggers installed at ~2.5 m below MSL; SE Australia only), topographic complexity (using the ratio of surface distance to linear distance of a 5 m chain within 10 haphazardly selected areas within each site), and substrate composition (within 30 haphazardly selected 0.25 m² quadrats, benthic habitats quantified using Underwood et al. 1991 and Bradbury & Young 1981). Wave-exposure values for sites were calculated using a fetch-based index (Hill et al. 2010) with MicroStation™ GIS. Fetch lines were constructed with 7.5° spacing around the midpoint of survey sites to a maximum of 650 km (i.e. minimum fetch distance for fully developed seas to form) and divided by the sum of fetch distances by the maximum possible total; index units are dimensionless, with exposure increasing from 0 to a maximum exposure value of 1 (Hill et al. 2010; see Fig. S1 in our Supplement). As a proxy for water parameters subjected to fishes within estuaries (e.g. nutrients, turbidity, oxygen), Google Earth™ was used to calculate the distance of each site from the mouth of the nearest estuary (i.e. minimum Manhattan distance).

Statistical analyses

Overall assemblage densities (i.e. individuals per 1000 m²) and species richness (i.e. total number of species per 1000 m²) for vagrant fish assemblages were compared between habitats (exposed, embayed: fixed), recruitment years (2011, 2012: random; Australia only), between countries (Japan and Australia: random) and among locations (locations nested within respective country: random) using uni-

variate permutational analysis of variance (based on Euclidean distances between sample data; Type III sums of squares; 9999 permutations under the reduced model; Anderson 2001). Density and species richness were calculated as total number of individuals and species divided by the area searched within each replicate survey, respectively (see Table S2 in the Supplement; both metrics expressed per 1000 m² due to rarity of many species). OT was excluded from analyses of population richness, diversity and densities since no exposed sites were surveyed there, but OT was included when exploring environmental influences on vagrant recruitment.

K-dominance plots were used to test whether species and trophic group diversity of vagrant fish assemblages differed between embayed and exposed reef habitats, years (SE Australia only) and locations (Clarke & Gorley 2006). As a diversity measure, *K*-dominance plots better account for species and trophic group evenness than single-value diversity indexes (Lambhead et al. 1983). *K*-dominance plots were constructed individually for survey replicates by cumulatively ranking 4th-root transformed species and trophic group densities, expressed as a percentage of all species density, in decreasing order of their density. Fourth-root transformations were used since there were many low and some high fish counts within survey replicates (Quinn & Keough 2002). Pairwise distances between values in *K*-dominance plots were calculated using DOMDIS (PRIMER v.6) (Clarke 1990, Clarke & Gorley 2006). *K*-dominance curves, both for species and trophic diversity, were compared between years (SE Australia only), habitats and amongst locations by permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008; same design as described in the paragraph above). Trophic groups that were important contributors to dissimilarity of fish assemblages between habitats were identified using the similarity percentages routine (SIMPER; Clarke 1993), then graphically explored by principal coordinate analysis (PCO) using Spearman's rank correlation (r_s). *A priori*, we considered species and trophic groups with $\bar{\delta}_i/SD(\bar{\delta}) > 1$, and % $\bar{\delta}_i > 4\%$ and 10% , respectively, as important contributors to overall dissimilarity between habitats, where $\bar{\delta}_i$ is the average contribution of the *i*th trophic group to the overall dissimilarity ($\bar{\delta}$) between the 2 groups and SD is standard deviation. Densities of these species and trophic groups, found by SIMPER as important contributors to variance in fish assemblages, were then compared between years (SE Australia only), countries, habitats and locations using PERMANOVA (as above).

Species found to be important (by SIMPER) in distinguishing assemblages between exposed and embayed temperate reefs were compared between shelter and exposed habitats of a coral reef, OTI. Densities of these species were compared between these reef habitats by PERMANOVA, including the factors year (random), exposure (protected and exposed reef aspects: fixed) and site (nested within exposure: random).

All survey data were inspected for homogeneity of variance using the PERMDISP procedure (PRIMER™), with data $\ln(x + 1)$, square- or 4th-root transformed where required. Data was converted to presence/absence prior to analysis where variances were still non-homogeneous following these transformations. PERMANOVA was used as it is more robust to heterogeneity of variances and assumptions of data normality than parametric analyses (Underwood 1997, Anderson & Walsh 2013). For all univariate analyses, factors were pooled with the residual, pertaining to the rule of pooling when $p > 0.25$ (Underwood 1997). Post hoc pairwise PERMANOVA tests were performed to identify differences in assemblage densities, richness and diversity amongst locations.

To determine environmental variables (i.e. minimum, maximum and mean water temperature, habitat rugosity, benthic composition, predator density, distance from estuary mouth, and latitude) that best predicted variance in trophic generalist and specialist fish assemblages between embayed and exposed temperate reef habitats, the best-fit DistLM procedure (PERMANOVA™; 9999 permutations pertaining to the Akaike information criterion with a correction for finite sample sizes, AIC_c ; maximum of 10 variables) was conducted using Bray-Curtis similarity measures on 4th-root transformed fish abundance data for all countries, years, locations, habitats and species (Clarke & Gorley 2006); trophic specialists (corallivores) were analysed separately, expecting coral habitats to be more important for their recruitment. Biophysical factors driving variance in vagrant assemblages were also analysed separately between SE Australia and W Japan, since water temperature was only measured in SE Australia. Moreover, W Japanese reefs are currently at a later stage of tropicalisation than SE Australia (Nakamura et al. 2013, Vergés et al. 2014), so factors impacting recruitment success of fishes may differ between these regions. We con-

sidered the most parsimonious model as the combination of environmental variables with an AIC_c value within 2 units of the overall best solution with the least number of variables (Burnham & Anderson 2002). Environmental data were checked for multicollinearity and dispersion using draftsman plots, $\ln(x + 1)$ or square-root transformed where required, then normalised prior to analysis (PRIMER v.6). Relationships amongst environmental data (post-transformation) were also checked for linearity prior to analysis. *A priori*, $p < 0.05$ was the set level of significance for all analyses.

RESULTS

A total of 4854 vagrant tropical fishes were surveyed within SE Australia and W Japan, encompassing 13 families and 69 species (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m546p197_supp.pdf). There was a 26.1% overlap in species between countries, with 6 families (i.e. Acanthuridae, Chaetodontidae, Labridae, Ostraciidae, Pomacentridae and Zanclidae) encompassing 18 species observed in both countries.

Association of vagrant assemblage with embayed and exposed temperate reefs

Overall density (total individuals), species and trophic diversity (K -dominance) and species richness (total species) of vagrant fishes were significantly greater in embayed than exposed reefs (PERMANOVA, $p < 0.05$ for these 4 metrics; Table 1, Fig. 2). Density and richness of vagrants was over 4.9 and 2.4 times greater, respectively, within embayed than

Table 1. PERMANOVA testing for differences in total vagrant tropical fish assemblage density, richness and diversity (i.e. K -dominance) between embayed and exposed temperate reefs (H = Habitat), locations (L = location, C = country) and years (Australia only), and interactions amongst these factors, within southeastern Australia and western Japan. Significant differences ($p < 0.05$) in **bold**. Where a variable was $p > 0.25$, it was pooled with the residual

Parameter	H			Other variables' p-values			
	Pseudo- F	df	p	C	L(C)	C × H	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

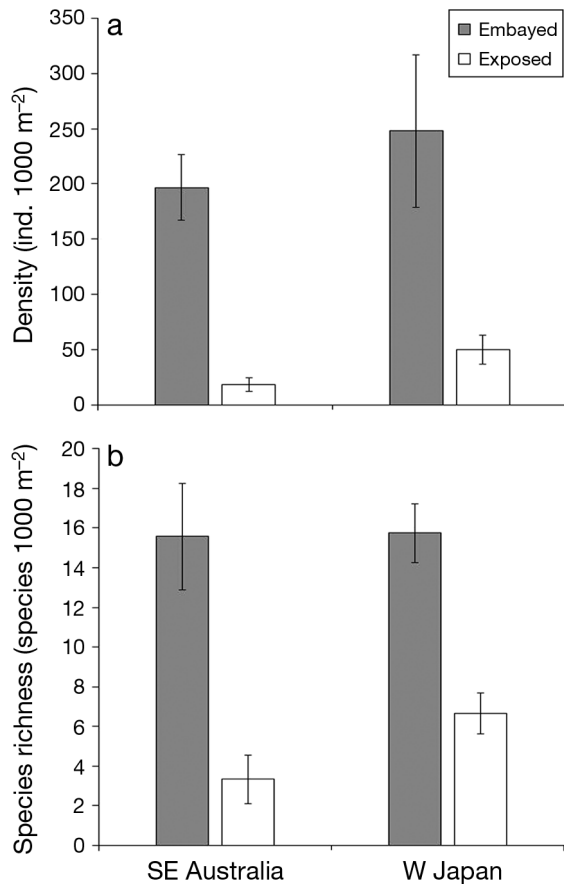


Fig. 2. Mean (\pm SE) (a) density and (b) species richness of vagrant tropical fishes within embayed and exposed reef habitats of southeastern (SE) Australia and western (W) Japan

exposed reefs for SE Australia and W Japan, after pooling data at the year (SE Australia only), location and site level (Fig. 2). Years surveyed were pooled prior to analysis for SE Australia since the factor 'year' did not significantly explain patterns of vagrant density, richness nor diversity (PERMANOVA, $p > 0.3$ for these metrics). All other interactions between factors within models were not significant ($p > 0.05$; Table 1).

Species and trophic composition of assemblages in embayed and exposed temperate reefs

Vagrant species assemblages differed between exposed and protected habitats in SE Australia (PERMANOVA; $p = 0.03$; Table 1) and (but not quite significant) W Japan (PERMANOVA, $p = 0.08$; Table 1). There was clear separation of species composition of assemblages between embayed and exposed habitats along PCO Axis 1, whilst species assemblages

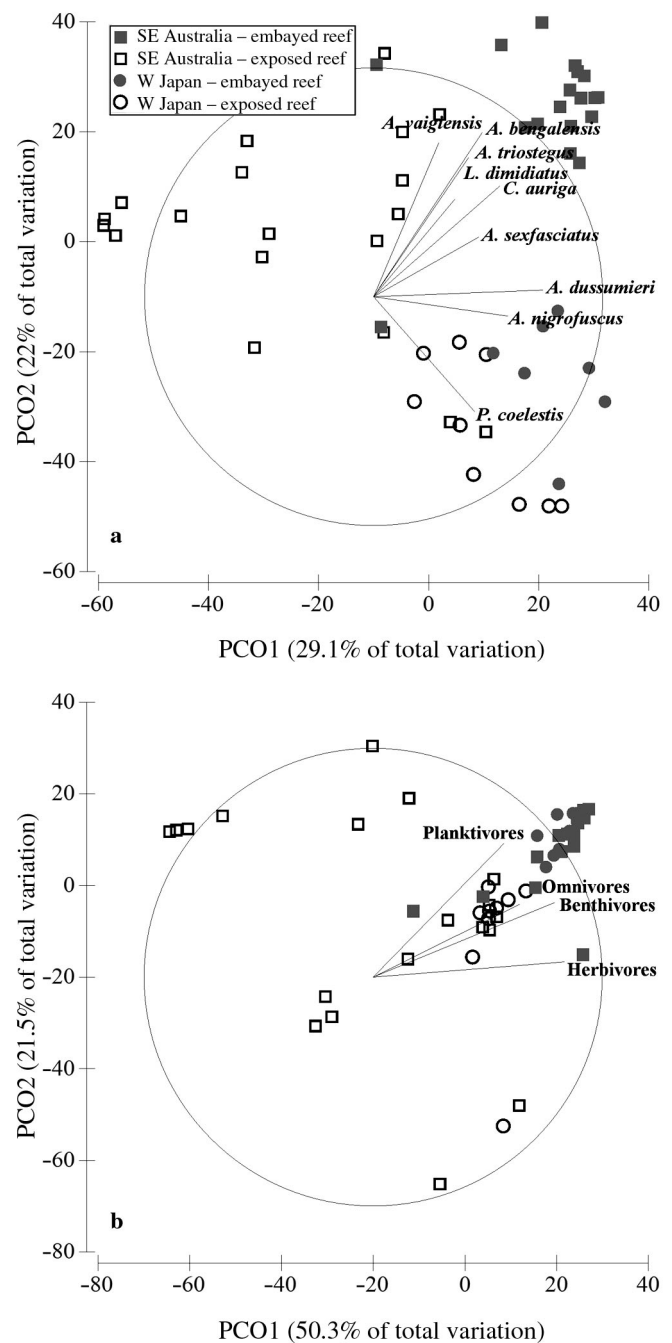


Fig. 3. Principal coordinate analysis (PCO) of vagrant tropical fish (a) species (*Abudefduf bengalensis*, *Abudefduf sexfasciatus*, *Abudefduf vaigiensis*, *Acanthurus dussumieri*, *Acanthurus nigrofuscus*, *Acanthurus triostegus*, *Chaetodon auriga*, *Labroides dimidiatus*, *Pomacentrus coelestis*) and (b) trophic groups within embayed and exposed reefs of southeastern (SE) Australia and western (W) Japan. Vectors overlaid display the primary (a) species and (b) diet groups responsible for division of sites along PCO Axis 1 (PCO1), determined by SIMPER analysis (see 'Results'). $N = 40$ and 21 replicate 30 min timed swims within SE Australia and W Japan, respectively. PCO2 = PCO Axis 2

were separated between countries along PCO Axis 2, explaining 29.1 and 21% of variance, respectively (Fig. 3a). In reducing order, *Abudefduf vaigiensis*, *Pomacentrus coelestis*, *Acanthurus dussumieri*, *Chaetodon auriga*, *Acanthurus nigrofuscus*, *Abudefduf bengalensis*, *Labroides dimidiatus*, *Abudefduf sexfasciatus* and *Acanthurus triostegus* primarily accounted for division of assemblages between habitats (SIMPER; % $\bar{\delta}_i > 4\%$, $\bar{\delta}_i/SD(\bar{\delta}_i) > 1$) and were positively associated with PCO Axis 1 ($r_S > 0.28$, $p < 0.05$ for these species; Fig. 3a). All 9 species were in significantly greater densities or more frequently observed in embayed than exposed reefs (see Table S3 in the Supplement).

Trophic generalists comprised entire vagrant assemblages in SE Australia and 98% of assemblages in W Japan. Planktivores were the most common generalist trophic guild in SE Australia (55.7%) and W Japan (86.9%), followed by herbivores (23.5% in Australia; 4.7% in Japan), benthivores (12% in Australia; 4.3% in Japan), omnivores (4.8% in Australia; 1.6% in Japan), parasite cleaners (1.5% in Australia; 0.3% in Japan) and piscivores (1.2% in Australia; 0.03% in Japan). Corallivores made up the remaining ~2% of vagrant assemblages in W Japan, but were not recorded within SE Australia.

Vagrant dietary preferences differed significantly between embayed and exposed reefs (PERMANOVA, $p = 0.006$; Table 1). Trophic composition of assemblages was separated between embayed and exposed habitats along PCO Axis 1, explaining 50.3% of variance in assemblages (Fig. 3b), whilst dietary composition of assemblages were separated between countries along Axis 2, explaining 21.5% of data variance (Fig. 3b). Of the habitat generalists, planktivores, herbivores, benthivores and omnivores primarily accounted for division of assemblages between habitats (SIMPER; % $\bar{\delta}_i > 10\%$, $\bar{\delta}_i/SD(\bar{\delta}_i) > 1$) and were positively associated with PCO Axis 1 ($r_S > 0.57$, $p \leq 0.01$ for each trophic group; Fig. 3b).

Embayed reefs supported greater densities of planktivores ($F_{1,42} = 45.5$, $p = 0.001$) and benthivores ($F_{1,42} = 53.6$, $p = 0.001$) than exposed reefs, with this consistent in SE Australia and W Japan (see Table S3 in the Supplement). Herbivores were in greater densities in SE Australian and W Japanese embayed reefs ($t = 7.05$, $p = 0.01$ and $t = 8.8$, $p = 0.03$, respectively), but omnivores were in greater densities in embayed than exposed reefs in SE Australia ($t = 7.36$, $p = 0.001$) but not W Japan ($t = 0.93$, $p = 0.37$). For herbivores and omnivores, there was a significant interaction between exposure and country ($F_{1,42} = 4.09$, $p = 0.02$ and $F_{1,42} = 8.52$, $p = 0.04$, respectively).

Dietary specialists (corallivores) were in significantly greater densities in embayed than exposed Japanese reefs ($F_{1,14} = 5.02$, $p = 0.006$).

Interactions of the factor 'habitat' with other terms in models were nonsignificant for all trophic groups and species reported here (i.e. $p > 0.05$ for all interactions between 'habitat' and 'location' and 'year' [SE Australia only]). Densities of planktivores, herbivores, benthivores and omnivores did not significantly differ between survey years in SE Australia ($p > 0.34$ for these trophic groups), allowing abundance data to be pooled for the above trophic analyses.

Influence of wave exposure on distribution of species on a coral reef

Of species that explained considerable variance in assemblages between embayed and exposed temperate reefs (see SIMPER result in the previous subsection), *A. sexfasciatus* and *L. dimidiatus* were in significantly greater densities in protected than exposed aspects of OTI ($F_{1,29} = 9.16$, $p = 0.015$ and $F_{1,30} = 4.69$, $p = 0.04$, respectively). *A. nigrofuscus* and *C. auriga* were only found on wave-protected reef ($n = 6$ and 47 individuals, respectively). There was no difference in densities of *P. coelestis* and *A. triostegus* between exposed and protected reefs; $F_{1,28} = 0.3$, $p = 0.84$ and $F_{1,28} = 0.7$, $p = 0.67$, respectively. *A. vaigiensis* was in significantly greater densities in exposed than protected reef aspects in 2011 ($t = 2.43$, $p = 0.012$), but not in 2012 ($t = 1.02$, $p = 0.36$); influence of exposure on *A. vaigiensis* densities depended on year ($F_{1,28} = 5.25$, $p = 0.03$). *A. bengalensis* and *A. dussumieri* were not detected. All interaction terms including the term 'reef exposure' not reported above were not significant (i.e. $p > 0.1$).

Environmental correlates and recruitment of tropical fishes to temperate reefs

Wave exposure best predicted variance in trophic generalist assemblages between embayed and exposed reefs within SE Australia (30.17%; $AIC_c = 297.53$) and W Japan (16.44%; $AIC_c = 157.24$). The richness and density of generalist assemblages in both countries increased monotonically with reducing wave-exposure of reefs (Fig. 4). In W Japan, wave exposure, independent of any other measured factor, best explained variance in the composition of trophic generalists (see Table S4 in the Supplement). In SE Australia, the overall best combination of fac-

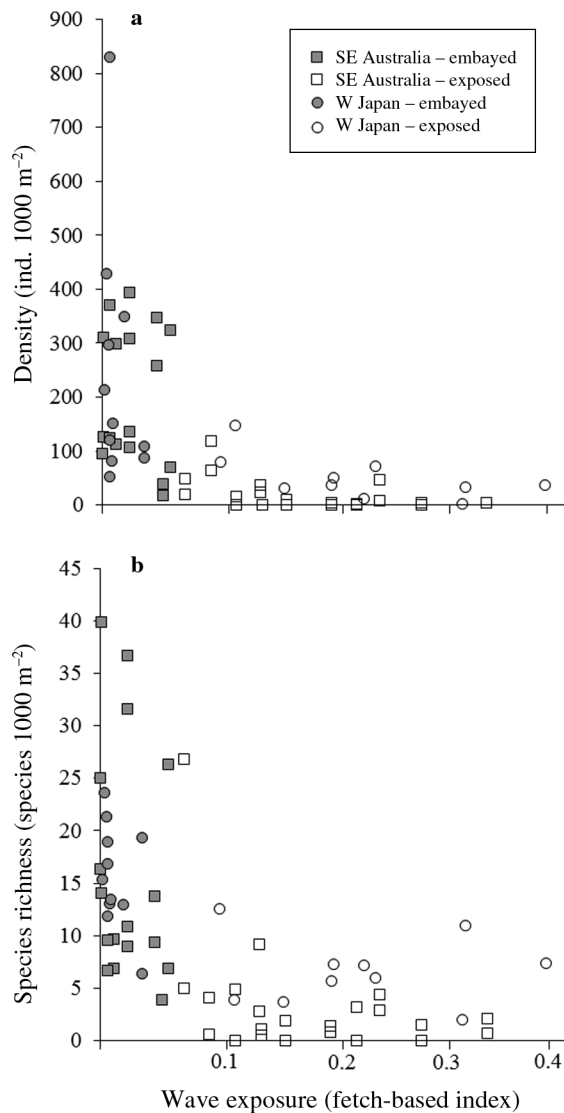


Fig. 4. Correlation of (a) densities and (b) species richness of tropical vagrant fish assemblages against wave exposure of sites within southeastern (SE) Australia and western (W) Japan. Fetch-based wave exposure indices calculated according to Hill et al. (2010). $N = 40$ and 21 replicate 30 min timed 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

tors explaining variance in vagrant assemblage also included predator density (22%) and latitude (7.5%) ($AIC_c = 294.06$; see Tables S4 & S5 in the Supplement). Richness and density of SE Australian generalist assemblages was significantly and positively correlated with predator density (density: $r_s = 0.64$, $p = 0.001$, richness: $r_s = 0.61$, $p = 0.001$; see Table S6 in the Supplement), but there was no significant corre-

lation with latitude (density: $r_s = -0.15$, $p = 0.35$; richness: $r_s = -0.09$, $p = 0.59$).

In W Japan, the presence of branching coral cover (39.9%) and sand (1.8%) best explained differences in densities of corallivore fishes amongst sites ($AIC_c = 129.15$; see Tables S4 & S5 in the Supplement). Richness and densities of corallivores were significantly and positively correlated with branching coral cover (density: $r_s = 0.74$, $p < 0.001$; richness: $r_s = 0.72$, $p < 0.001$; Fig. 5a), but there was no significant correlation with sand (density: $r_s = 0.07$, $p > 0.05$; richness: $r_s = 0.09$, $p > 0.05$). We found branching corals almost exclusively within highly embayed reefs; sites with branching corals had fetch-based wave exposure index values < 0.1 (our Fig. 5b; Hill et al. 2010).

DISCUSSION

To expand their range poleward with warming waters, some tropical fishes require reefs at temperate latitudes that support their recruitment (Figueira & Booth 2010). We show that availability of wave-sheltered reefs may strongly influence recruitment of many tropical reef fishes in temperate coastal regions. Specifically, we found that the density, species richness, and species and trophic diversity of newly recruited tropical fish communities was substantially higher on embayed than exposed temperate reefs. This result was consistent within both SE Australia (across 2 yr) and W Japan (during 1 yr). Prior to this study, larval supply (Booth et al. 2007, Soeparno et al. 2012), water temperatures (Figueira et al. 2009, Figueira & Booth 2010) and species traits (e.g. life history and diet: Luiz et al. 2013, Feary et al. 2014) were considered the major factors influencing range expansions of tropical fishes into temperate regions. However, our results suggest that even if tropical fishes are readily supplied as larvae to mid-latitude temperate regions where they may physiologically tolerate local water temperatures (Figueira et al. 2009) and access necessary resources (Feary et al. 2014), recruitment success (an important step to colonisation; Bates et al. 2014) may depend on the availability of moderately to highly embayed temperate reefs.

Of the environmental variables measured, wave exposure (estimated by a fetch-based index) was the primary factor organising tropical fish recruitment between embayed and exposed temperate reefs in our study. We showed that the density and richness of tropical fish assemblages was positively correlated with the degree of protection from wave action. This

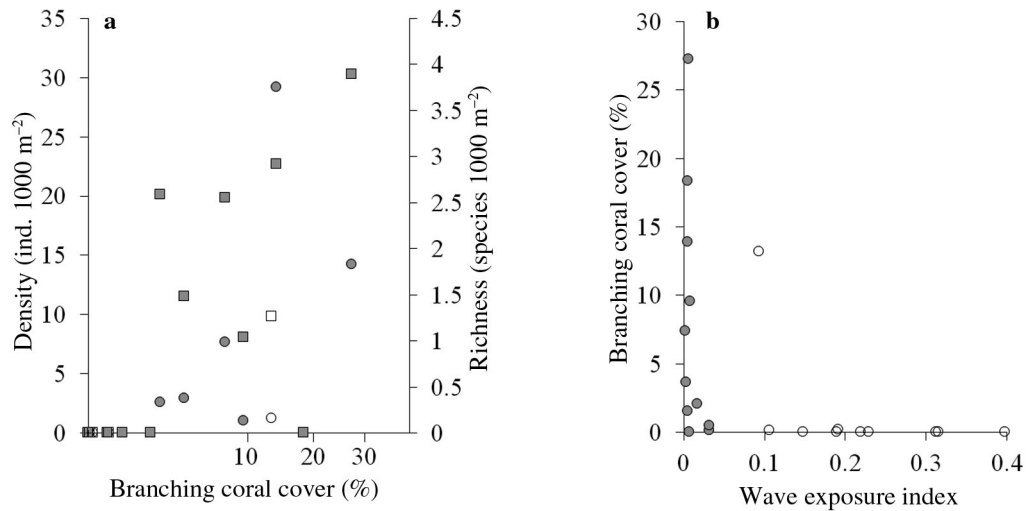


Fig. 5. Regression of (a) densities (circles, left axis) and species richness (squares, right axis) of corallivores with mean branching coral cover of reefs in embayed (grey markers) and exposed reef (open markers) of western (W) Japan, and (b) branching coral cover with wave exposure of embayed (grey markers) and exposed (open markers) sites within W Japan (N = 21 sites). Within each site, fishes were quantified by one 30 min timed swim survey and coral cover was quantified in 20 haphazardly arranged 0.5 m² quadrats. 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

influence of estimated wave exposure on tropical fish recruitment among temperate reefs appeared to outweigh other measured abiotic and biotic factors, shown to strongly determine reef fish recruitment success elsewhere. For example, habitat complexity, which may influence survival of reef fish recruits by determining refuge from predators, competition strength and/or environmental stress (Almany 2004, Johansen et al. 2008), did not explain differences in tropical fishes assemblages among sites in the present study. Water temperatures (at least in SE Australia) and distance from river mouth (i.e. estuarine influence) also did not explain such strong association with embayed reefs, despite the greater potential for physiological stress associated with high fluxes in salinity, oxygen, water temperature and nutrients associated with low flushing and rainfall influences that occur within these habitats (Figueira & Booth 2010, Wenger et al. 2012). Furthermore, although there is evidence that native predators may constrain colonisation of range-expanding marine fishes (Bates et al. 2013, Luiz et al. 2013, Beck et al. 2016), our results showed that the diversity and density of temperate predators also appeared to have little influence on tropical fish recruitment to embayed reefs, as densities of tropical fish recruits were positively correlated with predators in SE Australia, whilst vagrant assemblage composition did not vary with predator densities in W Japan (see Table S6 in the Supplement at [www.int-res.com/](http://www.int-res.com/articles/suppl/m546p197_supp.pdf)

[articles/suppl/m546p197_supp.pdf](http://www.int-res.com/articles/suppl/m546p197_supp.pdf)). Moreover, negative influences of wave exposure on tropical fish recruitment may have been underestimated here because surveys were conducted during periods of low swell (i.e. <1 m). Hence, we did not consider periods of high wave energy, which can occur during summer recruitment of tropical fishes in SE Australia (Short & Trenaman 1992) and W Japan (Sasaki et al. 2005), and may intermittently constrain reef fish populations from establishing in wave-exposed reefs (e.g. Friedlander & Parrish 1998).

Wave exposure appeared to have a stronger influence on tropical fish recruitment than latitude, suggesting habitat composition of temperate reefs may strongly influence colonisation, regardless of larval supply rates. Although larval supply may be spatially patchy throughout the W Japanese coast due to the sometimes almost perpendicular orientation of this coastline to the Kuroshio current and chaotic near-shore flow (Waseda & Mitsudera 2002), the East Australian Current (EAC) typically flows along the SE Australian coast (Fig. 1), leading to reducing vagrant diversity and density from north to south (Booth et al. 2007). Nevertheless, wave exposure of temperate reefs in SE Australia better explained spatial variation in vagrant assemblages among sites than latitude, at least on spatial scales of 100s of m to 5 km (studied here). It is possible that latitudinal trends in larval supply may be masked by sporadic, but reoc-

curing eddies in SE Australia (Matis et al. 2014), which form where the EAC encounters particular topographic features of the continental shelf and coastline in this region (Ridgway & Dunn 2003). However, patchiness of embayed and exposed reefs is at a much smaller scale than eddies (<5 km vs. 100s of km; Ridgway & Dunn 2003), so eddy effects did not confound our results. Hence, although larval supply is an important precursor/prerequisite to range expansions of tropical fishes, the influence of temperate reef habitats on recruitment success, such as exposed and embayed reefs, may ultimately control/limit colonisation at local scales.

Effects of wave exposure of temperate reefs on tropical fish recruitment may be mediated through wave motion effect on fish swimming ability. Many recruiting tropical fishes seek shelter from hydrodynamic stress to reduce energetic demand (Johansen et al. 2008) and/or to feed more efficiently (MacKenzie & Kjørboe 2000). Although there is considerable variance in swimming performance within and among tropical fish families (Fulton & Bellwood 2004, 2005, Fulton et al. 2005), most tropical fishes, independent of their swimming performance, may be forced into sheltered aspects of shallow reefs during periods of high swell activity (Friedlander et al. 2003, Fulton & Bellwood 2004). Alternatively, fishes may avoid hydrodynamic stress associated with wave action by moving to deeper reefs (Fulton & Bellwood 2004). However, a depth response to wave action by these range-expanding fishes was unlikely, at least at the forefront of their redistribution, since isotherms are typically warmer toward the surface, which best supports colonisation success of such warm-adapted, range-expanding species (Bates et al. 2014). This hypothesis was supported by a pilot study which found that tropical fishes assemblages were richer and more diverse in shallow (<4 m) than adjacent deeper (>4 m) reef, in at least 1 SE Australian site (H. J. Beck unpubl. data). Hence, the high wave energy of SE Australian and W Japanese reefs in this study may have been sufficient to force the majority of tropical fish recruits into highly wave-sheltered regions, and exclude them from using exposed sites due to the wave action exceeding these fishes' physiological tolerance for water movement, while also limiting their access to suitable resources. Nevertheless, many tropical fishes are highly mobile during their early life stages (Fisher et al. 2005, but see Lewis 1997), so some species may recruit to exposed reefs during calm conditions, moving to more sheltered reefs when ocean swells increased. For instance,

sheltering of reef fishes in response to high wave action was recently recorded by Munks et al. (2015), with the diversity and abundance of many reef fishes reducing on temperate reefs during periods of high swell activity. Although a strong swimming ability has been found to potentially benefit range expansion of marine fishes by aiding dispersal (Sunday et al. 2015), our results suggests that swimming abilities could further influence their colonisation success on fine spatial scales by determining the suitability of reef habitats for recruitment.

One salient result was a difference in habitat association of some damselfishes and surgeonfishes between their natal, tropical range and expanding, temperate range. Although *Abudefduf sexfasciatus*, *Labroides dimidiatus*, *Acanthurus nigrofuscus* and *Chaetodon auriga* associated with embayed reef on both coral and temperate reefs, *Abudefduf vaigiensis*, *Pomacentrus coelestis* and *Acanthurus triostegus* had a greater association with exposed reef in the coral reef than in temperate regions. Such a difference in habitat association of fishes between latitudes may be due to differences in hydrodynamic forcing between coral and temperate-rocky reef. For example, at least within shallow waters, wave energy may dissipate rapidly across a coral reef flat, as opposed to a temperate reef, where the surf zone is typically shorter, and hence potentially prone to higher wave energy on average (Fulton & Bellwood 2004, Fulton et al. 2005). However, physiological responses of tropical fishes to cool water temperatures may also account for differences in habitat use between latitudes. For example, the swimming performance of *A. vaigiensis* may be substantially reduced at temperate latitudes by suboptimal water temperatures (Figueira et al. 2009), potentially leading to greater sheltering from swell on temperate reefs. Such sheltering responses to cool waters are apparent even for some temperate fishes, which are more thermally tolerant to temperate waters than tropical species. For instance, although capable of high swimming performance, due to their body morphology and fin shapes, many temperate labrids still opt for sheltered temperate reefs, which is thought to result from a physiological response to cool temperate waters (Fulton & Bellwood 2004). Further work is required to better understand how swimming performance, thermal thresholds and other intrinsic characteristics of tropical fishes shape interspecific patterns of recruitment at temperate latitudes. This work should involve empirically tested wave energy models, and consider seasonal and interannual fluxes in wave energy and water temperatures.

As well as directly structuring tropical fish recruitment, wave action appeared to further influence colonisation success by determining the distribution and morphology of coral habitats at temperate latitudes. At least in W Japan, densities and richness of corallivore fishes were positively associated with branching corals. In SE Australia, corallivores were not detected, likely due to an absence of hard tropical corals in this region (Feary et al. 2014). This was consistent with our expectation, since corallivores typically depend on hard branching corals for food, but also living space and refuge (Syms & Jones 2000, Feary et al. 2007b). However, branching corals were exclusive to highly embayed W Japanese reefs (i.e. wave exposure index < 0.1; Fig. 5). Although branching coral cover increased monotonically with reducing wave action, so the positive response of tropical fishes to shelter may have been driven by hydrodynamic stress rather than coral habitats, we are confident that coral structure was important since all observed individual corallivores were found amongst branching corals (H. J. Beck unpubl. data). Factors organising range expansions of corals and their morphology are largely untested, but low wave action in embayed Japanese reefs was likely to be important for establishment of branching coral habitats. Such complex growth forms of corals (e.g. fine branching) are often preferred by coral-associated fishes but are highly prone to hydrodynamic stress (Madin et al. 2014), so that at least in shallow coastal waters prone to moderate to high wave energy, they often best establish in reef aspects protected from wave action (e.g. Sommer et al. 2014). Hence, by supporting the establishment of structurally suitable corals, embayed temperate reefs may indirectly assist the colonisation of tropical fishes that depend on these corals for resources.

This study identified the importance of reef exposure in organising tropical fish colonisation in temperate regions with moderate to high wave energy, yet these habitat influences may be weaker where regional and/or seasonal (i.e. through summer recruitment) wave action is lower (Santin & Willis 2007). However, while progressive warming of oceans may eventually lead to poleward expansions in temperate regions globally, where shifts have so far been documented, wave action should be sufficient to limit recruitment success, since many regions prone to tropical fish range expansions often have considerable wave energy. For example, the eastern continental boundaries of South America, Africa and USA, as well as the Western Australian coast, where poleward expansions of many tropical fishes are most rapid, all

receive moderate to high wave energy (Young et al. 2011, Vergés et al. 2014), similar to that of the SE Australian and W Japanese coasts studied here. Nevertheless, even in the presence of moderate to high swell, recruiting tropical fishes may establish where they can access natural shelter from wave action, such as where headlands and offshore reefs block swell. Anthropogenic disturbance associated with the development of rocky sea walls and other wave barriers may also increase the availability of embayed reef in temperate regions, and hence assist tropical fish recruitment. For instance, in W Japan, ~70% of shallow, embayed reefs are afforded shelter by artificial wave barriers, which include harbours, jetties, sea-walls and detached breakwaters (Walker & Mossa 1986). Protection of reefs from wave action, afforded by such constructions, may also promote recruitment success of coral-associated fishes because these relatively calm environments facilitate establishment of branching coral habitats (Iwas 2004).

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

Resource requirements and physiological performance of tropical fishes may change between their

early and later life stages, potentially leading to ontogenetic shifts in association with and impacts on temperate reef habitats. For example, individuals may shift from sheltered estuarine and back-reef nursery habitats to more exposed, offshore reefs in response to dietary changes, reduced predation risk, and greater physiological performance (Nagelkerken et al. 2000, Adams et al. 2006). Nevertheless, at least for some species of tropical fishes, their habitat requirements in temperate reefs appear consistent between recruit/early juvenile and later life-stages. For example, although rarely observed, mature-sized individuals of 26 species, belonging to Chaetodontidae, Labridae, Lutjanidae, Ostraciidae, Pomacentridae and Tetradonitidae, were only found in embayed reefs of W Japan and SE Australia (see Table S7 in the Supplement). Moreover, densities and richness of the entire adult tropical fish assemblage was greater in embayed than exposed temperate reefs, when data was pooled across countries, locations and survey years (see Table S7 in the Supplement). Such concentration of tropical fishes on embayed reefs may substantially impact native communities on sheltered temperate reefs by competing for resources, adding predation pressure and decimating habitat-forming macroalgae (Beck 2014, Vergés et al. 2014). Developing an understanding of temperate species that also associate with embayed reefs will allow us to better predict how colonising tropical fishes may impact these habitats.

CONCLUSION

Accurate predictions of species' range expansions are required for effective management of climate change impacts in natural ecosystems, but reliable projections of species' geographic responses to climate change are currently elusive (HilleRisLambers et al. 2013). Although propagule supply and species' thermal requirements are important considerations (Sorte 2013, Burrows et al. 2014), the timing and location of species' range expansions may be more accurately predicted by determining habitat requirements of species at higher latitudes (Cheung et al. 2010), yet field-based studies that test this are largely lacking (Wernberg et al. 2012). This study highlights the importance of understanding habitat constraints to recruitment of tropical fishes, such as wave action, not only larval supply and local environmental temperatures, when predicting where and when they may colonise with ongoing climate change. We show here that for many tropical fish species, failure to

consider wave exposure of low-latitude temperate reefs when predicting their future distribution may lead to vast overestimates of range expansion success. Further studies of physiological performance of tropical fishes in temperate waters, combined with empirically tested wave modelling, should better inform predictions of tropical reef fish distribution under climate change scenarios.

Acknowledgements. H.J.B. gratefully acknowledges funding from the Sydney Institute of Marine Science (SIMS) Doctoral Fellowship Program, and the University of Technology, Sydney. D.A.F. was funded by the University of Technology, Sydney under the Chancellors Postdoctoral Fellowship scheme. We are grateful for field support and/or advice provided by B. Curley, W. Figueira, B. Yui, L. Djurichkovic, R. Suzuki and K. Tose. Thanks to A. Fowler, J. Donelson and 3 anonymous reviewers for their helpful comments on the manuscript. Animal ethics approval for the research was granted by the University of Technology Sydney (UTS) Animal Care and Ethics Committee (ACEC) (Permit 2011-036A). This is contribution 173 of the Sydney Institute of Marine Science.

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*Editorial responsibility: Ivan Nagelkerken,
Adelaide, SA, Australia*

*Submitted: May 5, 2015; Accepted: January 1, 2016
Proofs received from author(s): March 2, 2016*