Temperate macroalgae impacts tropical fish recruitment at forefronts of range-expansion

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Abstract: 254

Total words: 8049

Abstract

Warming waters and changing ocean currents are increasing the supply of tropical fish larvae to temperature regions where they are exposed to range of novel habitats, namely temperate macroalgae and barren reefs. Here, we use underwater surveys on the temperate reefs of southeastern (SE) Australia and western Japan (~33.5° N and S, respectively) to investigate how temperate macroalgal and non-macroalgal habitats influence recruitment success of a range of tropical fishes.. We show that temperate macroalgae strongly effects recruitment of many tropical fish species in both regions, and across three years in SE Australia. Densities and richness of recruiting tropical fishes, primarily planktivores and herbivores, were over seven times greater in non-macroalgal compared to macroalgal reef habitat. Species and trophic diversity (*K*-dominance) were also greater in non-macroalgal habitat. Temperate macroalgal cover was a stronger predictor of tropical fish assemblages than temperate fish assemblages, reef rugosities or wave exposure. Tropical fish richess, diversity and density were greater in barren reef than reef dominated by turfing algae, at least in SE Australia. One common species, the neon damselfish (*Pomacentrus coelestis*), chose non-macroalgal habitat for settlement over temperate macroalgae in an aquarium experiment. This study highlights that temperate macroalgae may partly account for spatial variation in recruitment success of many tropical fishes, so that habitat composition of temperate reefs may need to be considered to accurately predict their geographic response to climate change.

Keywords: Climate change, kelp forest, novel habitat, poleward range-shift, temperate rocky reef, reef fishes

Introduction

Ocean warming is leading to rapid and widespread poleward shifts in the geographic distribution of many marine species (Thomas et al. 2004; Harley et al. 2006). This climate-driven redistribution of marine organisms is altering the composition and food web structure of coastal ecosystems, often negatively affecting human societies that depend on them for resources and economic stability (Cheung et al. 2009; Pereira et al. 2010). To manage ecological impacts of climate change, and alleviate associated socioeconomic consequences (Burrows et al. 2014), accurate predictions of the timing and location of species redistribution are required (Frusher et al. 2014). Nevertheless, factors regulating the colonisation of new ranges are largely unresolved (Hellmann et al. 2012; HilleRisLambers et al. 2013; Urban et al. 2013). Certainly, supply of larval propagules into new ranges (Keith et al. 2011; Gaylord and Gaines 2000) and climactic conditions at higher latitudes (Pinsky et al. 2013) may primarily? determine how species respond to shifting isotherms. However, independent of propagule input and background abiotic conditions, availability of habitats that support all species' benthic? life stages may ultimately determine whether they colonize higher latitudes (Hill et al. 2001; Warren et al. 2001; Honnay et al. 2002; Travis 2003; Cheung et al. 2010; Mair et al. 2014).

At forefronts of tropical fish range-expansion, temperate rocky reefs present a myriad of foreign biophysical conditions, which may determine where these fishes recruit (i.e., from settlement to reef habitat then survival to inclusion with existing assemblages). Although intensifying poleward-flowing currents are increasing thermal suitability of many temperate regions for such tropical species (including Australia, Japan, Korea, western Africa, Brazil and USA; Wu et al. 2012; Beck 2014), to colonise higher-latitudes tropical fishes need to access suitable resources and avoid predators in foreign, temperate rocky reef ecosystems.

Despite the rapid tropicalization of many temperate regions, roles of temperate habitats in influencing colonisation of tropical reef fishes are poorly understood (Beck 2014). To date, it has been shown that wave-protected temperate reefs offer a safe-haven for many tropical fish recruits (Beck et al. 2016a). Lower temperate predator densities, as well as higher winter water temperatures may also improve chances of overwinter success through facilitating greater physiological performance, and hence improved access to resources, including food (Beck et al. 2016b). However, one key question still remaining is how temperate macroalgae influences tropical reef fish recruitment. Differences in the habitat structure between temperate macroalgal forests (i.e., canopy, subcanopy and basal layers), and patches of algal turf and/or barren reef (covered by ephemeral or encrusting algae or bare reef) may influence patchiness in reef fish recruitment, at least on local scales. Patchiness may result from spatial heterogeneity in shelter (Shulman 1984, 1985), physical stress (Johansen et al. 2007; Johansen et al. 2008) and/or competition and predation pressure (Beukers and Jones 1998; Almany 2004).

On coral reefs, many tropical reef fishes avoid algae-dominated areas. Although the reason for such avoidance remains largely unresolved, it has been proposed that such avoidance is caused by physical movement of algal habitats in association with wave action, low availability of suitable fine-scale microshelter, higher predation risk in dense macroalgal areas and/or undesirable chemical cues from seaweed-dominated reefs (Hoey and Bellwood 2011; Lecchini et al. 2013; Dixson et al. 2014). On the other hand, a small proportion of tropical fish recruits have been found to positively associate with the structural complexity and potential food sources provided by macroalgal habitats in tropical regions??? , with lower recruitment success on reef devoid of macroalgae (Lecchini et al. 2007; Wilson et al. 2010; Evans et al. 2012; Yamada et al. 2012; Hoey et al. 2013). However, influences of temperate macroalgae on recruitment may not be simply assumed to also apply within temperate reefs. For instance, there are substantial structural differences between many temperate and tropical algae. The shape and movement characteristics common temperate brown algae, such as *Ecklonia* spp. and *Phyllosporum* spp. differ to tropical macroalgal communities, which is often dominated by *Sargassum* spp. Temperate macroalgae also supports a different suites of biological communities (including potential predators and competitors) than in the tropics (Kuiter 1993). Hence, we cannot predict how positive or negative interactions of tropical fishes with temperate residents may affect recruitment without field analysis in regions where these species distributions overlap.

By gaining an understanding at the seascape-level how temperate macroalgae influences recruitment success of invading tropical fishes, we may more accurately predict where and when tropical fishes may colonize, and hence where impacts resulting from these colonizing fishes may be most acute. So far, colonizing tropical fishes have been found to overgraze temperate algae, competing with natives for food/shelter and adding predation pressure in temperate reef ecosystems (Hiroyuki et al. 2000; Feary et al. 2014; Vergés et al. 2014). Moreover, as ocean warming facilitate greater overwinter survival of tropical fishes at temperate latitudes, increasing resource requirements for these tropical fishes would likely lead to more acute and diverse consequences (Beck 2014).

Temperate coastal reefs of southeastern (SE) Australia and western (W) Japan provide an opportunity to investigate how temperate macroalgal communities structure the density, richness and diversity of colonizing tropical reef fishes. Many tropical fishes are supplied to SE Australia and W Japan throughout summer by poleward flowing boundary currents [East Australian Current (EAC) in Australia, and the Kuroshio Current in Japan], where they recruit to coastal temperate reefs (Fig. 1). Although cool waters constrain many of these warm-adapted fishes from surviving during winter (Figueira et al., 2009; Figueira and Booth 2010), warming of these coastal waters is rapidly facilitating establishment of permanent populations; coastal waters in W Japan and SE Australia are warming at more than twice the global average rate (Wu et al. 2012). We examined whether temperate macroalgal cover influences recruitment of tropical reef fishes by comparing the density, richness and diversity of new recruit and juvenile tropical fishes (hereafter termed 'vagrants') between macroalgal dominated habitat (e.g., genera *Ecklonia, Phyllospora* and *Sargassum*) and non-macroalgal habitats. We considered non-macroalgal habitats as those that consisted of low-lying turfing algae (e.g., Class Rhodophyta and Phylum Phaeophyceae; both in turfing form) or barren rocky reef (rock covered in encrusting and ephemeral Rhodophyta and Phaeophyceae, or bare rock with no algae). To examine factors that possibly contributed to differences in recruitment of tropical fishes among non-macroalgal and macroalgal reef patches, reef structure (i.e., topographical complexity), wave exposure, temperate reef fish community (including likely competitors and predators) and benthic composition were also quantified. We conducted aquarium experiments using a common tropical damselfish (*Pomacentrus coelestis*) to test whether the observed habitat associations of vagrants resulted from preference during larval settlement (i.e. shift from pelagic to benthic life stage), rather than immigration and/or differential mortality.

Materials and methods

Field study: tropical fish recruitment to macroalgal-covered and non-macroalgal temperate reefs

Underwater visual surveys of new recruit and juvenile vagrant fishes were conducted in summer and early autumn; when they recruit to coastal temperate reefs of SE Australia (January - May 2011, 2012 and 2014) and W Japan (July 2013) (Kuiter 1993; Booth et al. 2007; Nakamura et al. 2013). Australian and Japanese study sites were located at ~33.5° S and N, respectively (Fig. 1). We quantified the density, richness and diversity of vagrant assemblages using haphazardly placed GPS-tracked timed swims (Garmin^{TM}; ≤ 3 m accuracy; 5 sec intervals), which allowed distances surveyed to be measured. Surveys were conducted on snorkel at 0 - 4 m water depths on reefs that were partially exposed to ocean swell (Beck et al. 2014). This survey method allows more accurate detection of richness and diversity of vagrants within temperate reefs than standard belt transects, with comparable accuracy and precision of density estimates (Beck et al. 2014). Macroalgal and non-macroalgal habitats were surveyed for vagrant fishes at seven SE Australian sites and three W Japanese sites, separated by 2.5 - 40 km within these countries. At each site, tropical fish recruits were surveyed using six, 5-min roaming surveys within each habitat. Surveys were repeated? in Australia once yearly during 2011, 2012 and 2014, whilst Japanese sites were only surveyed in 2013. In total, both habitats were surveyed 126 times in SE Australia (across the three years), whilst 18 patches of both habitats were surveyed in W Japan. Patches of macroalgal and non-macroalgal reef surveyed for vagrants were haphazardly selected visually prior to surveys and interspersed to avoid spatial pseudoreplication, ie to ensure influences of wave exposure on fish recruitment was comparable between sites and habitats (Beck 2016a). The dominant non-macroalgal or macroalgal habitat cover was classified and recorded for each survey replicate. Macroalgal habitats surveyed in SE Australia comprised *Ecklonia radiata*, *Sargassum* spp. and *Phyllospora comosa*, whist *E. cava* dominated W Japanese reefs. Macroalgal patches surveyed had > 75% cover and were 25 - 75 m^2 in area. Macroalgal patches surveyed were largely monospecific (i.e. one species of macroalgae comprised > 80% of the canopy assemblage). Non-macroalgal reef patches had < 20% cover of macroalgae and were either barren reef (bare or encrusted covered rock) or covered with with low (< 10 cm height, with a mean height of ~5 cm) ephemeral or turfing Rhodophyta and Phaeophyceae.

Vagrant fishes encountered within 1 metre either side of the observer were identified to species and their total length (TL) estimated visually. To avoid wrongly assigning individuals to a habitat due to the response of a fish to an observer, only individuals found more than 0.5 m from boundaries of macroalgal and non-macroalgal habitats were recorded (i.e., not in the vicinity of edges). Fishes found on edges of habitat through surveys were uncommon (< 1% of sightings). Individuals were identified as recruits of the present season (i.e. young-of-the-year) and juvenile based on family specific length-age criteria established by Booth et al. (2007), while trophic level? followed Froese and Pauly (2015), IUCN red list of threatened species (V2015.2) and a review of scientific literature (See Supplementary Information, Table S1). Where known, we assigned trophic groups based on feeding preferences during early life stages and/or within temperate reef habitats. However, we acknowledge that fish dietary preferences are likely to be more far more complex than documented and vary substantially between tropical and temperate ecosystems. Tropical “vagrant” species were considered as those found as breeding-aged adults only between the Tropics of Cancer and Capricorn (23°27' N and S, respectively), as determined by distribution data from Kuiter 1993; Froese and Pauly 2015 and and IUCN red list maps (V2015.2) (See Supplementary Information, Table S1). All surveys were conducted by the main author (HJB) between 9:00 and 17:00, when water visibility was > 5 m and swell was < 1 m.

Abiotic and biotic drivers of recruitment to non-macroalgal and macroalgal habitat

Factors influencing recruitment of vagrants to macroalgal and non-macroalgal patches were explored in SE Australia during 2014. To test if macroalgal cover *per se* influenced tropical fish recruitment to temperate reefs, benthic habitat composition (i.e. major temperate macroalgal species and non-macroalgal habitats), species richness and densities of the resident temperate reef fish community (estimated whilst surveying vagrant species using GPS-tracked surveyed, described above), reef rugosities (i.e., structural complexity) and wave exposure (using a fetch-based index, Beck 2014) were measured in each macroalgal and non-macroalgal reef patch surveyed for vagrant fishes. The composition of benthic habitats was estimated by recording the proportion of time the surveyor spent over each of the primary benthic habitats listed below?, whilst surveying fish assemblages. These habitats were categorised as either one of the dominant habitat-forming macroalgae (i.e. *Ecklonia radiata*, *Phyllosporum comosa* or *Sargassum* spp.), or as a non-macroalgal habitat (i.e. turfing algae or barren rock). Turfing algae was considered to be branching algae with a height < 10 cm, whilst 'barren' was reef where all branching algae was absent. The macroalgal canopy was typically monospecific in surveyed patches (e.g. of the seven sites surveyed, *Ecklonia radiata* comprised all macroalgal patches at four sites, whilst only

Phyllosporum comosa patches were surveyed at one site). Moreover, non-macroalgal reef habitat was consistent in ~80% of survey replicates, with the reef patch consisting of either turfing algae or an expanse of barren reef. Wave-exposure was calculated using a fetch??-based index (Hill et al. 2010); 7.5° rays around the midpoint of survey sites to a maximum of 650 km - the minimum fetch distance for seas to fully develop. Reef rugosities were averaged over areas within each reef patch (i.e., every ten swim kicks; measured immediately after fish surveys), using the ratio of surface distance to linear distance of a five metre chain (Risk et al. 1972; n = 126 in both macroalgal and non-macroalgal habitats).

Settlement choice of tropical fish larvae: macroalgal vs non-macroalgal habitat

To test settlement preferences of a common tropical vagrant fish, , habitat choice of late-stage? (or immediate presettlement??) larvae of the tropical damselfish *Pomacentrus coelestis* were assessed within aquarium trials at Yokonami Beach, W Japan (Fig. 1). *P. coelestis* was selected as the focal species due to its high abundance (Nakamura et al. 2013); this species is also one of the most common tropical species recruiting to both SE Australian and W Japanese temperate reefs (Booth et al. 2007; Nakamura et al. 2013; Soeparno et al. 2013).

P. coelestis larvae were collected by light-trapping (*sensu* Fisher and Bellwood 2002) on four consecutive nights (July 2013). Traps were set and collected each morning and evening, respectively. At 21:00 hrs on the night of collection, individual*P. coelestis* larvae were released into the middle of 85 L outdoor, rectangular aquaria containing one patch of encrusting algae covered rock and one patch of kelp, *E. cava*; these habitats were the most common non-macroalgal and macroalgal habitats in W Japan. Habitat patches were placed at opposite ends of the aquarium, with a similar coverage for each (each habitats covered 11 to 30% of aquaria bottom). Habitat choice of *P. coelestis* on non-macroalgal and macroalgal habitat were recorded at sunrise ~05:30 hrs (for 15 min). An individual fish was considered to have made a choice when it was found ≤ 2 cm from a habitat for at least 10 min We conducted 24 settlement trials, with different individuals used in a single trial. Between trials, habitats were randomly switched between ends of aquaria to reduce any potential 'tank' effect, and a new fish was used for each trial.

Statistical analyses

Because the number of survey occasions (three years in SE Australia, one year in W Japan), replicate surveys (126 in SE Australia, 18 in SE Japan) and number of sites (seven in SE Australia, three in W Japan) differed between regions, vagrant assemblages were separately evaluated within SE Australia and W Japan. To test if tropical vagrants avoided temperate habitats that are dominated by macroalgae, we compared total vagrant assemblage density (i.e., total individuals per m^2), species richness (i.e., total species per m^2), density and richness of trophic groups, between macroalgal and non-macroalgal habitat (fixed), site (random) and year (SE Australia only; random), using univariate permutation analysis of variance (PERMANOVA; 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 the total individuals and species divided by area searched within replicate surveys, respectively.

Species and trophic diversity of vagrant assemblages was compared between habitat site and year (SE Australia only) by *K*-dominance plots. As a diversity measure, *K*-dominance plots better account for species and trophic group evenness than single value diversity indexes (Lambshead et al. 1983). *K*-dominance plots were constructed individually for replicate surveys on forth root transformed density data (Clarke and Gorley 2006, Clarke et al 2006), cumulatively ranking species and trophic diversity, expressed as a percentage of all species, in decreasing order of their density. Fourth root transformations were used since there were many low and some high fish counts within survey replicates; as recommended by Quinn and Keough (2002). Pairwise distances between *K*-dominance plots, constructed for each survey using Manhattan distance metrics, were then calculated using DOMDIS (PRIMER™ v6) (Warwick 1986; Clarke 1990; Clarke and Gorley 2006). *K*-dominance curves, for species and trophic diversity, were then compared between habitats, years (SE Australia only) and amongst sites by PERMANOVA, using the same design as for richness and diversity (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 Principle Coordinate Analysis (PCO) using Spearman's rank correlation. *A priori*, we decided trophic groups with % $\bar{\delta}_i$ >10% were 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 two habitats. Densities of these trophic groups, identified by SIMPER as important contributors to variance in fish assemblages, were then compared between habitats and years (SE Australia only), and among sites using PERMANOVA (as above). To conform to the statistical assumption that variances were homogeneous, sites were excluded from trophic analyses where we observed fewer than five individuals belonging to a particular trophic group for each survey year.

All survey data were inspected for homogeneity of variance using the PERMDISP procedure (PRIMER^{TM} v6), with data ln(X+1), square- or forth root transformed where required. PERMANOVA was used here as it is typically more robust to heterogeneity of variances and assumptions of data normality than parametric analyses (Underwood 1997; Anderson and Walsh 2013). Where the *P* - value of a factor was > 0.25, it was pooled with the residual (following Underwood 1997). The Monte-Carlo p-value [*P*(mc)] was used when the number of unique permutations for a term within an analysis was < 100 (following Anderson 2001). Significant interactions between factors for all analyses of field parameters were explored using PERMANOVA *post-hoc* pairwise tests.

To determine the abiotic and biotic variables that best predicted difference in vagrant assemblages between macroalgal and non-macroalgal temperate reef habitats, a best-fit Distance-based linear model (DISTLM) was used . . The DISTLM focused on habitat variables measured during surveys of vagrant fishes in SE Australia during 2014, which were: trophic preference of temperate fish assemblages, reef complexity, overall macroalgal cover, cover of primary macroalgal species, overall extent of non-macroalgal habitat, extent of each non-macroalgal habitat and wave exposure. This analysis was conducted using Bray-Curtis similarity measures on forth root transformed vagrant abundance for all sites, habitats and species surveyed during 2014 in SE Australia (Clarke and Gorley 2006), pertaining to the AIC_c criterion with a maximum of 10 variables and using 9999 permutations (Clarke and Gorley 2006). We considered 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, as suggested by Anderson et al. (2008). Environmental data were checked for multicollinearity and dispersion using draftsmen plots, ln(X+1) or square-root transformed where required and then normalised prior to analysis. Relationships amongst environmental data (post-transformation) were also checked for linearity prior to analysis. Factors best explaining variance in SE Australian vagrant communities were graphically explored by PCO and Spearman rank correlation.

To test whether there was a preference for particular non-macroalgal, the density, richness and diversity of tropical fish assemblages were compared between barren (bare rock and sea urchin barren) and turfing algal dominated reef. These variables were also compared between patches of *Ecklonia*, *Phyllospora* and *Sargassum* sp. Due to the unbalanced replication of these habitats across survey years and locations, density, richness and diversity data were pooled together within each country prior to analysis. Density, richness and diversity (*K*-dominance) were analysed using PERMANOVA following the protocol detailed above.

To determine if vagrant habitat associations were caused by active preference at settlement to the reef, the proportion of *P. coelestis* that settled into the macroalgal and non-macroalgal habitats were compared by binomial tests, treating the probability of either outcome by chance as 50%. These proportional data were normalised by square root transformation prior to analysis. *A priori*, $P < 0.05$ was the set level of significance for all analyses. Field data were analysed using PRIMER™ v6 with PERMANOVA+ extension, whilst SPSS™ v20 was used to analyse settlement trial data.

Results

Tropical fishes recruits in non-macroalgal and macroalgal temperate rocky reef

Overall assemblages

A total of 3033 vagrant tropical fishes, from 36 species in seven families were surveyed within SE Australia (27 species and six families) and W Japan (20 species and five families) (See Supplementary Information, Table S1). There was a 44 % overlap in species observed in both SE Australia and W Japan; these species belonged to the families Pomacentridae (damselfishes, X species…), Acanthuridae (surgeonfishes), Chaetodontidae (butterflyfishes), Labridae (wrasses) and Zanclidae (Moorish idol).

Vagrant densities and species richness were over seven times greater in non-macroalgal than macroalgal reef habitats in both regions (PERMANOVA; species richness for both countries, $P \leq 0.007$; density in W Japan, $P < 0.001$; Fig. 2, Table 1). Vagrants were also significantly more abundant in non-macroalgal than macroalgal habitat within all three years studied in SE Australia (Pairwise test; $P \leq 0.002$ for all years), despite an interaction between habitat and year (PERMANOVA; $P = 0.02$; Table 1). Moreover, vagrants were more diverse within non-macroalgal than macroalgal habitats in SE Australia and W Japan (PERMANOVA; $P \leq 0.001$ in both countries; Table 1). There was no significant interaction with habitat and all other factors within the model for species diversity and species richness in either country, or density in W Japan ($P > 0.15$; Table 1). Mean ($\pm$SD) area searched within non-macroalgal and macroalgal patches per site was 197.93 (78.12) and 175.25 (63.48) m^2, respectively (n = six 5 minute replicate surveys in both non-macroalgal and macroalgal habitat per site).

Of the 36 species observed, 17 were more often in non-macroalgal habitat than that expected by chance (Binomial test; $P < 0.02$ for all species; See Supplementary Information, Table S1). Moreover, although sample numbers for15 species were too low for analysis (n < 5), these species were exclusively found in non-macroalgal habitat. There was no difference in frequencies of *Ctenochaetus striatus*, *Naso unicornis*, *Canthigaster rivulata* (Binomial test; $P > 0.05$) between macroalgal and non-macroalgal habitat. *Siganus fuscescens* was observed in significantly greater frequencies within macroalgal habitat (Binomial test; $P < 0.0001$).

Trophic assemblage and individual trophic groups

Planktivores were the most abundant trophic group within SE Australia (56%) and W Japan (64%), with each assemblage also comprising herbivores (31% Australia; 18% Japan), benthivores (5% Australia; 10% Japan), omnivores (4% Australia; 9% Japan) and ectoparasite feeders and piscivores (both < 1%, Australia only). The diversity and richness of trophic groups were significantly greater in non-macroalgal than macroalgal habitats in SE Australia and W Japan (Table 1; $P \leq 0.001$). There were no significant interactions between habitat and any other variable for either metric in either country ($P \geq 0.15$ for remaining terms in models).

PCO partitioned trophic assemblages between non-macroalgal and macroalgal habitats along PCO Axis 1, explaining 71.2% and 65.9% of variance in trophic assemblages within SE Australia and W Japan, respectively (Fig. 3). Planktivores and herbivores in SE Australia and W Japan, as well as benthivores and omnivores in W Japan, primarily accounted for differences in assemblages between non-macroalgal and macroalgal habitats (SIMPER; % $\bar{\delta}_i$ > 10%). These trophic groups were positively correlated with non-macroalgal reefs along PCO 1 within their respective countries (Spearman correlation; $P < 0.05$, $r_s > 0.48$; Fig. 3).

Planktivores and herbivores were in greater densities in non-macroalgal than macroalgal habitat in SE Australia (*Pseudo*-$F_{1,90} = 96.8$, $P = 0.01$ and *Pseudo*-$F_{1,170} = 214.4$, $P < 0.001$ for planktivores and herbivores, respectively). In W Japan, densities of omnivores [*Pseudo*-$F_{1,18} = 239.1$, P(MC) = 0.04] and herbivores [*Pseudo*-$F_{1,30} = 20.33$, P(MC) = 0.04] were significantly greater in non-macroalgal than macroalgal reefs. Densities of planktivores were significantly greater in non-macroalgal habitat in W Japanese sites of KA [P(MC) = 0.0001] and US [P(MC) = 0.001], but not TA [P(MC) = 0.22]. Benthivores were in significantly greater densities on non-macroalgae reef at TA [P(MC) = 0.02], but not US [P(MC) = 0.14]. Influence of habitat on planktivore and benthivore density depended on site in W Japan [planktivores, *Pseudo*-$F_{2,30} = 4.95$, P(MC) = 0.01; benthivores, *Pseudo*-$F_{2,20} = 5.34$, P(MC) = 0.03]. All interactions involving ‘habitat’ type with site and/or year (SE Australia only) not reported here were non-significant in both countries (i.e., $P > 0.05$ for all other interactions with habitat type not reported).

Abiotic and biotic influences on tropical fish recruitment

Of the environmental factors measured, the proportion of barren reef best predicted differences in the composition of vagrant fish assemblages (17.8%; Fig. 4; See Supplementary Information, Table S2 and S3). The composition of vagrant assemblages positively corresponded to the extent of barren reef within survey patches (Spearman rank; $r_s = 0.52$, $P = 0.001$), where branching algae was absent. The density and richness of the vagrant assemblages significantly increased with increasing proportion of barren within reef patches surveyed (density: $r_s = 0.46$; $t = 7.25$; $P < 0.001$; richness: $r_s = 0.27$; $t = 2.56$; $P = 0.006$). . The best combination of explanatory variables (AICc = 635.14) also included the density of the overall temperate fish assemblage (13.7%), but this failed to explain variance in vagrant assemblages, since overall temperate fish assemblages also positively corresponded with non-macroalgal reefs (Fig. 4).

Of the non-macroalgal habitats surveyed in SE Australia, the density ($Pseudo\text{-}F_{1,\,124} = 7.32$, $P = 0.007$), richness ($Pseudo\text{-}F_{1,\,124} = 6.33$, $P = 0.01$) and diversity ($Pseudo\text{-}F_{1,\,124} = 4.91$, $P = 0.04$) of tropical fishes was significantly greater on barren than turfing algae covered reef (Fig 5). Tropcial fish richness, diversity and density did not significantly differ between patches of *Ecklonia radiata*, *Phyllosporum comosa* or *Sargassum* spp. ($P < 0.05$ for all three variables). Non-macroalgal reefs surveyed in W Japan were all dominated by turfing algae, whilst macroalgal patches surveyed were dominated by *E. cava*.

Settlement choice of tropical fish larvae into macroalgal and non-macroalgal habitat

A significant proportion (87.5%) of *P. coelestis* larvae settled into the non-macroalgal reef (Binomial Test, $P < 0.001$), while only three of the 24 individuals settled into the macroalgal habitat. No individual changed habitat choice between sunrise (~5:30) and 8:00.

Discussion

To expand their range poleward with ocean warming, reef fishes must access reef habitats at higher latitudes that support their recruitment (Feary et al. 2014). But at the vanguard of range expansion of many tropical reef fishes, macroalgal cover of temperate reefs may influence where they can recruit (Feary et al. 2014). We show that temperate macroalgal patches may strongly inhibit?? tropical reef fish settlement since the overall density of assemblages, trophic and taxonomic diversity and species richness of new recruit and early juvenile tropical vagrants were greater within non-macroalgal than macroalgal patches of temperate SE Australian and W Japanese reefs. This result was consistent for three years in SE Australia. Our results suggest that at least in temperate reefs partially exposed to swell at range-expansion forefronts, colonisation of many tropical fishes would be organised, and potentially limited, by temperate macroalgal patches (Bates et al. 2014).

Cover of reef by macroalgae appeared to best explain the density, richness, diversity and trophic composition of vagrant fish assemblages among temperate reefs; vagrants were positively associated with reefs where all branching algae were absent. Despite potential effects of temperate reef fishes on recruitment of vagrant tropical reef fishes (e.g., heightened competition, predation and grazing; Bates et al. 2013; Beck 2014; Vergés et al. 2014), the overall assemblage density, densities of individual trophic groups and species/trophic richness of temperate reef fishes failed to significantly explain the observed strong association of tropical fishes with non-macroalgal reefs. Notably, we found densities of the temperate reef fishes was also positively associated with non-macroalgal habitats, which supported earlier findings by Curley et al. (2002). Hence, despite using the same habitats in which tropical fishes were found, temperate fishes did not appear to exclude tropical fishes from recruiting. However, we cannot discount a role for competition and predation between vagrants and temperate species post-settlement, and we did not evaluate the extent that these interactions may determine recruitment. Moreover, it may be possible that some temperate species facilitate recruitment of tropical reef fishes. For instance, the tropical planktivores *Abudefduf vaigiensis* and *Abudefduf whitleyi*, and grazers *Acanthurus dussumieri*, *Acanthurus olivaceus* and *Acanthurus nigrofuscus*, were observed schooling with temperate and sub-tropical fishes with similar dietary preferences (Beck HJ, personal observation). Such schooling behavior may promote colonisation of tropical fishes by reducing predation risk and enhancing foraging success (Feary et al. 2014). Influences of native species on vagrant recruitment could be assessed using manipulative experiments, where temperate reef communities are modified to test specific hypotheses. For instance, influences of temperate predator fishes on vagrant population dynamics and behaviors may tested by studying vagrants inside marine parks areas, where predator densities are typically high, and where predator populations are depleted by fishing (Beck et al. 2016b).

Although there are a range of factors which may favour vagrant settlement into non-macroalgal habitat patches, structural differences between areas lacking macroalgal habitat and macroalgal reef patches may be vital in determining tropical fish recruitment success. For example, there is a substantial literature showing structurally-stable tropical reef habitats, predominantly scleractinian coral communities, are an important habitat in which many tropical fishes will settle and recruit (Wilson et al. 2006; Pratchett et al. 2011). Such habitat-associated recruitment may be due to habitat structure, with stable and topographically complex reef often better mediating negative interactions with residents (Friedlander and Parrish 1998; Beukers and Jones 1998; Almany 2004; Gratwicke and Speight 2005; Wilson et al. 2010) and lessening effects of physical stressors, such as wave action (Johansen et al. 2007; Johansen et al. 2008). Stable reef habitats may also require less energy for marine organisms to associate with than non-stable, moving macroalgal dominated reef, and in some cases, abrasion caused by moving kelp may even prevent marine organisms from establishing (Velimirov and Griffiths 1979; Connell 2003; Gagnon et al. 2004). Nevertheless, macroalgae movement did not appear to influence habitat choice, at least for *P. coelestis*, since this species still avoided macroalgae in the aquarium experiment, where water/macroalgal movement was minimal. Open habitats, such as non-macroalgal reefs, also potentially increase visibility of predators for prey and abilities of prey to escape attacks compared to dense habitats, such as macroalgal patches, which can conceal predators and block escape efforts, as found for marine invertebrates (Konar and Estes 2003; Gagnon et al. 2003), and proposed for tropical reef fishes (Hoey 2010; Hoey and Bellwood 2011). Moreover, chemical odours released from macroalgae may deter recruitment of many tropical reef fishes, as found on some coral reefs (Lecchini et al. 2013; Dixson et al. 2014). We may discount potential influences of observer error from explaining the spatial patterns of fish recruitment detected, since most tropical species surveyed were non-cryptic and brightly colored, so were easily observed, even when associated with macroalgae (Beck HJ, Personal Observation). Moreover, the cryptic species *Siganus fuscescens* was clearly identifiable in the present study, with individuals more often found in macroalgae, suggesting that detected patterns of recruitment were not a sampling artefact.

Although our study applies to the dominant vagrant species, temperate macroalgae may still provide important recruitment habitat for tropical fishes, particularly for those that associate with tropical macroalgae. For instance, the rabbitfish *S. fuscescens*, a species whose close relatively commonly recruit to macroalgae (i.e. *Sargassum* spp.) in coral reefs (Hoey et al. 2013), was observed associating exclusively with the temperate macroalgae *E. cava* in the present study. Such association may be due to food availability, as the same species has been observed grazing *E. cava* on Japanese reefs, to the extent that these macroalgal communities decline (Hiroyuki et al. 2000).

Our study focused on the dominant benthic habitats in oceanic reefs, partially exposed to swell, whilst habitat associations of tropical fishes may differ in more embayed environments. Gaining knowledge of how macroalgae influences recruitment in embayed temperate reefs is important since highly embayed temperate reefs are recruitment hotspots for many tropical fishes (Beck et al. 2016). For instance, typically more elaborate kelp morphology and reduced movement of kelp in more sheltered reefs may influence their ability to support tropical fish recruitment. Other suitable habitats, not found in exposed temperate reefs, may also support tropical fish recruitment in embayments. For example, species that recruit to seagrass in the tropics may recruit to temperate seagrasses, which are often found in highly embayed areas, such as well-flushed estuaries along the SE Australian coast.

The active choice of non-macroalgal reef by settling *P. coelestis* larvae suggest that *in situ* associations of tropical vagrants with non-macroalgal reef, at least for this species, may reflect settlement preferences rather than higher post-recruitment mortality in macroalgal reef or post-settlement movement between habitats. Moreover, given the preference of *P. coelestis* for rubble habitats in coral reefs (Ohman et al. 1998) and other temperate regions (e.g. Wilson et al. 2010), it appears that this species seeks similar physical habitat properties, regardless of the geological origin of the reef and latitude. Certainly, further small-scale experiments are required to disclose the process underlying habitat associations of a wider range of tropical fishes in temperate reefs and habitat conditions. Cues driving associations would also be valuable in predicting important reef habitat for shifting tropical fishes. Based on this study, we may discount cues operating over large spatial scales, such as celestial references, magnetism and water movement (Leis et al. 2011), as important factors driving the observed habitat associations since macroalgal and non-macroalgal habitats surveyed were interspersed and separated by only 10s of metres. Conspecifics may also guide settlement of larvae (Jones 1987; Sweatman 1988; Booth 1992, 1995), but this was unlikely, at least in SE Australia, since established populations of tropical fishes are currently rare due to substantial overwinter mortality of most tropical species (Booth et al. 2007; Figueira and Booth 2010). In absence of conspecifics, and on such fine spatial scales, larval fishes may use olfactory, auditory and/or visual cues at settlement to differentiate macroalgal and non-macroalgal habitats (Kingsford et al. 2002; Lecchini et al. 2005; Wright et al. 2005).

Resource requirements and physiological performance of tropical fishes may change between their early and later life stages, leading to ontogenetic shifts in habitat and implications for temperate reefs. Fishes may shift reef habitat as they grow 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 tropical fishes, their habitat requirements may be consistent between recruit/early juvenile and later life-stages on temperate reefs. For example, 14 of the 15 species were mature-sized individuals (Labridae, Lutjanidae, Pomacentridae and Scaridae), and were observed only on non-macroalgal reef patches in W Japan and SE Australia (See Supplementary Information, Table S4). Furthermore, over 97% of the adult tropical fishes observed here only associated with non-macroalgal reef patches. Such concentration of tropical fishes on non-macroalgal reef, particularly those that use this habitat from recruitment to adulthood, may have implications for native communities. Tropical fishes may compete with natives for food and shelter, added predation pressure and decimation of habitat forming species, such as kelp (Beck 2014; Vergés et al. 2014).

Our results suggest that distribution of temperate macroalgal communities in thermally marginal temperate reefs should be considered when predicting where and when many tropical fishes may colonise with ongoing ocean warming. Such strong association of many recruiting tropical fishes with non-macroalgal habitat suggests that, at least for the dominant species, human-driven changes in temperate macroalgae assemblages may influence colonisation. Changes in macroalgal communities, with potential to influence tropical fish colonisation, may result from those warming waters, water pollution and/or increasing grazing pressure (Schiel et al. 2004; Ling 2008; Tait and Schiel 2011; Vergés et al. 2014). However, to more accurately determine how macroalgae influences poleward redistribution of tropical fishes s , we require an accurate understanding of larval supply, settlement rates and survivorship of tropical fishes on temperate reefs with varying levels of macroalgal cover (e.g. Bates et al. 2014). Moreover, impacts of macroalgae on tropical species redistribution may be better understood by studying how temperate and tropical macroalgae differentially influence tropical fish recruitment. As there are many species of tropical fishes that use habitats other than coral reefs at tropical latitudes, including seagrasses, mangroves and sponges, the potential for similar temperate benthic communities for supporting recruitment of these species also needs to be explored. Through gaining a more thorough understanding of interactions between tropical fishes and temperate habitats, management strategies may be effectively designed to alleviate undesirable impacts associated with the tropicalization of temperate reefs.

Acknowledgements

HJB gratefully acknowledges funding from the Sydney Institute of Marine Science (SIMS) Doctoral Fellowship Program, and the University of Technology, Sydney. DAF was funded by the University of Technology, Sydney under the Chancellors Postdoctoral Fellowship scheme. We appreciate the field assistance and advice from B. Curley, W. Figueira, R. Suzuki, K. Tose and B. Yui, and to A. Fowler for helpful reviews of 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 **XX** of the Sydney Institute of Marine Science.

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Figure Legends

Figure 1. Survey sites (open circles) within western Japan [(a) and b)] and south-eastern Australia [c) and d)]. Tropical reef fishes are supplied to temperate latitudes as larvae from tropical sources by the Kuroshio Current a) and East Australian Current c), where they recruit to novel reef habitats through summer within Japan and Australia, respectively. Juvenile tropical fishes were surveyed at sites by 5-min timed swims within kelp-free reef and kelp habitats, across three seasons in Australia [n = 126 per habitat; b)] and one season in Japan [n = 18 per habitat; d)]: SB = Shelly Beach; LR = Long Reef; NP = Newport; PB = Palm Beach; MB = Maitland Bay; TB = Terrigal Beach; TW = Toowoon Bay; TA = Tanoura; KU = Kutsuu and US = Usa. Settlement choice experiments were conducted at the Yokonami Rinkai Experimental Station (YO; filled circle).

Figure 2. Mean (±S.E.) a) total density and b) species richness of tropical vagrant fishes within non-macroalga1 (Grey bars) and macroalga1 reef habitats (White bars) within south-eastern (SE) Australia and western (W) Japan. n = 126, five-min timed swims per habitat, pooled across three years for SE Australia, and n = 18 per habitat for one recruitment season in W Japan. * Indicates a significant difference of $P < 0.05$ determined by PERMANOVA.

Figure 3. Principal co-ordinate analysis of tropical vagrant trophic groups within macroalgal and non-macroalgal reef habitats of a) SE Australia and W Japan. Vectors overlaid display the primary groups responsible for division of sites along PCO axis 1, determined by SIMPER analysis (result reported in text). Arrows denotes replicate surveys where no vagrants were detected: n = 110 and 23 in macroalgae and non-macroalgal patches in SE Australia, respectively, and n = 13 in macroalgae in W Japan. In total, n = 126 and 18

replicate surveys were conducted in both habitats within SE Australia and W Japan, respectively.

Figure 4. Principal co-ordinate analysis of tropical vagrant fish species within macroalgal (open markers) and non-macroalgal (grey markers) reef habitats of SE Australia, surveyed during 2014. Vectors overlaid display the environmental correlates that best explained variance in fish assemblage data, as determined by DISTLM (result reported in text); Barren = extent of barrens and Temperate Density = overall density of temperate fishes. Arrows denotes replicate surveys where no vagrants were detected: n = 34 and 5 in macroalgal and non-macroalgal patches in SE Australia, respectively, and n = 13 in macroalgae in W Japan. In total, n = 42 replicate surveys were conducted in both habitats.