Coral Reefs (2023) 42:1257–1262
https://doi.org/10.1007/s00338-023-02429-w

NOTE

Subtropical coral expansion into SE Australia: a haven for both temperate and expatriating tropical reef fishes

Max J. O'Connell[1] · Ashley M. Fowler[1,2] · Sam J. Allan[1] · Giglia A. Beretta[1] · David J. Booth[1]

Received: 23 April 2023 / Accepted: 18 September 2023 / Published online: 3 October 2023

Abstract We examined reef fish assemblages in and adjacent to a newly established coral bed (subtropical *Pocillopora aliciae*) in temperate south-eastern Australia, to understand whether novel coral habitat is facilitating assemblages of range-expanding tropical and local temperate fishes. This is the first comprehensive assessment of fish species associating with this novel coral habitat within a temperate environment. Twenty fish species were observed associating with the coral (8 tropical and 12 temperate). Both temperate and tropical species were observed at greater (up to 48 times higher) densities on the coral than on nearby temperate rocky reef in the area, suggesting that the corals generally concentrate fish and may aid in tropicalisation for species that use subtropical coral as habitat. Future research should investigate the ongoing expansion of this coral, the relative quality of coral habitat for fish in temperate regions and the potential implications for functioning of temperate rocky reef ecosystems.

Keywords Coral *Pocillopora aliciae* expansion · Tropical and temperate fish species · Tropicalisation

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-023-02429-w.

✉ David J. Booth
david.booth@uts.edu.au

[1] School of Life Sciences, Building 4, Level 6, University of Technology Sydney, Ultimo, NSW 2007, Australia

[2] New South Wales Department of Primary Industries, Sydney Institute of Marine Science, Mosman, NSW 2088, Australia

Introduction

The world's oceans have warmed significantly over the past several decades as a result of anthropogenic climate change (IPCC 2014). However, rates of warming vary among regions, with a number of coastal seas with poleward-flowing western boundary currents (WBCs) exhibiting warming two to three times faster than the global average (Wu et al. 2012)—termed 'global hot spots'. These hot spots warrant concerted research effort, because they will be the first affected by climate change, and they provide a model system for future scenarios in regions that are warming more slowly.

Tropicalisation has been a well-studied phenomenon over the last several years and refers to poleward migration and establishment of tropical marine species in subtropical and temperate environments (Pecl et al. 2017). Most marine fish, for example, have pelagic larvae that are dispersed over large distances (Leis 1991), and the expatriation and settlement of tropical larvae into temperate ecosystems are well documented (Booth et al. 2007; Nakamura et al. 2013; Fowler et al. 2018). Once settled, overwintering of tropical juveniles has been identified as a key bottleneck for the establishment of populations in temperate areas (Figueira and Booth 2010). However, as ocean temperatures continue to rise, greater overwinter survival of a broader range of species is expected, and habitat suitability may become a more important limiter of population establishment.

The poleward expansion of tropical habitat-forming species, such as scleractinian corals, may facilitate range extension of tropical fauna with complex and specific habitat requirements (Yamano et al. 2011; Vergés et al. 2014). The establishment of tropical coral in temperate areas is typically preceded by a reduction of macroalgae, often caused by the expansion of tropical grazers (Vergés et al. 2014; Kumagai et al. 2018) or disturbances (Wernberg

et al. 2016). In some cases, lost macroalgae is not replaced by structurally complex coral habitat, resulting in open 'barrens' of rocky reef habitat dominated by simple turfing algae (Agostini et al. 2021). The latter scenario is referred to as 'simplification', where the complexity of temperate reef habitat is essentially lost and not replaced (e.g. Tosa Bay, southern Japan; Pessarodona et al. (2021).

South-eastern Australia is a global hot spot for ocean warming, with the intensification of the East Australian Current (EAC) transporting warm tropical water from the Coral Sea further south (poleward) along the temperate coast (Ridgway 2007). While tropical reef fish species are shifting poleward in this region (Booth et al. 2018; Fowler et al. 2018), their key habitats such as corals have not kept pace (Baird et al. 2012), potentially limiting the range expansion of fishes that rely on specific habitat types. In SE Australia, colonies of subtropical *Pocillopora aliciae* (Pocilloporidae) (Schmidt-Roach et al. 2013) have recently been discovered in Cabbage Tree Bay Aquatic Reserve, Sydney, New South Wales (NSW) (Sydney Coral Gardens, hereafter 'SYCOGA', Fig. 1) (Booth and Sear 2018). *P. aliciae* is particularly abundant in the Solitary Islands (~ 450 km north–north-east of SYCOGA) (Smith and Simpson 2010), but has rarely been observed in Sydney until the last few years. The species is Sydney's only scleractinian branching coral species and has been observed proliferating and infilling urchin barrens and nearby kelp (*Ecklonia* spp.) habitat. Due to the recency of its establishment, the fish assemblages associated with this novel habitat have not been comprehensively investigated.

The aim of this study was to investigate the SYCOGA fish assemblage, specifically to: 1) identify fish species (both tropical and temperate) utilising novel *P. aliciae* habitat and 2) assess the potential importance of coral habitat for temperate and tropical species by comparing fish densities on coral to the surrounding kelp and urchin barren habitats. Findings will provide insights into the role of novel corals as habitat for both local temperate and range-expanding tropical fish species within a temperate rocky reef environment.

Materials and methods

The study was carried out at Sydney Coral Gardens (SYCOGA), Manly, NSW, Australia (33.800 S, 151.300 E), and nearby rocky reefs (Northern Sydney rocky reefs: see Supp. Fig. 1). The location is influenced by the seasonal western boundary current (EAC) and the associated eddies that form off of the EAC extension (Cetina-Heredia et al. 2014). SYCOGA is at 10–15 m depth on bare rock substrate, and the proliferation via local propagule release of *P. aliciae* has resulted in approximately 540 m^2 of novel coral habitat to date (*pers. obs.*). This habitat is expanding and infilling as shown in Fig. 1. Surrounding habitat westward (towards shore) is dominated by kelp *Eklonia radiata*, whereas the eastern, northern and southern habitat is predominantly urchin barren and encrusting algae.

Coral habitat surveys were conducted opportunistically between November 2019—May 2021 due to the exposed nature of the location and impact on suitable diving conditions. Each season (summer (December–February), autumn (March–May), winter (June–August) and spring (September–November)) comprised 2–3 sampling expeditions except for summer 2019–2020 ($n = 1$) and winter 2020 ($n = 1$) due to COVID-19 restrictions. A belt transect 6 m wide and 60 m long was laid which was subdivided into 6, sections that were surveyed on each expedition. A diver would slowly traverse the transect recording all fish found within each 10×6 m section.

Rocky reefs were also surveyed adjacent to the coral habitat at the SYCOGA, within typical temperate rocky reef habitat which included kelp (predominantly *Ecklonia radiata*), rock, turfing algae and sponges. In each of 4 months (February to May 2021), five 10×6 m transects were haphazardly placed in habitat adjacent to the coral gardens and surveyed as for the coral beds.

To further compare tropical assemblages on SYCOGA coral habitat to those on temperate rocky reefs, data on species density and species richness of tropical species from four additional rocky reef long-term monitoring sites ('Northern Sydney rocky reefs') nearby in Sydney

Fig. 1 Images of *Pocillopora aliciae* at the Sydney Coral Gardens (SYCOGA) showing coral coverage increase. Left image taken on 14 January 2019 and right image taken on 14 August 2021 (photograph cred. John Sear). Coloured circles indicate the same locations across both images

were included (Booth et al. 2018). To compare with assemblages from transects surveyed in the current study, the area of each roaming transect was calculated through known seabed features in Google Maps and measured as length surveyed (m) × 6 m transect width. Fish were surveyed in the same seasons at both SYCOGA and Northern Sydney rocky reefs.

Fish densities within SYCOGA coral habitat were compared to adjacent rocky reef habitat (2 levels: coral habitat vs rocky reef; Fixed) across the four monthly sampling expeditions during summer/autumn, 2021 (4 levels: February–May; random), through a two-way ANOVA utilising IBM SPSS software (IBM Corp 2019). Density of tropical and temperate species within this test were pooled since no tropical species were observed in the adjacent temperate habitat. Tropical species were defined as those with poleward distribution edges in central SE Australia and occur on the Great Barrier Reef while temperate species are long-term year-round adult residents [e.g. (Fishes of Australia: https://fishesofaustralia.net.au/) and pers. obs.].

To further compare the density of tropical species between SYCOGA coral and directly adjacent temperate rocky reef habitat, densities of the most abundant species were pooled and compared across years (2019–2021) and habitats (Northern Sydney rocky reefs vs SYCOGA coral) using a two-factor ANOVA. The most abundant tropical species were: *Dascyllus trimaculatus, D. reticulatus, Chaetodon auriga, C. flavirostris, C. kleinii, C. guentheri, Acanthurus nigrofuscus* and *Thalassoma lunare.* Since new fish would be observed each year, due to mortality in winter, years were considered to be independent. However, some individuals of *T. lunare* may have persisted through winter into the following years.

Results and discussion

Range-expanding coral *P. aliciae* habitat that has recently established in Sydney supported higher densities of both temperate and expatriating tropical reef fishes than nearby rocky reef habitat, indicating its potential importance as novel fish habitat in temperate south-eastern Australia.

Overall, 8 tropical and 12 temperate fish species were recorded from 11 families within SYCOGA over the study (Supplementary Table 1). Fifteen of the species were observed associating with coral habitat, while 18 were observed associating with rocky reef. Two species were exclusively observed on coral habitat, while five temperate species were exclusively observed on rocky reef habitat. Tropical species were sub-adult except for *T. lunare*, which was present in both sub-adult and adult life stages, and was seen to overwinter on the coral beds. Total fish density was significantly greater (3–10 times) on the coral habitat compared to adjacent temperate rocky reef habitat at SYCOGA (ANOVA, $F_{1,44} = 75.94$, $p = 0.003$, Fig. 2) and this pattern was consistent across the four sampling months (ANOVA, habitat × month, $F_{3,44} = 0.695$, $p = 0.559$).

The density of tropical species associated with SYCOGA coral increased each year, but remained stable at Northern Sydney rocky reef habitat, possibly due to the large increase (over double) in coral cover over that time (Fig. 1) as indicated by a significant interaction between year and location (ANOVA, interaction term, $F_{2,36} = 7.67$, $p = 0.002$, Fig. 3). In 2021, SYCOGA coral habitat supported 2.8 times greater key tropical vagrant densities than 2020 (Tukey's test, $p = 0.007$) and 5.4 times greater than 2019 (Tukey's test, $p = 0.0001$) (Fig. 3).

SYCOGA contained 48 times higher tropical vagrant densities than the Northern Sydney rocky reef during 2021 ($q = 9.187$, $p = 0.0001$) and 7 times greater in 2020 (Tukey's

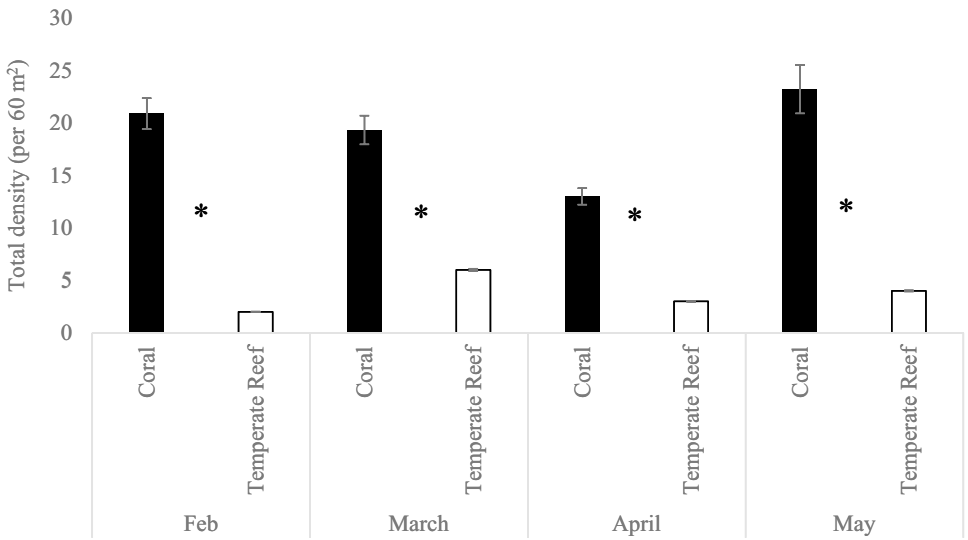

Fig. 2 Fish density (per 60 $m^2 \pm$ SE) of both tropical and adjacent temperate individuals combined on coral habitat vs temperate reef over four sampling months within SYCOGA. *Indicates significance at $p < 0.05$ (n's: coral $n = 6$, temperate reef $n = 5$)

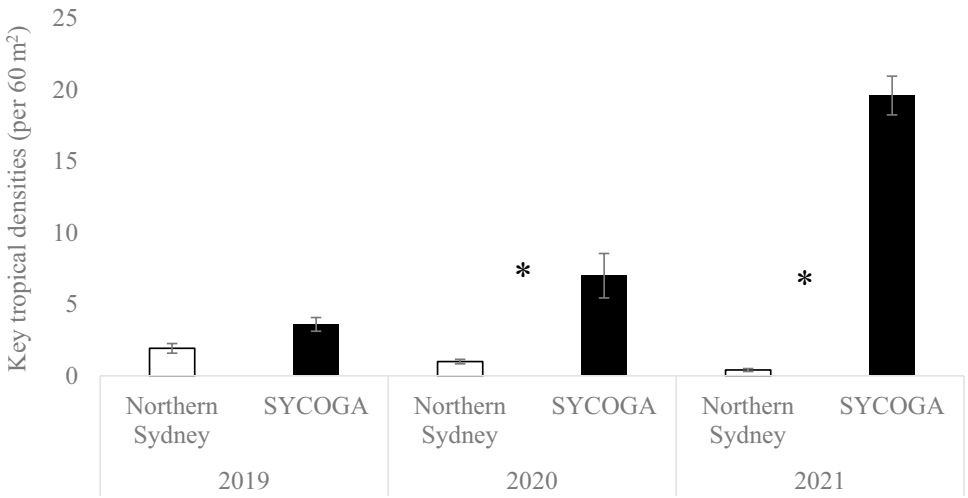

Fig. 3 Tropical vagrant fish species densities across years (2019–2021) between Northern Sydney temperate rocky reef sites and SYCOGA coral habitat. *Indicates significant differences between habitats within years (*n*'s. Northern Sydney $n=4$, SYCOGA $n=6$)

test, $q=5.014$, $p=0.001$); however, no significant differences were observed within 2019 ($p=0.064$) (Fig. 3). Figure 4 shows much higher densities of several key temperate rocky reef and vagrant coral reef fishes on SYCOGA compared to other rocky reef habitats in the area.

This study is the first to comprehensively describe tropical and temperate species associating with this novel coral habitat at its southern range edge. Our findings support a model of tropicalisation, not simplification (sensu Agostini et al. 2021), within SYCOGA. There has been an infilling of barren areas that may have been stable for a long period (e.g. Kingsford and Byrne 2023), with habitat-forming corals on which both tropical and temperate fish species were in much higher density than surrounding barren rock and crustose algae. Therefore, the newly established coral gardens in Sydney provide relatively complex habitat that concentrates (higher densities, more vagrant species) of fish and may facilitate tropicalisation while still providing suitable habitat for temperate fish assemblages. A similar phase shift has been reported from Japan's Tosa Bay, where grazing has removed kelp forests, but infilling of tropical corals has maintained some habitat complexity and resulted in the dominance of tropical fish within temperate communities (Nakamura et al. 2013).

Thalassoma lunare was consistently the most abundant tropical species observed in the current study and similarly abundant throughout the tropical Indo-Pacific region (Parenti and Randall 2011). It was the only tropical species observed in both sub-adult and adult phases at SYCOGA and therefore the only species likely to have survived the winter during the

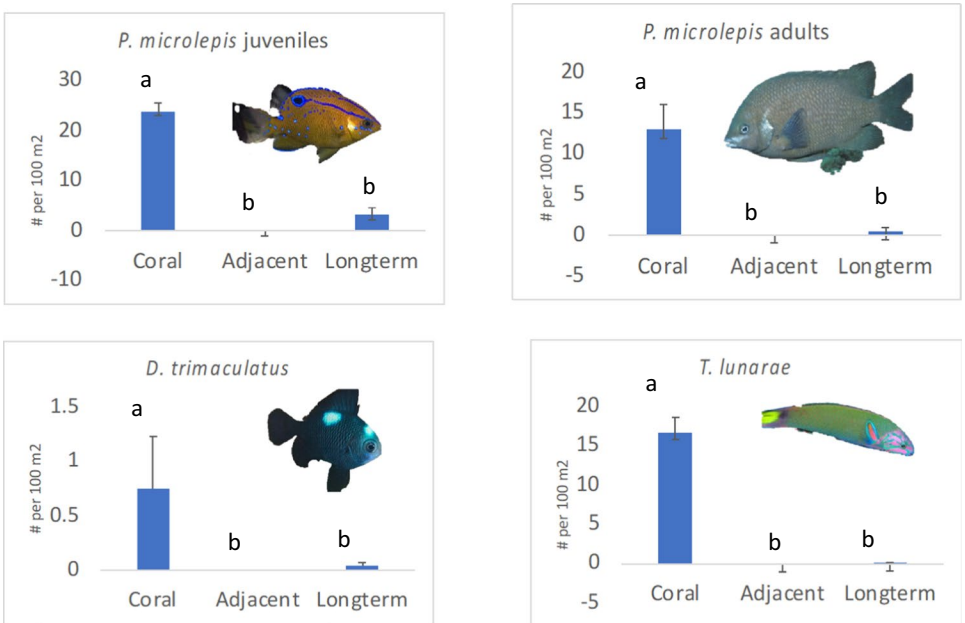

Fig. 4 Comparisons of fish density between SYCOGA coral, SYCOGA rocky reef ('adjacent') and long-term (Northern Sydney rocky reef) survey sites outside of SYCOGA for four key tropical fish taxa during 2021 (Year 2021: mean ± SE) [*P.microlepis* juveniles: ANOVA $F=115.6$, $p=0.00003$; *P. microlepis* Adult $F=167.6$, $p=0.001$; *D. trimaculatus* $F=9.0$, $p=0.007$; *T. lunarae* $F=6.81$, $p=0.01$] (*n*'s: SYCOGA corals: $n=6$; adjacent rocky reef $n=5$; long-term Northern Sydney: $n=4$)

study period. This species is also potentially the first expatriated tropical species to form reproducing populations within SYCOGA, as mating behaviours have been observed there (W. Gladstone *pers. obs.*). Despite some persistence through winter at SYCOGA, densities of *T. lunare* were still reduced during the cooler months of April and June 2020.

In 2022–2023, we have observed further expansion of *P. aliciae* beds at SYCOGA but also at a number of nearby sites, including outer Sydney Harbour, suggesting that its significance as a refuge for tropical and temperate fish species may expand rapidly. Other tropical species, such as *Chaetodon speculum* and *Paracanthurus hepatus*, have bene photographed by amateur divers on the coral, but we only included species we observed during the study period. Therefore, we predict the coral will act as a major vector for tropicalisation and a reef fish hot spot, so whether it should be managed to ensure its protection from human disturbance, or not, given its expansion as a result of human-caused climate change, is unclear. Future investigations should examine the quality of habitat provided by tropical corals in temperate environments, such as those in SYCOGA, and why some but not all local temperate fish species occupy the coral beds, to understand the mechanisms driving higher fish densities on coral relative to natal temperate reef and the potential implications for temperate fish populations as the coral habitat expands.

Acknowledgements The authors would like to thank the University of Technology Sydney technical staff in particular Helen Price and UTS Dive Officer Penelope McCracken for all assistance with field work-related diving safety and gear acquisitions. Furthermore, we would also like to thank Geoff and the team at Dive Centre Manly for the ongoing partnership with UTS. Finally, we would like to thank John Sear for his local expertise and willingness to lend a hand at any moment.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

References

Agostini S, Harvey BP, Milazzo M, Wada S, Kon K, Floc'h N, Komatsu K, Kuroyama M, Hall-Spencer JM (2021) Simplification, not "tropicalization", of temperate marine ecosystems under ocean warming and acidification. Glob Change Biol 27:4771–4784

Baird A, Sommer B, Madin J (2012) Pole-ward range expansion of *Acropora* spp. along the east coast of Australia. Coral Reefs 31:1063–1063

Booth DJ, Sear J (2018) Coral expansion in Sydney and associated coral-reef fishes. Coral Reefs 37:995–995

Booth DJ, Figueira WF, Gregson MA, Brown L, Beretta G (2007) Occurrence of tropical fishes in temperate southeastern Australia: role of the East Australian Current. Estuar Coast Shelf Sci 72:102–114

Booth DJ, Beretta GA, Brown L, Figueira WF (2018) Predicting success of range-expanding coral reef fish in temperate habitats using temperature-abundance relationships. Front Mar Sci 5:31

Cetina-Heredia P, Roughan M, Van Sebille E, Coleman M (2014) Long-term trends in the East Australian Current separation latitude and eddy driven transport. J Geophys Res: Oceans 119:4351–4366

Figueira WF, Booth DJ (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. Glob Change Biol 16:506–516

Fowler AM, Parkinson K, Booth DJ (2018) New poleward observations of 30 tropical reef fishes in temperate southeastern Australia. Mar Biodivers 48:2249–2254

IPCC (2014) Climate change 2013: the physical science basis: working Group I contribution to the 5th assessment report of the intergovernmental panel on climate change. Cambridge University Press

Kingsford MJ, Byrne M (2023) New South Wales rocky reefs are under threat. Mar Freshw Res 74:95–98

Leis JM (1991) The pelagic stage of reef fishes : the larval biology of coral fishes. Ecol Fishes Coral Reefs

Nakamura Y, Feary DA, Kanda M, Yamaoka K (2013) Tropical fishes dominate temperate reef fish communities within western Japan. PLoS ONE 8:e81107

Parenti P, Randall JE (2011) Checklist of the species of the families Labridae and Scaridae: an update. Smithiana 15:29

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I-C, Clark TD, Colwell RK, Danielsen F, Evengård B (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355:eaa214

Pessarodona A, Filbee-Dexter K, Alcoverro T, Boada J, Fehan C, Fredricksen S, Grace SP, Nakamura Y, Narvaez CA, Norderhaug KM, Wernberg T (2021) Homogenization and miniaturization of habitat structure in temperate marine forests. Glob Change Biol 27:5262–5275

Ridgway KR (2007) Long-term trend and decadal variability of the southward penetration of the East Australian Current. Geophys Res Lett 34 L13613. https://doi.org/10.1029/2007GL030393

Schmidt-Roach S, Miller KJ, Andreakis N (2013) *Pocillopora aliciae*: a new species of scleractinian coral (Scleractinia, Pocilloporidae) from subtropical Eastern Australia. Zootaxa

2013(3626):576–582. https://doi.org/10.11646/zootaxa.3626.4.11. (**PMID: 26176158**)

Smith SD, Simpson R (2010) Nearshore corals of the Coffs Harbour region, mid north coast, New South Wales. Wetlands Aust 11: 15–25

Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KL, Booth DJ, Coleman MA, Feary DA, Figueira W, Langlois T, Marzinelli EM, Mizerek T, Mumby PJ, Nakamura Y, Roughan M, van Sebille E, Gupta AS, Smale DA, Tomas F, Wernberg T, Wilson SK (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B: Biol Sci 281:20140846

Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353(6295):169–172. https://doi.org/10.1126/science.aad8745. (**PMID: 27387951**)

Wu L, Cai W, Zhang L, Nakamura H, Timmermann A, Joyce T, McPhaden MJ, Alexander M, Qiu B, Visbeck M (2012) Enhanced warming over the global subtropical western boundary currents. Nat Clim Chang 2:161–166

Yamano H, Sugihara K, Nomura K (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. Geophys Res Lett 38. https://doi.org/10.1029/2010GL046474