Habitat preference and low water temperature tolerance:
key determinants in the successful colonization of tropical reef fishes in temperate waters under climate change

気候変動下での温帯域における熱帯性魚類の定着条件
としての生息場所選好性と低水温耐性の重要性

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Chapter 1: General Introduction

The persistent increase in ocean temperatures globally significantly affected the range distribution of most tropical marine organisms (Brierly and Kingsford 2009), causing range shifts on species sensitive to sea surface temperature (SST) increases—if not adapting—to avoid extinction (i.e., range contraction; Thomas et al. 2004, Brierly and Kingsford 2009; Maggini et al. 2011; Bates et al. 2014). However, most tropical reef fishes expanding ranges experienced conditions outside from their native range, e.g., different habitat structure, high thermal variability (Feary et al. 2014). Hence, this may require strategies and traits, e.g., ecological generalization, phenotypic plasticity, and physiological tolerance, to survive, adapt, and successfully colonize marginal novel environments (Sorte et al. 2010; Bates et al. 2014; Feary et al. 2014; Estrada et al. 2016).

Many of the tropical reef fishes were observed in temperate waters as a response to the favorable condition of the coral-tropicalized reef habitats (Nakamura et al. 2013; Booth and Sear 2018), which have successfully expanded ranges consequent to the persistent ocean warming (Precht and Aronson 2004; Yamano et al. 2011). However, the role of reef habitats in organizing the successful expansion of tropical marine organisms remains unresolved (Bates et al. 2014). In which, the lack of suitable habitat may potentially limit the range-expansion of tropical reef fishes with specific habitat requirements (i.e., habitat specialist Feary et al. 2014), despite the persistent increase of winter temperatures and the consistent transport of poleward-flowing boundary currents.

The constant larval supply of tropical reef fishes to higher latitudes facilitated by poleward-flowing boundary currents (Soeparno et al. 2012) serves as a prerequisite for their range expansion (Booth et al. 2007). However, the wider range of thermal variability and the low water temperatures in temperate waters during winter are known to physiologically limit the performance of most tropical reef fishes (Figueira et al. 2009; Johansen et al. 2015), impairing them to survive and become susceptible to potential predators (Figueira et al. 2009). Hence, this potentially caused constraints on the successful poleward expansion of many tropical reef fishes (Figueira and Booth 2010; Feary et al. 2014). Of which, winter remains the population bottleneck for most range-shifting tropical reef fishes (Figueira et al. 2009; Figueira and Booth 2010; Hirata et al. 2011; Nakamura et al. 2013). Yet, as the water temperature is predicted to increase amidst climate change (Yara et al. 2011), this may potentially favor the successful range expansion of tropical reef fishes, withstanding warmer winters (Figueira and Booth 2010).

This thesis tried to address the potential factors influencing the latitudinal distribution variability of range-shifting tropical reef fishes along the Kuroshio Current by assessing their distribution pattern in three climatic regions—tropical, subtropical, and temperate (Chapter 2), and further subjected representative congeneric species with varying occurrence in temperate-Kochi (southwestern Japan) to low water temperatures in a tank experiment (Chapter 3). Of which, both the habitat availability, and suitability, and the low water temperatures appeared to have a significant impact on the assemblage structure of range-shifting tropical reef fishes in temperate waters, as revealed by the unprecedented occurrence of the extreme cold event in Kochi (Chapter 4). This thesis demonstrates that climatic changes not only alter the system functioning of marine ecosystems but also caused the contemporary range-shifts of many organisms. Of which, the key role of physiological climatic tolerance to winter water temperatures and ecological generalization (e.g., habitat generalist) are crucial factors in predicting a successful range-shifts. Thus, the extent as to which climate change may impact the marine ecosystems (e.g., fisheries and ecosystem services) is critical since ocean temperatures and frequencies of extreme events are predicted to increase amidst climate change, where impacts are inevitable and irrevocable (Chapter 5).

Chapter 2: Latitudinal distribution pattern of tropical reef fishes across three latitudinal climatic regions along the Kuroshio Current

Range-shifts in tropical marine organisms, including reef fishes, are more pronounced in western boundary regions. However, latitudinal distribution patterns of tropical reef fishes along the Kuroshio Current are poorly known, and despite evidence showing their range-shifts, many of tropical reef fish species are still found non-occurring in temperate waters. Since latitudinal population and environmental gradients are important predictors in understanding vagrancy of tropical reef fishes in temperate waters, this chapter aimed to determine the latitudinal distribution pattern of tropical reef fishes in the three climatic regions—tropical, subtropical, and temperate—along the Kuroshio Current.

This chapter selected three separate locations representing the three climatic regions along the Kuroshio Current, i.e., Philippines for tropical, Okinawa for subtropical, and Kochi for temperate. Fish assemblage structures were assessed in all the reef habitats within the respective regions in two different seasons (cool/winter and hot/summer) by the underwater visual census, using SCUBA. Among the habitats identified in each region, coral habitats significantly harbored higher species richness and abundance, including the coral-tropicalized habitats in temperate-Kochi. Each climatic region had different fish assemblage structure, and dominant species, wherein Kochi appeared to have the least species richness and abundance, despite the noticeable occurrence of tropical reef fishes in the area. Also, the notable non-occurrence of some tropical reef fishes in temperate-Kochi may indicate that not all tropical reef fishes have successfully colonized temperate waters. Whereas, the clear seasonal pattern in higher latitudes—subtropical and temperate—and the significant declines in the abundance of some species in Kochi during winter, may indicate that winter water temperature is still a population bottleneck for most vagrant tropical reef fishes. The presence of coral habitats may have considerably facilitated the colonization of most tropical reef fishes in temperate waters. However, the latitudinal distribution pattern and the varying occurrence of some congeneric species in temperate-Kochi may be due to their difference in tolerance to low water temperatures. In this chapter, species with year-round occurrences (with possible reproduction in temperate waters; Hirata et al. 2011; Tose et al. 2017) were referred as adapted species while species showing low abundance to complete absence—during and after winter—and with no adult population in temperate-Kochi (Hirata et al. 2011; Tose et al. 2017) were tagged as non-adapted species.

Chapter 3: Physiological and behavioral responses of tropical reef fishes to low water temperature: differences between temperate water adapted and non-adapted species

Many of the tropical fishes transported to higher latitudes exhibited high mortality rate during winter (Nakazono 2002; Booth et al. 2007; Figueira and Booth 2010; Hirata et al. 2011; Tose et al. 2017). However, the recent significant ocean warming may allow some of these tropical vagrant species to tolerate winter conditions in temperate waters (e.g., Figueira et al. 2009; Figueira and Booth 2010; Nakamura et al. 2013). Despite the mounting evidence of tropical fishes expanding ranges to temperate regions globally, little is known how these species adapt to local conditions (e.g., winter), (Feary et al. 2014), and how closely-related species differ in physiological tolerances to low temperatures. Since winter mortality *in situ* is difficult to quantify (Figueira et al. 2009), this chapter aimed to demonstrate the temperature-specific physiological performances and behavioral responses of congeneric adapted and non-adapted tropical fishes to low temperatures in a tank experiment.

This chapter subjected congeneric adapted and non-adapted species from two fish families, Pomacentridae and Chaetodontidae. Each of which has different latitudinal distribution pattern and occurrence in temperate waters of Kochi, central Tosa Bay (see Chapter 2). Results have shown that low water temperatures affected both the adapted and non-adapted species resulting in declines on their feeding rate as the temperature approached 15°C (lowest winter temperature in Tosa Bay). However, non-adapted species had significantly higher mortality rates than their congeneric adapted species. Most of which also have resulted in a marginally higher temperature ranges on behavioral responses, e.g., minimum acclimation temperature, feeding cessation, and critical thermal minimum, compared with their congeneric adapted species. This indicates that adapted species may physiologically tolerate winter water temperatures than non-adapted species, thereby potentially allowing them to survive and colonize higher latitudes. Such trait is important and a known prerequisite for successful colonization (Bates et al. 2014). Winter temperatures are predicted to increase amidst persistent ocean warming (Yara et al. 2011), thereby potentially allowing not only the adapted but may favorably allow non-adapted species to thrive and colonize temperate waters.

Chapter 4: Unpredictable extreme cold events: a threat to range-shifting tropical reef fishes in temperate waters

Tosa Bay, southwestern Japan is one of the global hotspots of tropicalization, where habitat-forming tropical corals have become established as a result of ocean warming (Yamano et al. 2011). The poleward establishment of corals may have been facilitating the successful colonization of tropical reef fishes in the temperate waters (Nakamura et al. 2013; Booth and Sear 2018). However, climate change has also caused an increasing occurrence of extreme weather events, e.g., extreme cold events (Timmermann et al. 1999; Easterling et al. 2000; Wang et al. 2010; Meehl and Tebaldi 2004). Such cold events are known to have adverse consequences on corals greater than the effects of elevated temperatures (Lirman et al. 2011). However, no published information demonstrated how such cold events affect range-shifting tropical reef fishes in temperate waters.

This chapter semiannually assessed (in winter and summer) the tropical reef fish assemblage structure in Tosa Bay for two years (2017-2018), fortuitously covering the unprecedented extreme cold event that occurred in the bay during the winter of 2018. The event caused an extremely low sea surface temperature (SST) during the winter resulting in a rapid coral bleaching and the subsequent mortality of more than 90% coral during summer. Both the extremely low SST and the massive coral loss resulted in significant declines on the species richness and abundance of tropical reef fishes in the area. In which, the extreme winter affected both the breeding and the non-breeding population while the massive coral loss substantially impacted the coral-associated species, primarily the corallivore fishes. This chapter is the first to elaborate the potential impact of the extreme cold event on the persistent establishment of tropical reef fishes in temperate waters, thus highlighting its potential threat on the stability of temperate waters as a refuge for range-shifting species amidst increasing ocean warming.

Chapter 5: General Discussion

Climate change has caused adverse consequences to the earth's ecological system structure and functioning (Jentsch et al. 2007). Of which, many marine organisms (e.g., corals and reef fishes) are the most affected as they are more vulnerable to rapid changes in ocean temperatures (Munday et al. 2008), thus, resulted in their contemporary range-shifts.

Establishments of marine protected areas (MPAs) may have provided conservation to commercially exploited species and contributing to reef resilience as well as benefits to fisheries through leakage of 'surplus' adults (spillover) and larvae (larval replenishment), (Boersma and Parrish 1999). Of which, effects of climate change and the climate-mediated contemporary range-shifts might be of less concern when it comes to fisheries management since most of the reef fishes are the small-sized non-commercially targeted species where impacts may not directly affect large-bodied commercially important species (Pratchett et al. 2008). However, these MPAs offer limited protection from the impacts of extrinsic disturbances, e.g., climate change (Munday et al. 2008). Wherein, commercial fisheries may still be susceptible to additional impacts from the contemporary range-shifts of reef fishes as they constitute part of its trophic niche. Nevertheless, as climate change causes significant changes to the coral reef ecosystem, this could have implications on fisheries given that corals serve as a source of food and refuge to many marine organisms. This may subjectively affect the biomass of all trophic levels in the marine ecosystem (including the targeted fisheries) and may likely increase the risk of fisheries collapses (Munday et al. 2008) and may affect the services it provided (Booth et al. 2018; Woodhead et al. 2019). Hence, understanding how organisms (e.g., reef fishes) respond to contemporary climatic changes may help facilitate in effectively managing the impacts of climate change and develop sustainable planning and management strategies.

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