Marine Biology (2021) 168:93
https://doi.org/10.1007/s00227-021-03875-2

ORIGINAL PAPER

Cold thermal tolerance as a range-shift predictive trait: an essential link in the disparity of occurrence of tropical reef fishes in temperate waters

Janice C. Leriorato[1] · **Yohei Nakamura**[1] · **Wilfredo H. Uy**[2]

Received: 3 July 2020 / Accepted: 4 April 2021 / Published online: 22 May 2021

Abstract

There is increasing empirical evidence of the shifting range distributions of tropical reef fishes as a response to persistent climatic warming. However, the link between the observed disparity of closely related species' occurrence in temperate waters and their trait-based responses to winter thermal conditions is unclear. This study focuses on congeneric tropical reef fishes with similar dispersal potential (pelagic larval duration) but with varying occurrence in Kochi, southwestern Japan. The studied species include the abundantly occurring, overwintering, and reproductively established species in Kochi (adapted) and the less abundant species with no recorded overwintering and adult populations (non-adapted). This study assessed the responses of congeneric adapted and non-adapted species from two genera of Pomacentridae (*Pomacentrus* and *Dascyllus*) and one from Chaetodontidae (*Chaetodon*) to the winter seawater thermal range in Kochi by subjecting them to the decreasing temperature from 25 to 15 °C (1 °C d^{-1}) in the laboratory. Both the adapted and non-adapted species demonstrated swimming and feeding reductions when temperatures approached 18 °C. However, stress-related behaviors were observed at 17 °C in the non-adapted species compared with 16 °C in their adapted congeners. The non-adapted species also exhibited relatively lower growth rates and higher mortality rates of > 50% during the 3-d exposure to 15 °C, indicating that the minimum winter temperature in Kochi is often lethal to these species. Thus, the present study highlights the species-specific cold thermal tolerance of tropical reef fishes to winter conditions at the leading edge as a useful predictor of a given specie's range-shift capacity.

Introduction

Ocean waters have been undergoing significant warming, turning many temperate marine ecosystems into a global biodiversity hotspot for tropicalization consequent in rapid poleward shifts in tropical organism's geographic distribution (Last et al. 2011; Yamano et al. 2011; Tanaka et al. 2012; Wernberg et al. 2016). Most of these ecosystem transformations occur in regions influenced by poleward-flowing boundary currents (Vergés et al. 2014). Significant warming might allow tropical reef fishes to survive winter conditions in temperate waters (Figueira et al. 2009; Figueira and Booth 2010), as evidenced by their increasing numbers (Booth et al. 2007, 2018; Nakamura et al. 2013). However, not all tropical reef fishes can be found in temperate waters (Feary et al. 2014). In that, post-arrival mortalities in marginal novel environments are complex, and responses to factors contributing to their survival and establishment are species-specific in most teleost fishes (Johnston and Dunn 1987).

Tropical reef fishes are generally warm-adapted species. Hence, the high seasonal thermal variation in temperate waters often subject these fishes to climatic conditions that are very different from those experienced in the tropical coral reefs where they originate (i.e., winter; Feary et al. 2014). Mid-latitude seawater temperatures during winter are typically below the native thermal range of range-shifting tropical reef fishes. Thus, it could be a potential constraint

---

Responsible Editor: S. Hamilton.

Reviewers: undisclosed experts.

✉ Janice C. Leriorato
leinice2000@yahoo.com

[1] Graduate School of Integrated Arts and Sciences, Kochi University, 200 Monobe, Nankoku, Kochi, Japan

[2] Institute of Fisheries Research and Development, Mindanao State University At Naawan, 9023 Naawan, Misamis Oriental, Philippines

on their migration and colonization in temperate waters despite the availability of necessary resources (e.g., food and habitat; Feary et al. 2014). Low water temperatures during winter often cause significant changes in the behavioral and physiological functions of fish (Beitinger and McCauley 1990), which result in high mortality in expatriate tropical reef fishes compared with temperate resident fishes (Figueira et al. 2009). These thermal conditions physiologically challenge tropical reef fishes, affecting their performance/fitness (Figueira et al. 2009; Johansen et al. 2015; Djurichkovic et al. 2019) and metabolic responses (Johnston and Dunn 1987; Guderley 2004; Kingsbury et al. 2019) and often require adaptation strategies for survival (Stevens 1989). Hence, winter temperature, particularly during the first exposure, is thought to be the primary population bottleneck for the survival and establishment of most expatriate tropical reef fish populations at the leading edges (Booth et al. 2007; Hurst 2007; Figueira et al. 2009; Figueira and Booth 2010), regardless of the long-distance dispersal facilitated by poleward-flowing boundary currents (Soeparno et al. 2012).

Many of the expatriated tropical reef fishes in various global biodiversity hotspots have successful overwintering (Booth et al. 2007; Figueira and Booth 2010; Nakamura et al. 2013) and reproduction (Pearce et al. 2016; Tose et al. 2017). The temperate waters of Kochi, southwestern Japan, is one of these global hotspots, where tropical reef fishes mainly occurred in tropicalized coral habitats and are abundant during summer and throughout the autumn season (Hirata et al. 2011; Nakamura et al. 2013; Tose et al. 2017). Most of these tropical reef fishes are presumably a recruit of mixed populations from the southern regions (e.g., Okinawa and Philippines) since they are believed to have been transported by the Kuroshio Current during the larval stage (Soeparno et al. 2012). However, it remains unclear why few tropical reef fishes occur and establish populations in temperate waters despite contemporary ocean warming (Feary et al. 2014). A few studies have tested the performance of tropical reef fishes under low water temperature conditions, demonstrating that winter temperatures are a potential barrier for the occurrence of some tropical teleost fishes at higher latitudes (Eme and Bennett 2008; Figueira et al. 2009; Johansen et al. 2015). These studies suggest that species-specific cold thermal tolerance could be an essential driver of the range-shift success of tropical reef fishes. However, to our knowledge, no studies have directly compared and assessed the direct linkage of mid-latitude winter thermal tolerance and the range distribution disparity of closely related tropical reef fishes (particularly their occurrence in temperate waters).

In the present study, we classified tropical reef fishes according to their latitudinal distribution and occurrence, particularly in the temperate waters of Kochi (as temperate-established and temperate non-established). We hypothesized that temperate-established species had developed tolerance to mid-latitude winter thermal conditions, even at temperatures below 16 °C. Hence, they are referred to as adapted species since they exhibit year-round occurrences with overwintering records, adult populations, and reproduction in temperate Kochi (Hirata et al. 2011; Tose et al. 2017). On the other hand, we hypothesized that temperate non-established species are incapable of adapting to mid-latitudinal winter thermal conditions where the minimum seawater temperature in Kochi (c. 15 °C) is presumed lethal to them. This is because they are present in low abundance to complete absence during and after winter, with no recorded adult populations or reproduction in Kochi (Hirata et al. 2011; Tose et al. 2017), hence referred to as non-adapted species. Our study addresses the individual responses of tropical reef fishes to low seawater temperatures as a possible limiting factor in the variation in range shifts among closely related species. We compared the performance (feeding and growth), activity levels, and thermal tolerance of adapted and non-adapted congeneric species to the decreasing water temperature as well as their thermal resistance (i.e., time to death or survival) to the average recorded minimum seawater winter temperature at Kochi (15 °C).

Materials and methods

Selection of fishes

Before the experiment, we conducted a 2-year fish survey (underwater visual census) in coral habitats in three climatic regions of the northwestern Pacific—i.e., the tropical Philippines, subtropical Okinawa, and temperate Kochi—to determine the latitudinal distribution and seasonal occurrences of tropical reef fishes, particularly in Kochi (see Fig. S1 site maps and sampling details). We then classified tropical reef fishes based on their occurrence throughout and after Kochi’s winter season (during the fish survey and their previous occurrence records), as well as the presence of adult and reproducing populations (see Table S1 list of tropical reef fishes; Hirata et al. 2011; Nakamura et al. 2013; Tose et al. 2017). The abundantly occurring tropical reef fishes in Kochi, with records of overwintering, adult, and reproducing populations, were presumed to have adapted to mid-latitudes winter thermal conditions, hence identified as the temperate-established species (referred to as adapted species, Table S1). Contrarily, species with no reported records of overwintering and adult populations and are less abundant or rarely occurring species in Kochi were assumed to be incapable of adapting to the mid-latitude winter conditions, hence identified as temperate non-established (referred to as non-adapted species).

We then selected a congeneric adapted and non-adapted species pair from three genera: *Pomacentrus*, *Dascyllus* (family Pomacentridae), and *Chaetodon* (family Chaetodontidae)—with similar behaviors and diets to avoid different interpretations of the results owing to trait discrepancy. These were: *P. coelestis* and *P. moluccensis*, *D. trimaculatus* and *D. aruanus*, and *C. auriga* and *C. vagabundus*, as the adapted and non-adapted species of each genus, respectively (Table S1). Although *C. vagabundus* are regularly found at Kochi, they are less abundant, with no recorded overwintering and adult individuals in the area (Hirata et al. 2011; Nakamura et al. 2013), hence categorized in this study as non-adapted species. Juvenile individuals of the selected tropical reef fishes were obtained from aquarium fish traders. The traders collected the targeted species from low-latitude waters in subtropical Okinawa (*D. trimaculatus*, *D. aruanus*, and *P. moluccensis)* and the tropical Philippines (*C. auriga*, *C. vagabundus*, and *P. coelestis)*. They immediately transported the collected fishes to the experimental site after obtaining the desired number of individuals (c. 23–25 per species), which were acclimated and maintained at 25 °C before and during transport (per our instructions).

Experimental design

Okinawa island, the largest of the island chain off the coast of southwest Japan (i.e., the Ryukyu Islands), is located along the path of the Kuroshio Current (Uchiyama et al. 2018), where it has an average minimum sea surface temperature (SST) of 21 °C during winter (Hongo and Yamano 2013; Sakai et al. 2019). Conversely, the Philippine Archipelago is among the tropical islands in the northwest Pacific where the Kuroshio Current originates (i.e., at its northeast coast, off Luzon; Nitani 1972; Su et al. 1990). Its coastal waters experience an average minimum SST of 26 °C during the cold season (i.e., from December−March; https://seatemperature.net/current/philippines/manila-sea-temperature). Thus, the purpose of collecting fishes outside of Kochi was mainly to assess the mid-latitude winter thermal responses of tropical reef fishes from areas that have a potential source of larvae yet have thermal conditions that are different from Kochi. This approach prevented the maternal effects of heritability to survival (i.e., local adaptation traits to mid-latitudinal winter thermal conditions; Vehviläinen et al. 2008; Nielsen et al. 2010; Prchal et al. 2018) while ensuring that their first exposure to mid-latitude winter seawater thermal conditions was through the experimental simulation trials. This approach also eliminated potential difficulties in collecting rarely occurring non-adapted fishes from Kochi (e.g., *P. moluccensis* and *D. aruanus*; Hirata et al. 2011; Tose et al. 2017). All experiments were performed in a temperature-controlled laboratory at the Usa Marine Biological Institute, Kochi University (33°26′19″N, 133°26′34″E), from late autumn to early spring (Nov 2017 to Mar 2018).

After receiving the fish, we directly placed them in a 70 L holding tank filled with seawater and maintained it at 25 ± 1.0 °C (using a GEX aquarium temperature controller). We then selected 20 fish individuals per species (unfed) with nearly equal body sizes and measured their weight to the nearest 0.01 g using a millimeter-calibrated mini-aquarium (halfway filled with seawater) on a top-loading balance. Photos were collectively captured during each fish's weight measurement and analyzed using an image processing tool, FIJI (Fiji Is Just Image-J 1.52a; Schindelin et al. 2012), for fish length measurements. Despite our use of juvenile individuals, the size ranges used in this study were typical of those found during the autumn and winter months in Kochi (Hirata et al. 2011). Half of the selected fish individuals (c. $n = 10$ per species) were randomly placed for each temperature treatment (control and cold) where they were individually housed in separate glass aquariums ($15 \times 15 \times 15$ cm^3), i.e., yielding a total of ten aquariums for adapted and ten for non-adapted species per treatment. The selected species are typically social or schooling species, while our experimental set-up's densities did not precisely mimic reef conditions. However, individual housing of fish was used to avoid any social interactions with conspecifics (e.g., feeding competition, Ward et al. 2006) that might affect an individual's behavior and performance (Réale et al. 2007). Such an approach is commonly used in thermal performance experiments (e.g., Eme and Bennett 2008; Figueira et al. 2009; Johansen et al. 2015). Each aquarium contained a piece of coral rubble and was visually isolated from other aquariums and observers using plastic divisions and sheeting to avoid any influence of neighboring environments on performance measures during the experiment.

We then performed the experiments on congeneric (adapted and non-adapted) species separately for each genus. The control fishes were maintained at 25 ± 0.2 °C (using aquarium heaters and cooler, Zensui ZC-200α) throughout the entire 12-d experimental period (Fig. 1). Cold test fishes, on the other hand, were subjected to a temperature decrease rate of 1 °C d^{-1} (Zensui ZC-200α) using the dynamic temperature tolerance method (i.e., minimum chronic lethal methodology, CLM$_{\mathrm{min}}$; Beitinger et al. 2000; Fig. 1). Digital aquarium tetra thermometers were used to monitor real-time temperature fluctuations, while temperature loggers (HOBO Pendant UA-001-08, Onset Computer Corp., USA; logged every 15 min) were used to record the temperature fluctuations in both treatments (control and cold) during the experimental trials (see Fig. 1). While the temperature change rate in this study (1 °C d^{-1}) might not mimic natural daily decreases in the wild, this method is known to generate better estimations of a specie's lower temperature tolerance (Beitinger et al. 2000). This method is also

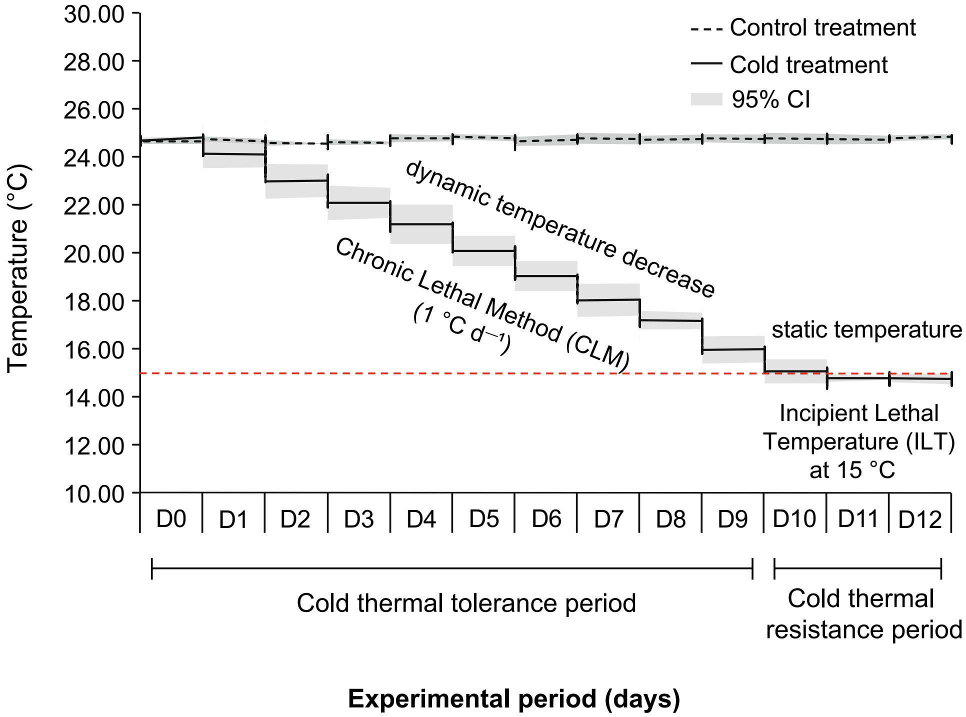


Fig. 1 Water temperature set-up for each treatment (control and cold) within the experimental period (~ 12 d; D: day). Control temperatures were maintained at 25 °C, and cold temperatures were decreased at a constant rate (1 °C d^{-1}) using the chronic lethal method (CLM) for 10 d (cold thermal tolerance period) and maintained at 15 °C for 3 d (cold thermal resistance period) using the incipient lethal temperature method (ILT). The black solid and broken lines represent average temperatures, and the gray-shaded areas are 95% confidence intervals of the logged temperatures (pooled) in each treatment tank. The red broken line indicates the lowest temperature limit used for the cold treatment set-up (15 °C)

applied in determining feeding cessation (Eme and Bennett 2008), and other behavioral characteristics in fishes where death is typically employed as the endpoint (Kimball et al. 2004; Eme and Bennett 2009) since in situ winter mortality is difficult to quantify (Figueira et al. 2009). Here, we chose 25 °C as the control temperature because it represents the average seawater temperatures of early autumn in Kochi (occurrence peak of tropical reef fishes; Hirata et al. 2011; Nakamura et al. 2013). The selection of 15 °C as the lowest test temperature for CLM_{min} was based on the average recorded winter seawater minima at Kochi (Nakamura et al. 2013; Leriorato and Nakamura 2019). The recorded minimum winter seawater temperature in Kochi typically persists for 3 d during the current winter condition (Nakamura et al. 2013; Leriorato and Nakamura 2019). Because time and temperature are significant lethality elements (Fry 1971), fish individuals that reached 15 °C were kept at this temperature (SD = 0.1–0.5 °C) for 3 d to evaluate their thermal resistance (i.e., time to 50% mortality) using the incipient lethal temperature (ILT) technique (Fry 1947). Hence, this was the basis for determining whether the minimum seawater temperature in Kochi is lethal to expatriated tropical reef fishes. The gradual decrease rate of 1 °C d^{-1} (using CLM_{min}), before fishes were kept at 15 °C for 3 d, is a more ecologically realistic method than acutely plunging them in low-temperature levels (Beitinger et al. 2000). This method also moderately exposes fishes to changing temperature conditions that are enough (neither too slow nor too fast) for them to track the environmental temperature—i.e., unlike the rate change used in the critical thermal method (CTM), which is usually biased toward low or high temperatures (Beitinger et al. 2000). We also simulated the winter photoperiod with a 10 h (0800–1700)/14 h (1700–0800) light/dark cycle using artificial lighting with a digital program timer (Revex PT70DW), as photoperiod could also be a factor in seasonal variation (Hoar 1956; Guderley et al. 2001). During the experimental period, pH levels for all treatment set-up were daily measured while ammonia levels were monitored every 2–3 d using NH3/NH4 + test kit (TETRA Co. Ltd.), wherein both parameters were kept at recommended values for reef aquaria (ammonia: 0 ppm; pH: between 7.80 and 8.50). Uneaten food and feces were siphoned daily, and 20–30% of the aquarium water was replaced with clean seawater at temperatures similar to those of the treatment aquaria.

Performance measures

Before temperature manipulation trials, transferred fish individuals (from the holding tank to the individual aquarium) were acclimated to experimental conditions (25 ± 1.0 °C) using an aquarium heater and aquarium cooler (Zensui ZC-200α) and were allowed to recover from the effect of handling for 24–72 h (Black 1955; Smit et al. 1971; Beitinger and McCauley 1990; Pike et al. 2008). During this period, the fish were fed ad libitum with commercial small-sized dry pellets (Megabite red, Kyorin Co. Ltd.). Fish individuals that died during this period were replaced with extra acclimated individuals, except for species with no individuals available for replacements (yielding a sample of $n < 10$). Experimental trials were started briefly after the fish became accustomed to the experimental aquarium conditions, at least 24 h of initial acclimation. The fish in both treatments (control and cold) were fed twice daily (morning and afternoon, with the food introduced during acclimation). Swimming activity and feeding behavior were collectively assessed during afternoon feeding (and between 1–3 min before and after the afternoon feeding) both visually and via video recordings (using GoPro cameras). This approach reinforces the efficiency of quantifying feeding rates in fishes while concurrently quantifying different responses that they exhibited before and after feeding, as the temperature decreased. As fishes tend to eat a lot and fast enough to be visually quantified, the feeding rates of individual fish was analyzed using a video editing tool (Adobe Premiere Pro CC v12.0, Kentos) to count the number of pellets ingested min^{-1} after the first bite was initiated and to ensure that the feeding rates were fairly quantified for all the test fishes. During low temperatures in the cold-experimental trials, the period and temperature during which an individual fish became unresponsive to food or failed to ingest pellets were noted. Hereafter, these individuals were referred to as fishes that exhibited feeding cessation (Beitinger et al. 2000; Eme and Bennett 2008). This information was collected for every individual fish of each species in the cold-experimental trials. Thus, observed feeding cessation periods were categorized as FC_{10} when 10% of individuals within the population exhibited feeding cessation, FC_{50} when at least 50% of the population exhibited this behavior, and FC_{min} when at least 90% of the population exhibited this behavior. During the period at which each individual demonstrated feeding cessation, the logged temperature was used to calculate the average temperatures of FC_{10}, FC_{50}, and FC_{min} for each species.

Conversely, since different species (particularly from different genera) demonstrated different behavioral responses to decreasing temperature, we grouped the observed responses into five categories: normal activity, reduced activity, stressed behavior, critical behavior, and death point. We defined the normal activity category as having the optimal temperature range or a normal physiological range (Elliot 1981). In this category, fishes demonstrated free-swimming behavior, attentiveness during feeding, and/or other considered normal activities, i.e., without demonstrating abnormal behaviors or any observable signs of thermal stress (Elliot 1981). Cold test fishes then exhibited various "non-normal" progressive responses as the water temperature approached and reached below 18 °C (i.e., the onset of winter seawater temperature in Kochi). Hence, we categorized these responses into three phases, from the least obvious to the critically obvious thermal stress signs. The first phase (referred to as the reduced activity category) includes subtle clinical signs of thermal stress in individual fish, such as reduced swimming and/or feeding activity. We then noted the minimum temperature during which a fish exhibited a significant reduction in swimming and feeding activities (i.e., before the onset of feeding cessation) and labeled it as the minimum acclimation temperature, AT_{min} (Eme and Bennett 2008). In the second phase (referred to as the stressed behavior category), most cold test fishes exhibited "abnormal behavior" or indicative thermal stress responses. These include body discoloration (e.g., darkening or paling), frequent rapid muscle twitches, erratic or agitated swimming, indications of stimuli disorientation or loss of visual, olfactory, and/or physical stimuli—that often result in the inability to locate and determine food or barriers, incidental light wall bumps, and/or unsuccessful capture and ingestion of pellets—and exhibiting feeding cessation (Elliot 1991; Beitinger et al. 2000; Kimball et al. 2004). We recorded the minimum temperature before fishes demonstrated critical behaviors as the minimum thermal stress (ST_{min}). Lastly, the third phase (referred to as the lower critical thermal range or the critical category) was the period at which individual fish demonstrated critically apparent behavioral disturbances (Elliot 1981) or experienced locomotory disorganization and inability to maintain dorso-ventral orientation (loss of equilibrium, LOE; Beitinger et al. 2000). These are leaning at the sides, vertical swimming, stationary movement coupled with sporadic, sudden swimming bursts when startled (which often result in frequent collisions into the wall), and coma (termed as the final LOE; where fish had no reactions when prodded; Elliot 1991; Kimball et al. 2004). We then recorded the temperature and period at which fishes exhibited final LOE or vertical swimming for at least 1 min as the critical thermal minimum, CT_{min} (Bennett and Beitinger 1997; Beitinger and McCauley 1990; Beitinger et al. 2000). In most critical thermal (CTM) experiments, the third phase is commonly used as the endpoint to represent the sublethal (near-lethal tolerance) stage of fishes (Beitinger et al. 2000). It is also considered as the ecological death (known as the pre-death thermal point; see a review by Beitinger et al. 2000), where fishes usually recover after being gradually subjected to increasing temperatures until they reach their acclimation temperature (Eme and Bennett 2008). Conversely, a death point (DP) was identified when fish demonstrated a complete cessation of fin and opercular movements and a loss of touch response (Beitinger et al. 2000). Although we did not want a fish to die in this study, the addition of DP to CT_{min} was intended to generate and compare both the sublethal and lethal estimates of adapted and non-adapted congeneric species at 15 °C. Of which, the subsequent application of CLM's dynamic decreasing temperature rate ($1\ ^{\circ}\text{C d}^{-1}$) and ILT's static temperature at 15 °C in this study was to determine a fish's thermal tolerance to Kochi's winter thermal range and their thermal resistance (i.e., time to death after exhibiting critical behaviors) to the area's persistent periods of minimum winter seawater temperatures (c. 3 d, Leriorato and Nakamura 2019). Thus, if the mortality rate was low for a given species throughout the cold-experimental trials, the temperature (CT_{min}) and period (exposure day) at which final LOE occurred in at least 50% of their population were considered ecologically lethal (Beitinger et al. 2000). At the end of the experiment, the temperature was gradually increased (at a rate of 0.5 °C h^{-1}) to the control temperature (25 °C). The lengths and weights of both the surviving and dead fish were again quantified during the gradual increase of temperature, and the survival ratios for adapted and non-adapted cold test species were noted. We only obtained the weight and length measurements twice (before and after the experiment) for unfed fish individuals, and the differences in the lengths were non-significant. Hence, to determine the growth of the individual fish, we utilized the final mass (M2), initial mass (M1), and time (Δt, in days) using the following instantaneous growth formula (G_{inst}; Figueira et al. 2009).

$$G_{inst} = \frac{\ln\left(\frac{M_2}{M_1}\right)}{\Delta t}$$

Statistical analyses

The mean temperatures at which minimum thermal responses occurred in fish individuals of each species, e.g., minimum thermal acclimation (AT_{min}), minimum thermal stress (ST_{min}), minimum feeding cessation (FC_{min}), and critical thermal minima (CT_{min}), were calculated from each cold-experimental trial and analyzed using general linear model (GLM) univariate analysis (overall and per congeneric species pair). For AT_{min}, species type (adapted and non-adapted) was treated as a fixed factor, and for ST_{min} and CT_{min}, the 3 d exposure to 15 °C was dummy-coded and included as a fixed factor. The correlation effect of decreasing temperature and species type (adapted and non-adapted) on the behavioral responses of cold test fishes (e.g., the transition of active swimming to reduced, stressed, and critical behaviors) was determined using the chi-squared test for independence (Phi/Cramer's V on satisfied assumptions) and Fisher's exact test (Fisher–Freeman–Halton; on violated chi-squared assumptions). The differences in behavioral responses (i.e., active swimming, stressed behavior, and critical behavior) exhibited by individual cold test fish [expressed as the percentage (%)] between each congeneric species pair were further compared using a GLM repeated measures analysis where the decreasing temperature (experimental days) was treated as the within-subject variable. The feeding rate was also analyzed using a GLM repeated measures analysis, and the results were interpreted based on the satisfied assumptions of sphericity (Mauchly's). Alternative adjustments (e.g., Huynh–Feldt correction: epsilon > 0.75; Greenhouse–Geisser: epsilon < 0.75; Girden 1992) were then interpreted for unsatisfied sphericity of within-subject designs to mitigate an increase in the Type I error rate. Trial time in days (or decreasing temperatures in the cold treatment) was treated as a within-subject variable, and the treatment (control and cold) and species type (adapted and non-adapted) were treated as between-subject factors (for the overall and per congeneric species pair). The mean and relative (percentage) differences in each specie's daily feeding rate between the control and cold treatments were calculated and compared using an independent sample *t* test. Fish individuals that did not eat from the start of the experiment (i.e., at warmer temperatures for cold trials) or only ingested a few pellets intermittently throughout the experimental period were referred to as "non-feeding individuals" and were excluded only from the computations of the feeding rate and the mean temperature of feeding cessations in the cold treatment (FC_{10}, FC_{50}, and FC_{min}). The mean temperatures of FC_{50} and FC_{min} between each congeneric adapted and non-adapted species pair were compared using an independent samples *t* test. GLM univariate analysis was also used to compare the growth rates of test fishes (per species, congeneric species pair, and overall) between treatments (control and cold) and the difference between each congeneric adapted and non-adapted species pair in each treatment. Datasets were tested for normality (using the Kolmogorov–Smirnov test and the Jarque–Bera test) and homogeneity of variance (using Levene's test) before performing all analyses. Appropriate transformations were performed on non-normal data depending on the degree of skewness and kurtosis (Tabachnick and Fidell 2013) and alternative transformations (e.g., box-cox, Osborne 2010; two-step, Templeton 2011) for substantially non-normal datasets. No control test fishes died during the experimental trials, and the survival (mortality) distributions in cold test fishes for each congeneric species pair (adapted and non-adapted) were compared using Kaplan–Meier survival analysis [log-rank (Mantel–Cox)]. Survival (mortality) analysis was further expanded using Cox stratified (no-interaction) model regression analysis, i.e., the best model fit to consider additional risk factors of the behavioral responses and to determine cause-specific covariates for mortality and the occurrence of the final LOE in cold test fishes during the 3-d exposure to 15 °C. Species type was used as the strata variable (i.e., adapted = 1, non-adapted = 0), and the assumption for the no-interaction model was checked via −2 log-likelihood difference with the interaction model (Kleinbaum and Klein 2012). Behavioral response variables (feeding cessation, reduced activity, and stressed and critical behaviors) were treated as binary covariates based on their occurrence (i.e., yes = 1, no = 0) and were tested for proportional hazard assumptions via Schoenfeld residuals (partial residuals in SPSS) and log–log plots prior to the analysis. The rest of the analyses were conducted using the software SPSS version 23 (IBM Corp. 2015) except for the normality tests and data transformations, which were performed using the software PAleontological STatistics version 2.17 (Hammer et al. 2001) and SPSS.

Results

Behavioral responses of tropical fishes to the mid-latitude winter seawater thermal range

Control test fishes maintained free-swimming behaviors at 25 °C throughout the entire experimental period, which was considered normal for comparison with test fishes that exhibited reductions in swimming activity in the cold-experimental trials (Fig. 2a). Swimming reduction in cold test fishes strongly correlated to decreasing temperature (Cramer's $V=0.75$, $p<0.001$), and despite no correlation to species type (Phi = 0.01, $p=0.774$), many individuals of non-adapted species reduced swimming earlier compared to that in their adapted congeners, particularly when the temperature approached 18 °C (i.e., the onset of winter water temperature in Kochi; Fig. 2a). Some *D. aruanus* individuals (non-adapted) reduced swimming at 21 °C, which was three degrees significantly higher than its adapted congener, *D. trimaculatus* (Greenhouse–Geisser, $F=4.93$, $p=0.006$; Fig. 2a). Hence, this significantly resulted in a 67% difference between the *Dascyllus* species pair at 19 °C (GLM: $t=-3.62$, $p=0.006$) and 90% at 18 °C (GLM: $t=-4.15$, $p=0.003$; Fig. 2a). Although non-significant, some individuals of non-adapted *C. vagabundus* and *P. moluccensis* also exhibited swimming reductions earlier, i.e., one degree higher than their adapted congeners (Fig. 2a). Thus, this resulted in a significantly higher overall recorded minimum acclimation temperature (mean $AT_{min} \pm SD$) for non-adapted species, i.e., 16.8 ± 1.09 °C, compared to the overall mean $AT_{min} \pm SD$ in the adapted species, i.e., 16.2 ± 1.02 °C, (GLM: $t=-2.10$, $p=0.041$; see Table 1 for values in each species). The mean AT_{min} differed significantly among genera ($F=5.45$, $p=0.009$), and only *Dascyllus* showed significantly different mean $AT_{min} \pm SD$ between species type, i.e., 15.5 ± 0.73 °C ($n=10$) for *D. trimaculatus* and 17.5 ± 0.93 °C ($n=9$) for *D. aruanus* (GLM: $t=-6.44$, $p<0.001$; Table 1).

Stress-related behaviors (i.e., mainly correlated with low temperatures, Fisher's exact test = 292.96, $p<0.001$) started to occur in cold test fishes when the temperature dropped below 18 °C (Fig. 2b–d). Most non-adapted species exhibited higher stressed behavior as compared with their adapted congeners (Huynh–Feldt, *Chaetodon*: $F=6.88$, $p=0.001$; *Dascyllus*: $F=3.67$, $p=0.018$), which typically started at 17 °C (compared to 16 °C in adapted species, except for *C. auriga*: $n=1$). More than 80% of the population in most non-adapted species exhibited significantly increased stressed behaviors on day 1 (*Chaetodon*: $t=-2.16$, $p=0.049$; *Dascyllus*: $t=-3.55$, $p=0.006$) and day 3 (*Chaetodon*: $t=-6.71$, $p=0.001$) of exposure to 15 °C (Fig. 2c–d). Although 88% of *D. trimaculatus* (adapted) exhibited stressed behaviors, which was significantly higher than *D. aruanus* (non-adapted) on day 3 of exposure to 15 °C (Fig. 2c), none of its individuals exhibited critical behavior (with no mortality recorded) on the same day. Nevertheless, the difference in the overall mean ST_{min} values for the adapted and non-adapted species was non-significant ($F=0.23$, $p=0.634$), and *D. trimaculatus* still had a significantly lower average ST_{min} than *D. aruanus* ($F=10.50$, $p=0.006$; Table 1).

Some individuals in cold test fishes started exhibiting critical behaviors on day 1 of exposure to 15 °C, which typically increased on days 2 and 3 (GLM: $t=-7.59$, $p<0.001$; Fig. 2b–d) as its occurrence strongly correlates with low temperature (Fisher's exact test = 57.46, $p<0.001$). Regardless of the non-significant difference in the average CT_{min} values of adapted and non-adapted species ($F=1.17$, $p=0.294$) and no correlation of occurrence of critical behavior with species type (Fisher's exact test = 1.12, $p=0.611$), most non-adapted species exhibited relatively higher critical behavior on days 2 and 3 of exposure to 15 °C compared with their adapted congeners (Fig. 2b–d). The 0% occurrence of critical behavior in *C. vagabundus* (non-adapted) on day 3 of exposure to 15 °C was a result of the death of its individuals that experienced critical behavior on day 2 where 100% of its remaining alive individuals ($n=3$) exhibited stressed behavior on day 3 (Fig. 2d). Behaviors of all the remaining live individuals of each cold test fish slowly reverted to normal conditions (e.g., normal coloration and swimming activity) after reaching their AT_{min} temperature ranges during the gradual temperature increase back to 25 °C after the experiment.

Although the feeding rates for all the control test fishes demonstrated an increasing and persistently high pattern throughout the experimental period, the feeding rates in all adapted and non-adapted species in the cold treatment significantly reduced with the decreasing temperature ($F=101.67$, $p<0.001$; Fig. 3). This decreasing feeding pattern correlated with the reduction in swimming activity and responses in all cold test fishes (Figs. 2a, 3). During reduced swimming activity, cold test fishes still effectively captured food but at a reduced rate compared to that of the control test fishes. The significant feeding reductions in most adapted and non-adapted cold test fishes were typically observed at 21 °C as compared to the control (GLM: $t=3.38$, $p=0.001$; Fig. 3). However, non-adapted cold test fishes experienced a steep decline in feeding rates at higher temperatures (i.e.,

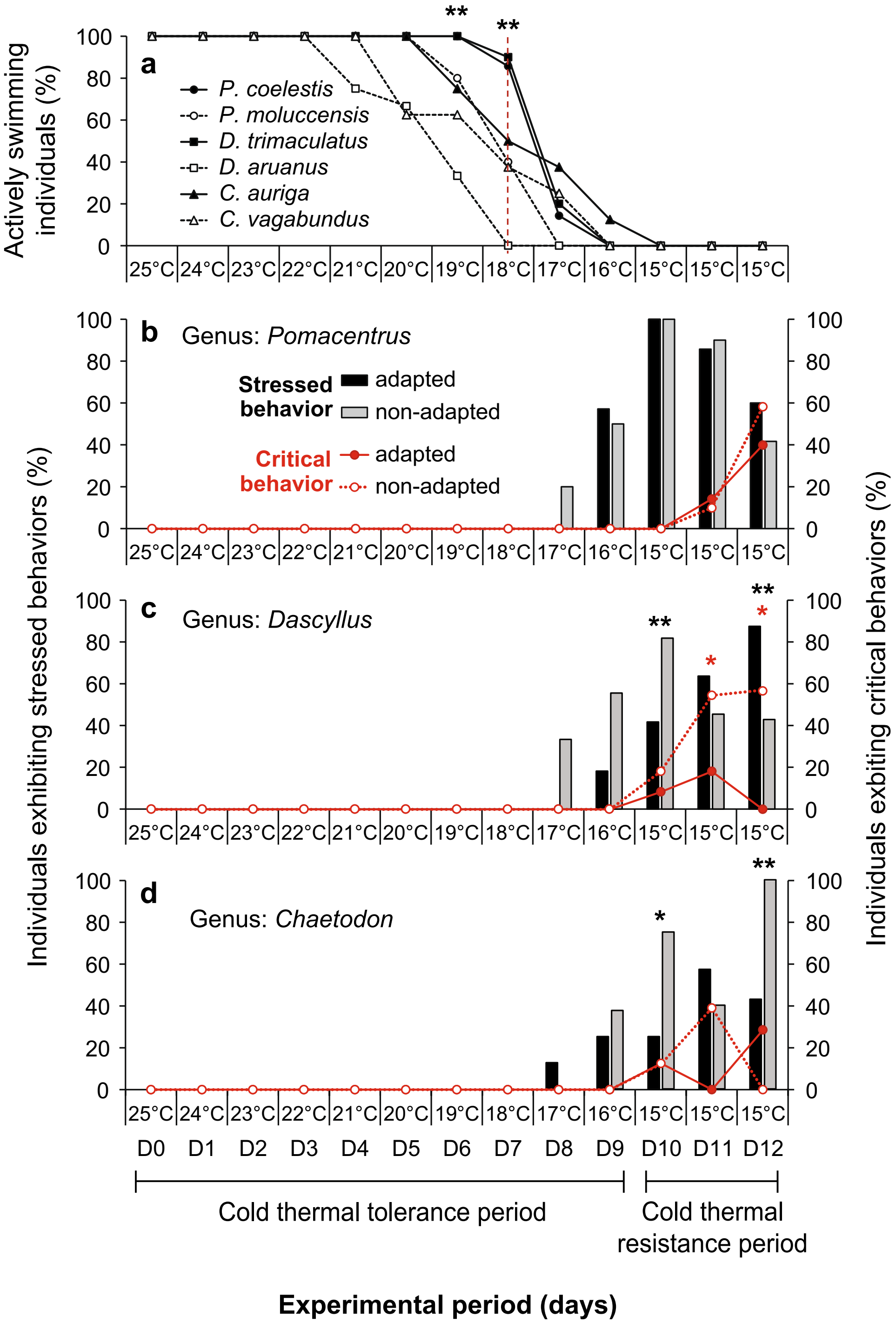


Fig. 2 **a** Percentage of fish individuals that were actively swimming within each population of congeneric adapted (solid black markers and lines) and non-adapted (empty markers and broken black lines) species pair of the three genera: *Pomacentrus* (circle markers: *P. coelestis* and *P. moluccensis*), *Dascyllus* (square markers: *D. trimaculatus* and *D. aruanus*), and *Chaetodon* (triangle markers: *C. auriga* and *C. vagabundus*) during decreasing temperatures (25–15 °C; cold thermal tolerance period). The red long-dash line represents the 18 °C thresholds (onset of winter seawater temperatures in Kochi). Asterisks denote significant differences in the percentage between the congeneric species pair of *Dascyllus* per day (**$p < 0.01$). **b–d** Percentage of fish individuals that exhibited stressed behavior (bar chart) and critical behavior (line chart) at low temperatures, particularly during the 3 d exposure to 15 °C (cold thermal resistance period), within each population of the species pairs of genus **b** *Pomacentrus*, **c** *Dascyllus*, and **d** *Chaetodon*. The black bar denotes the percentage of stressed individuals for adapted species, and the gray bar represents non-adapted species. The solid red line (and marker) is the percentage of individuals from the adapted species exhibiting critical behaviors, and the red dotted line (and empty marker) is for the individuals of non-adapted species. Asterisks denote significant differences in stressed (black) and critical (red) behaviors between congeneric species pair per day (*t* test: *$p < 0.05$; **$p < 0.01$)

24 °C until 21 °C, days 1−4) compared to that in their adapted congeners (Fig. 3 right panels). This resulted in an earlier occurrence of feeding reductions of > 40% in most non-adapted species, i.e., *D. aruanus*: at 22 °C; *C. vagabundus*: at 20 °C), as compared to their adapted congeners (*D. trimaculatus*: 20 °C; *C. auriga*: 19 °C; Figs. 3, 4). It generally took 3–5 days of decreasing temperature (1 °C d^{-1}) for 10% of the population in each cold test fish to exhibit feeding cessation (FC_{10}) from the significant reduction of at least 40% in feeding rates (Fig. 4). However, non-adapted species initially exhibited feeding cessation (FC_{10}) at mean temperatures of approximately 17 °C (i.e., *P. moluccensis*: 16.6 ± 0.63 °C; *D. aruanus*: 17.5 ± 0.72 °C; *C. vagabundus*: 16.9 ± 0.68 °C; Table 1), which was a degree higher than that of their adapted congeners (Fig. 4). Most feeding cessations of ≥ 50% of the population (FC_{50}) in non-adapted

Table 1 Number of samples (n; in control and cold treatments), thermal response minima, surviving fish individuals, and mortality rate

Family	n (Mean initial length: SL, mm ± SD)		Mean thermal response minima, °C (± SD)						Cold treatment	
Species	(control)*	(cold)	AT_{min}	ST_{min}	Feeding cessation			CT_{min}	Total number of mortalities	Total number of final LOE
(common name)					FC_{10}	FC_{50}	FC_{min}			
Pomacentridae										
Pomacentrus coelestis (Neon damselfish)[a]	9 (30.3 ± 0.13)	7 (28.5 ± 0.25)	16.6 (± 0.51)	14.8 (± 0.11)	16.0 (± 0.76)	15.3 (± 0.48)	15.0 (± 0.44)	14.8 (± 0.06)	1/7	3/7
Pomacentrus moluccensis (Lemon damselfish)[b]	10 (38.7 ± 0.44)	10 (38.1 ± 0.39)	17.4 (± 0.79)	15.0 (± 0.18)	16.6 (± 0.63)	16.4 (± 0.38)	15.9 (± 0.71)	14.8 (± 0.19)	1/10	6/10
Dascyllus trimaculatus (Three-spot dascyllus)[a]	10 (27.6 ± 0.48)	10 (28.4 ± 0.41)	15.5 (± 0.73)	14.9 (± 0.11)	16.0 (± 0.76)	15.2 (± 0.39)	15.0 (± 0.39)	14.7 (± 0.26)	2/10	2/10
Dascyllus aruanus (Whitetail dascyllus)[b]	8 (28.0 ± 0.48)	9 (30.4 ± 0.40)	17.5 (± 0.93)	15.2 (± 0.41)	17.5 (± 0.72)	16.8 (± 0.48)	16.0 (± 0.97)	15.0 (± 0.52)	6/9	6/9
Chaetodontidae										
Chaetodon auriga (Threadfin butterflyfish)[a]	10 (53.2 ± 0.55)	8/6[c] (58.5 ± 0.35)	15.4 (± 0.90)	14.9 (± 0.87)	15.9 (± 0.67)	15.3 (± 0.51)	15.0 (± 0.58)	14.7 (± 0.25)	2/8	3/8
Chaetodon vagabundus (Vagabond butterflyfish)[b]	8 (52.3 ± 0.51)	8/5 [c] (55.0 ± 0.55)	16.2 (± 0.91)	15.1 (± 0.71)	16.9 (± 0.68)	16.4 (± 0.70)	15.6 (± 0.83)	14.7 (± 0.18)	5/8	5/8

Thermal response minima include the minimum acclimation temperature (AT_{min}), minimum feeding cessations: in 10% population (FC_{10}), ≥ 50% population (FC_{50}), and ≥ 90% population (FC_{min}), minimum thermal stress (ST_{min}), critical thermal minima (CT_{min})

*No fish died during the experimental period

[a] Classified as adapted species

[b] Classified as non-adapted species

[c] Dual numbers of threadfin and vagabond butterflyfishes represent the number of test fish individuals vs. the number of feeding fish individuals, respectively

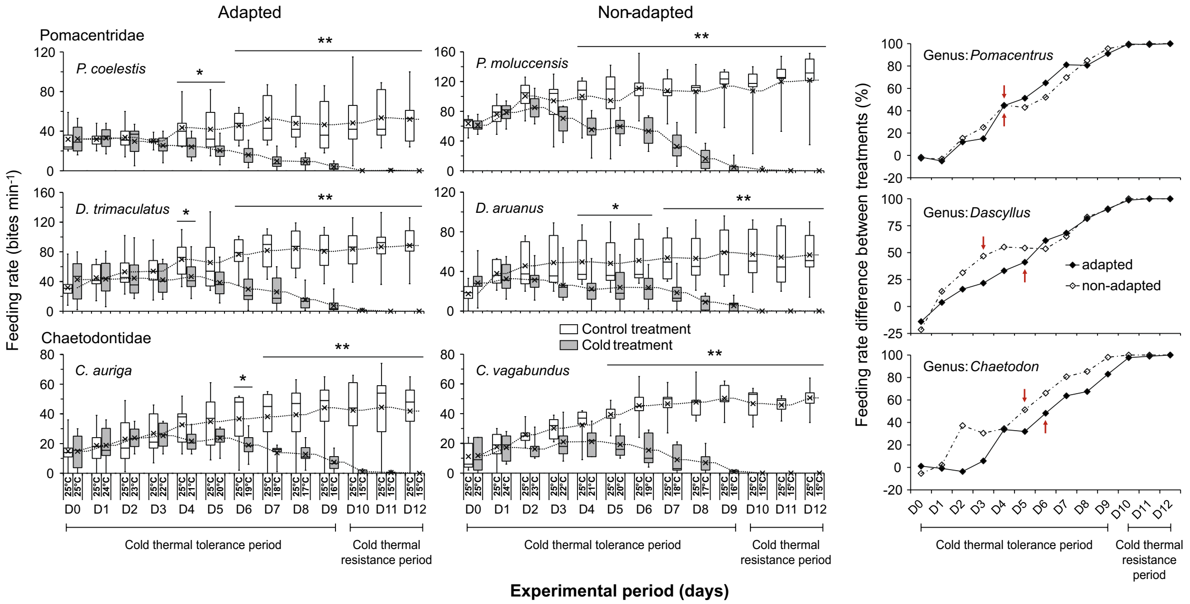


Fig. 3 Feeding rates of each congeneric adapted (left panels) and non-adapted (middle panels) species pair of genera *Pomacentrus*, *Dascyllus*, and *Chaetodon* in the control and cold-temperature treatments during the experimental period (~ 12 d; D: day), and the relative difference (percentage difference) in the feeding rate of each cold test fish with the decreasing temperature as compared with their control counterparts (right panels). Black "×" markers in the left and middle panels indicate mean values, boxes are the interquartile ranges, middle lines are the median values, whiskers are the min/max values, and dotted lines are moving average lines for each treatment. Empty boxes indicate the control treatment, and the gray-shaded boxes represent the cold treatment. Asterisks denote a significant difference in the average feeding rate between the control and cold treatments for each species per day (*t* test: *$p<0.05$; **$p<0.01$). Red arrows in the right panels indicate > 40% significant feeding rate reductions in each cold test species (as compared to the control)

species subsequently occurred at an average of approximately 16 °C (Table 1), which was also significantly higher than that of their adapted congeners by a degree (overall: $t=-7.41$, $p<0.001$; *Pomacentrus*: $t=-4.17$, $p=0.003$; *Dascyllus*: $t=-5.81$; $p<0.001$; Fig. 4). More than 90% of the population in each group of non-adapted species exhibited feeding cessation (FC_{min}) on days 1 and 2 of exposure to 15 °C, which was 1 day earlier than that of the adapted species (Fig. 4). This has resulted in significantly higher mean FC_{min} temperature values in non-adapted species as compared with their adapted congeners (overall: $t=-4.55$, $p<0.001$; *Pomacentrus*: $t=-2.90$, $p=0.011$; *Dascyllus*: $t=-2.73$, $p=0.024$; Table 1).

Effects of cold winter waters on growth

Significantly lower growth rates were typically noted in cold test fishes as compared to the control test fishes (GLM, overall: $t=-3.35$, $p=0.001$; adapted: $t=-5.76$, $p<0.001$; non-adapted: $t=-2.58$, $p=0.013$; Fig. 5). This relative change in growth between treatments was significant among genus (treatment × genus: $F=6.97$, $p=0.001$) and species type (treatment × species type: $F=10.61$, $p=0.002$). Of which, *P. coelestis* ($F=34.20$, $p<0.001$), *P. moluccensis* ($F=11.60$, $p=0.003$), and *D. trimaculatus* ($F=53.80$, $p<0.001$) had a significantly different growth rate between treatments among the test species. Although the difference in the overall growth rate between species type was only significant for the control (particularly for the species pair of *Pomacentrus* and *Dascyllus*; $F=17.74$, $p<0.001$, Fig. 5), the growth rates of most adapted cold test fishes were still relatively higher (GLM: $t=2.07$, $p=0.044$) compared with their non-adapted cold test congeners. This was particularly evident for the cold test species pair of genus *Chaetodon* (although the difference was non-significant; Fig. 5) and *Pomacentrus*, where *P. coelestis* (adapted) exhibited a significantly higher growth rate (GLM: $t=2.23$, $p=0.042$) compared with its non-adapted congener, *P. moluccensis* (Fig. 5), even though the latter had a significantly larger body size than that of the former, i.e., initial length ($F=22.79$, $p<0.001$; Table 1) and weight (*P. moluccensis*: 4.22 ± 0.88 g; *P. coelestis*: 1.48 ± 0.27 g; $F=63.07$, $p<0.001$).

Effects of minimum winter seawater temperature on survival

No mortalities were recorded from the control test fishes throughout the experimental trials, whereas mortalities in cold test fishes occurred during the 3 d exposure to 15 °C (Fig. 6). Although the difference in mortality rates appeared

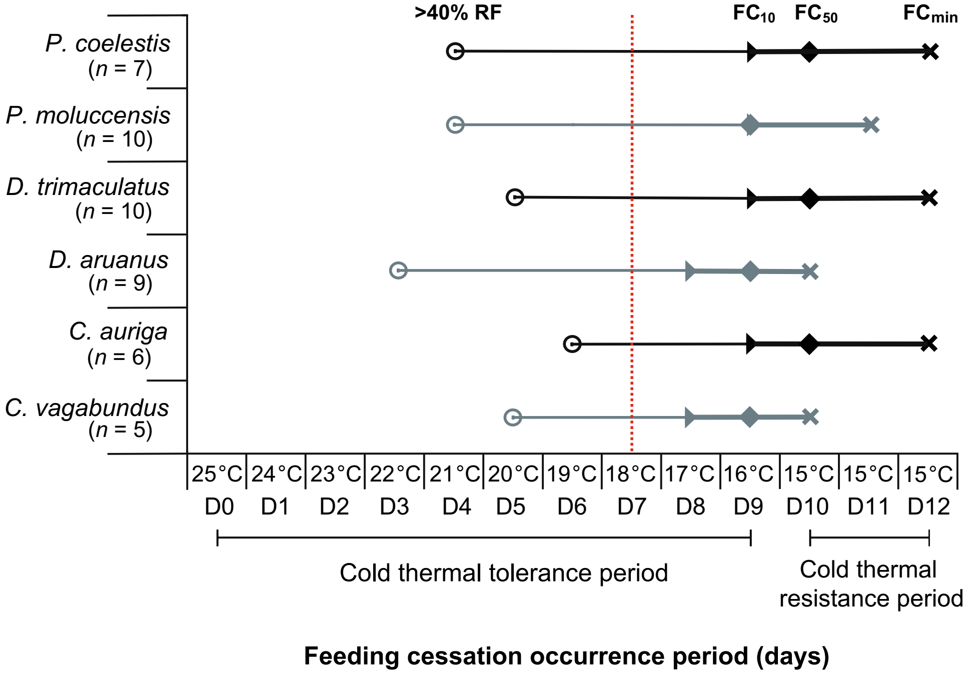
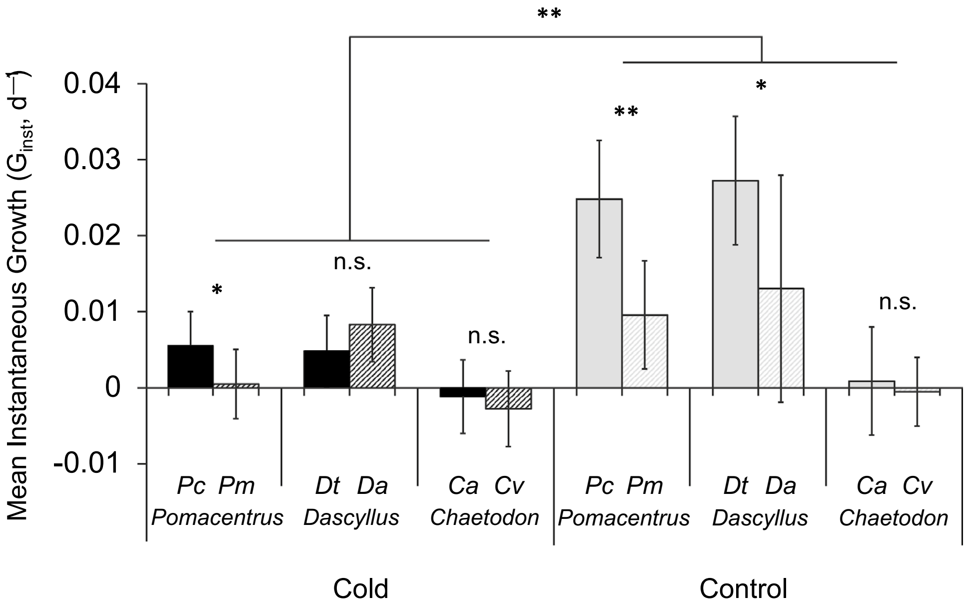


Fig. 4 Occurrences of feeding cessation in congeneric adapted (black lines and markers) and non-adapted (gray lines and markers) species from three genera, namely, *Pomacentrus*, *Dascyllus*, and *Chaetodon*, under cold treatment during the experimental period (*D* day). The empty circle marker denotes the start of > 40% reduction in the feeding rate (RF) of cold test fishes as compared to the control, the arrowhead marker denotes the onset of feeding cessation in at least 10% of the population (FC_{10}), the diamond marker denotes feeding cessation in ≥ 50% of the population (FC_{50}), and the "×" marker denotes the lowest period where feeding cessation occurred in ≥ 90% of the population (FC_{min}). Thin solid lines indicate the period from the > 40% feeding rate reduction until the onset of the first occurrence of feeding cessation for each group, and bold lines indicate the start of FC_{10} until FC_{min}. The red dotted line represents the 18 °C thresholds (onset of winter seawater temperatures in Kochi)

to be statistically non-significant between adapted and non-adapted species [Kaplan–Meier log-rank (Mantel–Cox)], overall: $\chi^2 = 3.29$, $p = 0.07$; *Pomacentrus*: $\chi^2 = 0.07$, $p = 0.79$; *Dascyllus*: $\chi^2 = 3.46$, $p = 0.06$; and *Chaetodon*: $\chi^2 = 2.19$, $p = 0.14$), non-adapted species generally appeared to have 55% higher relative mortality risks at 15 °C than their

Fig. 5 Mean (± SD) instantaneous growth, G_{inst}, of congeneric species of genera *Pomacentrus*, *Dascyllus* (Pomacentridae), and *Chaetodon* (Chaetodontidae) under each temperature treatment (control and cold). Solid bars indicate adapted species, and bars with diagonal lines indicate non-adapted species. Asterisks denote significance level comparisons between adapted and non-adapted species, and between control and cold set-ups (*$p < 0.05$; **$p < 0.01$; *n.s.* not significant)



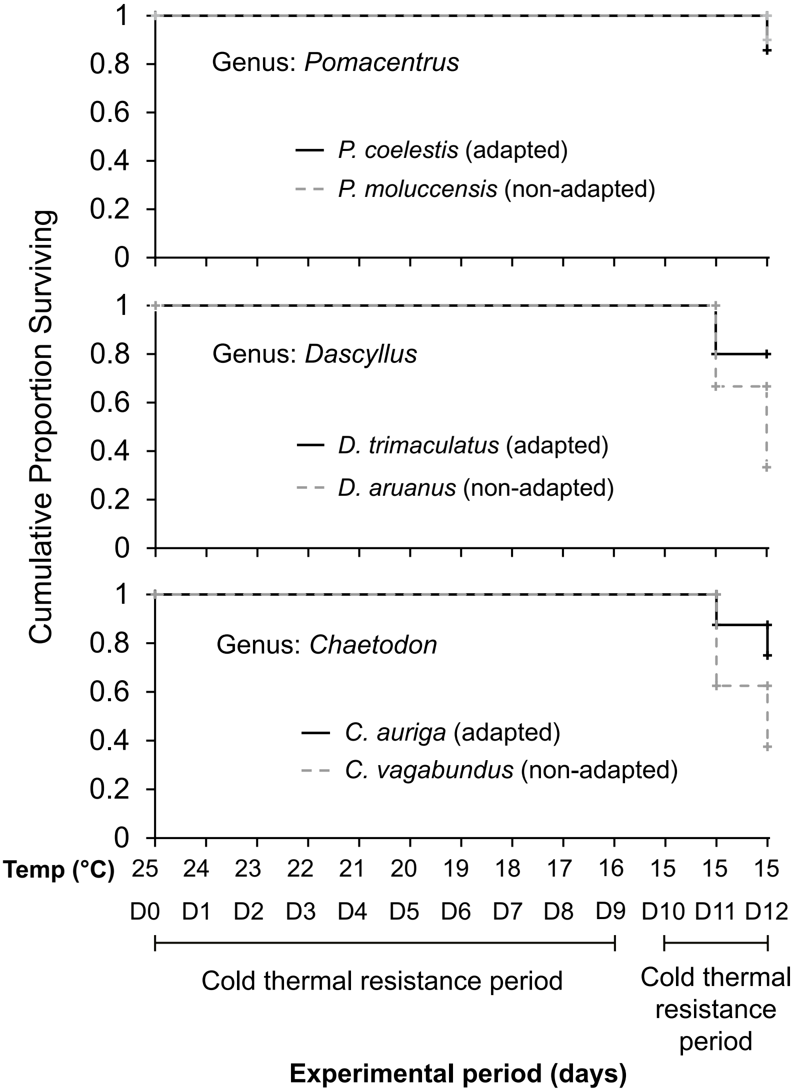


Fig. 6 Cumulative proportion surviving (Kaplan–Meier) of adapted (solid lines) and non-adapted (broken lines) species pair in each genus (*Pomacentrus*, *Dascyllus*, and *Chaetodon*) throughout the cold-experimental period (~ 12 d; D: day)

adapted congeners [overall, Cox hazard ratio for death ($HR_{(death)}$): 0.45 (95% CI: 0.16−1.28); Table S2; Fig. 6]. The initial mortality rate of the non-adapted species *C. vagabundus* on day 2 of exposure to 15 °C (37.5%, $n = 3$) was 25% higher compared with its adapted congener (*C. auriga:* 12.5%, $n = 1$; Fig. 6). On day 3 of exposure to 15 °C, *C. vagabundus* also had a similar mortality rate of 40% ($n = 2$), which yielded a cumulative mortality rate (CMR) of 62.5%, as compared to 14.3% ($n = 1$) mortality rate in *C. auriga* on the same day with a CMR of 25% (Fig. 6). Hence, it appears that *C. vagabundus* had a 60% higher relative risk of mortality than its adapted congener when exposed for at least 2−3 days to 15 °C [$HR_{(death)}$: 0.40 (0.08−2.06); Table S2]. Similarly, *D. aruanus* (non-adapted) had a 33.3% ($n = 3$) mortality rate on day 2 and 50% ($n = 3$) on day 3 of exposure to 15 °C, which was 10–50% higher than that of *D. trimaculatus* with only 20% mortality on day 2 and no further recorded mortality on day 3 (Fig. 6). This resulted in a 70% higher relative mortality risk [$HR_{(death)}$: 0.30 (0.61−1.49); Table S2] in *D. aruanus* than in *D. trimaculatus* (Fig. 6). No deaths were recorded from the species pair (adapted and non-adapted) of genus *Pomacentrus* on day 2 of exposure to 15 °C. Despite the 43% relatively higher mortality risk in *P. coelestis* than *P. moluccensis* [$HR_{(death)}$: 1.43 (0.09−22.84)], both species had similar mortality ($n = 1$) on day 3 (Fig. 6). Subsequently, non-adapted species also demonstrated approximately 50% relatively higher occurrences of final LOE (or inability to maintain dorso-ventral orientation) than the adapted species did [overall Cox hazard ratio for final LOE ($HR_{(LOE)}$): 0.51 (0.22−1.18); Table S2]. Of these, *D. aruanus* had a 70% higher relative risk to experience final LOE at 15 °C than its adapted congener [*Dascyllus*, $HR_{(LOE)}$: 0.30 (0.06−1.49)], *C. vagabundus* had 40% higher relative risk than *C. auriga* [*Chaetodon*, $HR_{(LOE)}$: 0.60 (0.14−2.51)], and *P. moluccensis* had 29% higher final LOE than *P. coelestis* [*Pomacentrus*, $HR_{(LOE)}$: 0.71 (0.18−2.86)], (Table S2). Although no response behaviors significantly correlated to the occurrence likelihood of mortality and final LOE among fish individuals per genus (except for final LOE in the mortality of *Dascyllus* individuals; Table S2), most mortalities and final LOE in individuals of both genus *Dascyllus* and *Chaetodon* appeared to be attributed to the prior occurrence of stressed and critical behaviors (Table S2: significant model improvements). These two behaviors were also the only response behaviors that significantly contributed to all cold test fish's mortality and final LOE (Table S2: fitted models for overall cold test fishes). However, between the two behaviors, stressed behavior appeared to have less effect on the occurrence likelihood of mortality and final LOE in cold test fishes (with < 1 h value, Table S2). Of which, only the critical behavior significantly contributed to > 50 times the occurrence of final LOE [$HR_{(LOE)}$: 54.67 (7.31−408.93)] and five times the probability of mortality in cold test fishes [$HR_{(death)}$: 4.87 (1.67−14.20); Table S2]. Mortalities of which the probability risk was significantly increased to approximately six times with the occurrence of final LOE [$HR_{(death)}$: 5.77 (2.09−15.92); Table S2].

Discussion

Tropical organisms, including reef fishes, are believed to have been transported by poleward-flowing boundary currents (e.g., Kuroshio Current) in temperate regions from lower latitudes during the larval stage (Soeparno et al. 2012). Potential for long-distance dispersal and the presence of suitable habitats are among the prerequisites for the successful poleward migration and colonization of tropical reef fishes (Feary et al. 2014). The selected congeneric adapted and non-adapted species pairs in this study have similar pelagic larval durations (PLDs) (Wellington and Victor 1989; Wilson and McCormick 1999; Soeparno et al. 2012), and tropical corals have colonized in temperate Kochi since the late 1990s (Yamano et al. 2011; Nakamura et al. 2013; Vergés et al. 2014). Nevertheless, the identified non-adapted species rarely occur or decline in abundance during winter and diminish after winter compared with their adapted congeners, which occur in high abundance and with recorded adult populations or reproduction in the area (see Table S1; Hirata et al. 2011; Nakamura et al. 2013; Tose et al. 2017). Hence, thermal conditions during winter in Kochi, which usually reach a low of about 15 °C during normal conditions (Leriorato and Nakamura 2019), might plausibly be responsible for the rare occurrences and low abundance of some tropical reef fishes in temperate Kochi (Table S1; Hirata et al. 2011; Tose et al. 2017).

Irrespective of their family and genus, congeneric adapted and non-adapted cold test species exhibited similar responses to decreasing water temperatures by displaying swimming and feeding reductions, whereas control test fishes exhibited normal behavioral activities during the entire experimental period. Reductions in the activity that prominently occurred in all cold test fishes when the temperature reached 18 °C (i.e., the onset of winter seawater temperatures in Kochi), particularly in non-adapted species, indicates that surviving the first exposure to winter is crucial for most teleost fishes (Hurst 2007) and vagrant tropical reef fishes in temperate waters (Figueira and Booth 2010). The decrease in swimming activity and occurrences of stressed behaviors in cold test fishes under low temperatures occur in most tropical teleost fishes until a temperature of around 15 °C is reached (Johnston and Dunn 1987; Kimball et al. 2004), reflecting the deterioration of sustained swimming muscular performance (i.e., red muscle; Sidell and Moerland 1989; Johnson and Bennett 1995). This indicates that cold waters during winter are generally stressful for fish (Fry 1971; Elliot 1981; Cunjak 1988; Johnson and Evans 1996). However, reductions in the activity that occurred at a significantly higher temperature (c. 18 °C) and the generally earlier occurrence of stressed behaviors in most non-adapted species (Fig. 2a) indicate that low temperatures exerted detrimental effects (e.g., limiting, inhibiting, and loading stress effects, sensu Elliot 1981) earlier as compared to that of their adapted congeners. Although this study illustrates different ranges for AT_{min}, FC_{min}, and CT_{min} than were previously reported for tropical reef fishes (*cf.* results of Eme and Bennett 2008), this could be due to differences in the methods and temperature rate changes that were used. The rate of heating or cooling in critical thermal (CTM) experiments (e.g., –1 °C min^{-1}) only reflected an acute cause of death (Fry 1971) as the rate change is too rapid for a fish's body to track water temperature (Beitinger et al. 2000). Contrarily, the temperature rate change in chronic lethal methodologies (CLM, e.g., 0.5–1.0 °C d^{-1}) better estimates the lower thermal tolerances in fish (Bennett et al. 1997; Beitinger et al. 2000). Thus, the rate of temperature change plays a vital role in the fish's tolerance to low temperatures (Beitinger and McCauley 1990), wherein acute short-term temperature drops in the CTM (e.g., in Eme and Bennett 2008) typically yield lower temperature tolerance values as compared to the slower transitions in the CLM (Beitinger et al. 2000). Nevertheless, the application of both the CLM_{min} for the dynamic temperature rate change (1 °C d^{-1}) and the static temperature method (set to 15 °C in this study) not only provide a better estimation of the lower thermal tolerances (i.e., independent with the pretest acclimation temperature; Beitinger et al. 2000) in the tested fishes exposed to mid-latitude winter thermal ranges but may also provide a better estimate on the thermal resistance of vagrant tropical reef fishes to the persistence periods of minimum winter seawater temperatures in Kochi.

The significant reduction in feeding rates might also be attributable to low water temperatures, despite differences in the feeding mechanisms among genera (Wainwright and Bellwood 2002), since feeding rates of control fishes remained at persistently higher rates throughout the experimental period. The initial low feeding rates of test fishes in both treatments (control and cold) might have resulted from their indecisive response to the presence of a potential disturbance (i.e., video camera; Hutchinson 1976). Thus, a general increase in the feeding rate (2–3 d after introducing a camera) possibly indicates habituation to its presence. It could also be an indication that test fishes experienced an adjustment period as they became accustomed to commercial pellet food since they were used to eating natural live foods. Nevertheless, non-feeding individuals of *Chaetodon* spp. in the cold-experimental trial even at the start of the experiment (or at warmer temperatures) is not uncommon, as this response was exhibited by lionfish subjected to low water temperatures (Kimball et al. 2004). Hence, the occurrence of such response behavior in some cold test fishes in this study was presumed to be a compensatory response of the fish whereby they entered a torpid or dormant state (see review by Johnston and Dunn 1987) since they reached temperatures beyond their winter thermal threshold (i.e., 17−19.5 °C, Figueira and Booth 2010), as did the other cold test fishes (where $n=1$ survived). Feeding cessation in fishes presumably occurred due to a cost of acclimatization at low temperatures as the blood glucose levels continued to increase (i.e., hyperglycemia-stress response; Cunjak 1988), which may have occurred in most reef fishes that exhibit similar behavior when exposed to cold temperatures (Kimball et al. 2004; Eme and Bennett 2008; Figueira et al. 2009). It is also presumed to be one of the causes of mortality, typically known as winter starvation (Figueira et al. 2009). However, this study showed that feeding cessation does not substantially affect the overall mortality of cold test fishes. This corroborates some studies that observed little effect of overwintering temperature on unfed fish (Moles et al. 1997). Hence, this might be the reason why not all cold test fishes that demonstrated feeding cessation died within the 3-d exposure period to 15 °C, as well as the survival of non-feeding individuals of *C. auriga* ($n=1$).

Water temperatures lower than a fish's optimum thermal range typically cause exhaustion that limits their activity and growth (i.e., acts as the loading stressor, Elliot 1981) and often leads to energy depletion (Johnson and Evans 1996; Schultz and Conover 1999; Hurst 2007). Combined with marked feeding reduction or feeding cessation, this has a distinctive impact on fish's growth and survival (Elliot 1981). Thus, the colder water might have caused a deficit in the bodyweight of cold test fishes compared with that of the control test fishes, which then resulted in the significantly lower growth rate of *P. moluccensis* compared to that of its adapted congener, *P. coelestis*, as well as the negative growth of C*haetodon* spp. (see Fig. 5). Similarly, low temperatures also suppress a fish's ability to maintain normal functions (homeostasis; Hurst 2007), consequently reducing their survival probability (i.e., acting as an inhibiting stressor, Elliot 1981). The comparatively high occurrence of stressed behaviors in most non-adapted cold test fishes (e.g., *D. aruanus* and *C. vagabundus*) may have partly contributed to their high mortality rate as compared to that of their adapted congeners. However, the high occurrence of critical behaviors and final LOE substantiates the high probability of mortality in all cold test fishes (see Table S2). Although the difference in the mortality rates of the cold test adapted species (*P. coelestis*) and non-adapted species (*P. moluccensis*) of genus *Pomacentrus* was non-significant (with both $n=1$), the latter species exhibited higher occurrences of final LOE on day 3 of exposure to 15 °C as compared to its adapted congener, despite the significantly larger body sizes of the individuals of *P. moluccensis* than that of *P. coelestis* (in both treatments, Table 1). Hence, it indicates that the minimum seawater temperature in Kochi during winter (c. 15 °C) is ecologically lethal for *P. moluccensis*, despite being collected from Okinawa where winter temperatures typically drop until 21 °C compared to that of *P. coelestis* (collected from the Philippines), which only experienced minimum temperatures at approximately 26 °C during the cold months in the area. While the species pair of genus *Pomacentrus* had different source collection, the indication of high final LOE occurrence in *P. moluccensis* at Kochi's persistent periods (2–3 d) of low temperatures during winter (c. 15 °C) may not only prevent them from escaping predation (Hurst 2007; Figueira et al. 2009; Booth et al. 2011; Johansen et al. 2015). It may also eventually lead to their physiological death (Bennett and Beitinger 1997; Beitinger and McCauley 1990; Beitinger et al. 2000) since extreme cold events are no longer an uncommon phenomenon with the recent climate change, where low temperatures typically persist at extended periods (e.g., two months of below 15 °C in Tosa Bay, Leriorato and Nakamura 2019). The bioenergetic cost of persistent periods of sublethal temperatures in the natural environment may subject fishes to higher minimum tolerable temperatures (Hurst and Conover 2002). Various interacting factors may also potentially regulate their thermal tolerance, such as hypothermia (McBride and Able 1998); acute or chronic cold stress (Johnson and Evans 1996; Schultz and Conover 1999), hyperglycemia-stress responses (Cunjak 1988); metabolism-related causes (Johnston and Dunn 1987; Guderley 2004); decreased locomotor performance (Sidell and Moerland 1989; Johnson and Bennett 1995); depletion of energy reserves (Johnson and Evans 1996; Schultz and Conover 1999); and inability to maintain homeostasis (Hurst 2007).

Our study demonstrates that cold waters during winter in Kochi (< 18 °C) are stressful for both adapted and non-adapted species as they displayed reductions in feeding and swimming activity, particularly when the temperature approached 18 °C. This finding corroborates previous records of the substantial decreases in the abundance and species richness of tropical reef fishes in Kochi after December, i.e., at temperatures ≤ 18 °C (Nakamura et al. 2013), wherein the disappearance of most tropical reef fishes after the winter season (Hirata et al. 2011) coincides with the limited ecological and physiological survival of most non-adapted species exposed to the minimum winter temperature in this study. The shorter thermal resistance time (i.e., time to 50% mortality or occurrence of final LOE) in most non-adapted species within the persistence period (3 d) of the average minimum winter temperature (c. 15 °C) in Kochi plausibly causes their rare occurrence (e.g., *P. moluccensis* and *D. aruanus*, Table S1; Hirata et al. 2011; Tose et al. 2017) or declining abundance (e.g., *C. vagabundus;* Hirata et al. 2011; Nakamura et al. 2013) during and after the winter season in Kochi. Hence, this study suggests intrageneric variations in the thermal tolerance and resistance to cold temperatures, whereby non-adapted species might have higher minimum ecological thermal limits than their adapted congeners. The survival of most tropical reef fishes during their first exposure to the mid-latitudinal winter temperatures presumably allows them to survive harsher winter conditions in the future due to establishing lower thermal tolerance (Figueira and Booth 2010). This is commonly attributable to the significant heritability of survival that fishes exhibit after successfully surpassing the adverse effects of winter conditions (Vehviläinen et al. 2008; Nielsen et al. 2010; Prchal et al. 2018). Thus, the significant abundance (and establishment of a viable reproducing population) that adapted species have achieved in temperate Kochi may be due to their ability to survive cold temperatures during winter, which facilitated their successful colonization at higher latitudes (Figueira and Booth 2010). Indeed, temperate-established (adapted) species still occurred in Kochi during an extreme cold event in Tosa Bay (i.e., 2-month low seawater temperatures of 14–15 °C, which dipped to approximately 12 °C) in the winter of 2018, while the identified non-adapted species completely disappeared during the event (Leriorato and Nakamura 2019). Despite the continued increase in SSTs due to climate change, this study reveals that the successful poleward colonization of tropical reef fishes is contingent on their capacity to tolerate and resist mid-latitude cold seawater temperatures during winter, regardless of their pelagic larval duration (PLD), the availability of suitable marginal habitats, and accessibility of nearby larval sources.

Predicting range shifts in tropical reef fishes must be challenging, considering the various contributing factors (biotic and abiotic) and the generally species-specific responses of most fishes to these factors. Nevertheless, our results demonstrate supporting evidence of the difference in winter thermal tolerance (and resistance to minimum temperatures) between the temperate-established (adapted) and non-established (non-adapted) expatriate congeneric tropical reef fishes on their first exposure to the mid-latitude winter seawater temperature range. Although the low number of test fishes may limit the strength of inference drawn from our results, our study obtained comparable results to previous studies using a similar number of samples (*cf.* Kimball et al. 2004). Winter thermal tolerance capacity could be a range-shift predictive trait as temperate winter waters remain a population bottleneck to most range-shifting tropical reef fishes despite contemporary ocean warming. Hence, a specie's inability to physiologically persist mid-latitudes cold thermal conditions during winter (particularly during their first exposure) may inevitably increase their contraction or extinction risks (Cheung et al. 2009) since the persistent ocean warming increases the unsuitability of their current geographic ranges, affecting both their performance and the stability of their habitat (e.g., coral degradation; Pratchett et al. 2008; Rummer et al. 2014). Effects of which could significantly impact their population structure and biogeographic distributions (Munday et al. 2008; Nilsson et al. 2009) that may be exacerbated as episodes of extreme weather events intensify with climate change (Easterling et al. 2000; Wernberg et al. 2013, 2016; Leriorato and Nakamura 2019).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-021-03875-2.

Acknowledgements We are grateful to the Mindanao State University at Naawan (MSUN) for supporting the logistics during the field-based fish surveys in Mindanao and to Eugene Moleño, Darwin Baslot, and Daryl Baslot of MSUN for their kind assistance. This study was implemented under the auspices of the research collaboration between MSUN and Kochi University. We thank the anonymous reviewers for their helpful comments and Enago (www.enago.jp) for the English language review.

Author contributions JCL and YN designed the study. JCL and YN performed the laboratory experiment, and JCL analyzed the data. JCL, YN, and WHU conducted the field survey. JCL wrote the paper with the help of YN and WHU. All the authors have approved the contents of this paper and have agreed to its submission to Marine Biology.

Funding This study was supported by a grant from the Japan Society for the Promotion of Science (KAKENHI 15K07529) through the Climate Change Impacts Project.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest All the authors declare that they have no conflict of interest.

Ethical approval Although the Animal Experiment Committee of the Kochi University ruled that no ethical clearance or approval of research ethics was required for this study because experimental work was conducted with an unregulated fish species, we followed all applicable institutional and/or national guidelines for the care and use of animals in this study. A minimum number of fish were used to test the hypothesis. After the experiment, fish were kept in home aquariums where they demonstrated normal conditions (e.g., unstressed body color and actively swimming).

References

Beitinger TL, McCauley, (1990) Whole-animal physiological processes for the assessment of stress in fishes. J Great Lakes Res 16(4):542–575. https://doi.org/10.1016/S0380-1330(90)71445-1

Beitinger TL, Bennett WA, McCauley RW (2000) Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environ Biol Fish 58(3):237–275. https://doi.org/10.1023/a:1007676325825

Bennett WA, Beitinger TL (1997) Temperature tolerance of sheepshead minnow, *Cyprinodon variegatus*. Copeia 1:77–87. https://doi.org/10.2307/1447842

Bennett WA, Currie RJ, Wagner PF, Beitinger TL (1997) Cold tolerance and potential overwintering of the red-bellied piranha *Pygocentrus nattereri* in the United States. Trans Am Fish Soc 126(5):841–849. https://doi.org/10.1577/1548-8659(1997)126%3c0841:CTAPOO%3e2.3.CO;2

Black EC (1955) Blood levels of hemoglobin and lactic acid in some freshwater fishes following exercise. J Fish Res Bd Can 12(6):917–929. https://doi.org/10.1139/f55-048

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. https://doi.org/10.1016/j.ecss.2006.10.003

Booth DJ, Bond N, Macreadie P (2011) Detecting range shifts among Australian fishes in response to climate change. Mar Freshw Res 62(9):1027–1042. https://doi.org/10.1071/mf10270

Booth DJ, Feary D, Kobayashi D, Luiz O, Nakamura Y (2018) Tropical marine fishes and fisheries and climate change. In: Phillips BF, Perez-Ramirez M (eds) Climate change impacts on fisheries and aquaculture: a global analysis, vol II. Wiley, West Sussex, pp 875–896. https://doi.org/10.1002/9781119154051.ch26

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish 10:235–251. https://doi.org/10.1111/j.1467-2979.2008.00315.x

Cunjak RA (1988) Physiological consequences of overwintering in streams: the cost of acclimatization? Can J Fish Aquat Sci 45(3):443–452. https://doi.org/10.1139/f88-053

Djurichkovic LD, Donelson JM, Fowler AM, Feary DA, Booth DJ (2019) The effects of water temperature on the juvenile performance of two tropical damselfishes expatriating to temperate reefs. Sci Rep 9:13937. https://doi.org/10.1038/s41598-019-50303-z

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068–2074. https://doi.org/10.1126/science.289.5487.2068

Elliot JM (1981) Some aspects of thermal stress in freshwater teleosts. In: Pickering AD (ed) Stress and fish. Academic Press, New York, pp 209–245

Elliot JM (1991) Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. Freshwat Biol 25:61–70. https://doi.org/10.1111/j.1365-2427.1991.tb00473.x

Emme J, Bennett WA (2008) Low temperature as a limiting factor for introduction and distribution of Indo-Pacific damselfishes in the eastern United States. J Therm Biol 33:62–66. https://doi.org/10.1016/j.jtherbio.2007.10.003

Emme J, Bennett WA (2009) Critical thermal tolerance polygons of tropical marine fishes. J Therm Biol 34:220–225. https://doi.org/10.1016/j.jtherbio.2009.02.005

Factors influencing thermal tolerances of individual organisms. In: Esch GW, McFarlane RM (eds) Thermal Ecology, vol. II, ERDA Symp Ser CONF-750425 Natl Inf Serv, Springfield, Va, pp 10–26

Feary DA, Pratchett MS, Emslie MJ, Fowler AM, Figueira WF, Luiz OJ, Nakamura Y, Booth DJ (2014) Latitudinal shifts in coral reef fishes: why some species do and others don't shift. Fish Fish 15:593–615. https://doi.org/10.1111/faf.12036

Figueira WF, Booth DJ (2010) Increasing ocean temperature allow tropical fishes to survive overwinter in temperate waters. Glob Change Biol 16:506–516. https://doi.org/10.1111/j.1365-2486.2009.01934.x

Figueira WF, Biro PA, Booth DJ, Valenzuela VC (2009) Performance of tropical fishes recruiting into temperate habitats: role of ambient temperature and implications for climate change. Mar Ecol Prog Ser 384:231–239. https://doi.org/10.3354/meps08057

Finch C, Pike M, Witten M (1990) Slow mortality rate accelerations during aging in some animals approximate that of humans. Science 249:902. https://doi.org/10.1126/science.2392680

Fry FEJ (1947) Effects of the environment on animal activity. Univ. Toronto Studies in Biol., Series No. 55, Publ Ont Fish Res Lab 68:1–62.

Fry FEJ (1971) The effect of environmental factors on the physiology of fish. In: Hoar WS, Randall DJ (eds) Fish physiology, environmental relations and behavior, vol 6. Academic Press, New York, pp 1–98

Girden ER (1992) ANOVA: repeated measures. Sage University Paper Series on quantitative applications in the social sciences, 07-084. Newbury Park, CA: Sage.

Guderley (2004) Metabolic responses to low temperature in fish muscle. Biol Rev 79(2):409–427. https://doi.org/10.1017/s1464793103006328

Guderley H, Houle-Leroy P, Gagne A (2001) Thermal acclimation, growth and burst swimming of threespine stickleback: enzymatic correlates and influence of photoperiod. Physiol Biochem Zool 74:66–74. https://doi.org/10.1086/319313

Hammer O, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis, version 3.08 (8/2015). Paleontol Electron 4(1):9. https://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hirata T, Oguri S, Hirata S, Fukami H, Nakamura Y, Yamaoka K (2011) Seasonal changes in fish assemblages in an area of hermatypic corals in Yokonami, Tosa Bay, Japan. Jpn J Ichthyol 58:9–64

Hoar WS (1956) Photoperiodism and thermal resistance of goldfish. Nature 178:4529. https://doi.org/10.1038/178364a0

Hongo C, Yamano H (2013) Species-specific responses of corals to bleaching events on anthropogenically turbid reefs on Okinawa Island, Japan, over a 15-year Period (1995–2009). PLoS ONE 8(4):e60952. https://doi.org/10.1371/journal.pone.0060952

Hurst TP (2007) Causes and consequences of winter mortality in fishes. J Fish Biol 71:315–345. https://doi.org/10.1111/j.1095-8649.2007.01596.x

Hurst TP, Conover DO (2002) Effects of temperature and salinity on survival of young-of-the-year Hudson River striped bass (*Morone saxatilis*): implications for optimal overwintering habitat. Can J Fish Aquat Sci 59(5):787–795. https://doi.org/10.1139/f02-051

IBM Corp (2015) IBM SPSS Statistics for Windows, Version 23.0. Armonk, NY: IBM Corp.

Johansen JL, Steffensen JF, Jones GP (2015) Winter temperatures decrease swimming performance and limit distributions of tropical damselfishes. Conserv Physiol 3:39. https://doi.org/10.1093/conphys/cov039

Johnson TP, Bennett AF (1995) The thermal acclimation of burst escape performance in fish: an integrated study of molecular and cellular physiology and organismal performance. J Exp Biol 198:2165–2175

Johnson TB, Evans DO (1996) Temperature constraints on overwinter survival of age-0 white perch. Trans Am Fish Soc 125:466–471. https://doi.org/10.1577/1548-8659(1996)125%3c0466:ntcoos%3e2.3.co;2

Johnston IA, Dunn J (1987) Temperature acclimation and metabolism in ectotherms with particular reference to teleost fish. Symp Soc Exp Biol 41:67–93

Kimball ME, Miller JM, Whitfield PE, Hare JA (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. Mar Ecol Prog Ser 283:269–278. https://doi.org/10.3354/meps283269

Kingsbury KM, Gillanders BM, Booth DJ, Coni EOC, Nagelkerken I (2019) Range-extending coral reef fishes trade-off growth for maintenance of body condition in cooler waters. Sci Total Environ 703:134598. https://doi.org/10.1016/j.scitotenv.2019.134598

Kleinbaum DG, Klein M (2012) Survival analysis: a self-learning text (3rd edn). Statistics for biology and health. Springer, New York, pp 201–240

Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, Pecl G (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Glob Ecol Biogeogr 20:58–72. https://doi.org/10.1111/j.1466-8238.2010.00575.x

Leriorato JC, Nakamura Y (2019) Unpredictable extreme cold events: a threat to range-shifting tropical reef fishes in temperate waters. Mar Biol 166:110. https://doi.org/10.1007/s00227-019-3557-6

McBride RS, Able KW (1998) Ecology and fate of butterflyfishes, *Chaetodon* spp, in the temperate, western North Atlantic. Bull Mar Sci 63(2):401–416

Moles A, Korn S, Rice S (1997) Effects of low temperatures and starvation on resistance to stress in presmolt coho salmon. In: Reynolds J (ed) Fish Ecology in Arctic North America, AFS Symp 19, Bethesda, MD, pp 148−154

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. Fish Fish 9:261–285. https://doi.org/10.1111/j.1467-2979.2008.00281.x

Nakamura Y, Feary DA, Kanda M, Yamaoka K (2013) Tropical fishes dominate temperate reef fish communities within western Japan. PLoS ONE 8:e81107. https://doi.org/10.1371/journal.pone.0081107

Nielsen HM, Ødegård J, Olesen I, Gjerde B, Ardo L, Jeney G, Jeney Z (2010) Genetic analysis of common carp (*Cyprinus carpio*) strains I: genetic parameters and heterosis for growth traits and survival. Aquaculture 304:14–21. https://doi.org/10.1016/j.aquaculture.2010.03.016

Nilsson GE, Crawley N, Lunde IG, Munday PL (2009) Elevated temperature reduces the respiratory scope of coral reef fishes. Glob Change Biol 15:1405–1412. https://doi.org/10.1111/j.1365-2486.2008.01767.x

Nitani H (1972) Beginning of the Kuroshio. In: Stommel H, Yoshida K (eds) Kuroshio–its physical aspects. University of Tokyo Press, Tokyo, pp 129–163

Osborne J (2010) Improving your data transformations: applying the Box-Cox transformation. Pract Assess Res Eval 15(12):1–9. https://doi.org/10.7275/qbpc-gk17

Pearce A, Hutchins B, Hoschke A, Fearns P (2016) Record high damselfish recruitment at Rottnest Island, Western Australia, and the potential for climate-induced range extension. Reg Stud Mar Sci 8:77–88. https://doi.org/10.1016/j.rsma.2016.09.009

Pike TW, Samanta M, Lindström J, Royle NJ (2008) Behavioural phenotype affects social interactions in an animal network. Proc R Soc B 275:2515–2520. https://doi.org/10.1098/rspb.2008.0744

Pitchaimani M, Eakin T (2008) Unique estimation of Gompertz parameters with mortality deceleration rate. Math Comput Model 47:104–114. https://doi.org/10.1016/j.mcm.2007.02.005

Pratchett MS, Munday PL, Wilson S, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes-ecological and economic consequences. Oceanogr Mar Biol Annu Rev 46:251–296. https://doi.org/10.1201/9781420065756.ch6

Prchal M, Kause A, Vandeputte M, Gela D, Allamellou JM, Kumar G, Bestin A, Bugeon J, Zhao J, Kocour M (2018) The genetics of overwintering performance in two-year old common carp and its relation to performance until market size. PLoS ONE 13:e0191624. https://doi.org/10.1371/journal.pone.0191624

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. Biol Rev 82:291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Rummer JL, Couturier CS, Stecyk JAW, Gardiner NM, Kinch JP, Nilsson GE, Munday PL (2014) Life on the edge: thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. Glob Change Biol 20:1055–1066. https://doi.org/10.1111/gcb.12455

Sakai K, Singh T, Iguchi A (2019) Bleaching and post-bleaching mortality of Acropora corals on a heat-susceptible reef in 2016. PeerJ 7:e8138. https://doi.org/10.7717/peerj.8138

Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B, Tinevez JY, White DJ, Hartenstein V, Eliceiri K, Tomancak P, Cardona A (2012) Fiji: an open-source platform for biological-image analysis. Nat Methods 9:676–682. https://doi.org/10.1038/nmeth.2019 (**PMID 22743772**)

Schultz ET, Conover DO (1999) The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. Oecologia 119:474–483. https://doi.org/10.1007/s004420050810

Seatemperature.net (2020) Sea temperature in Manila, Philippines. World Sea temperature and water surface temperature. Available: https://seatemperature.net/current/philippines/manila-sea-temperature Accessed Oct 2020

Sidell BD, Moerland TS (1989) Effects of temperature on muscular function and locomotory performance in teleost fish. Adv Comp Environ Physiol 5:115–156. https://doi.org/10.1007/978-3-642-74510-2_5

Smit H, Amelink-Koutstaak JM, Vijverberg J, Von Vaupel-Klein JC (1971) Oxygen consumption and efficiency of swimming goldfish. Comp Biochem Physiol 39:1–28. https://doi.org/10.1016/0300-9629(71)90343-4

Soeparno, Nakamura Y, Shibuno T, Yamaoka K (2012) Relationship between pelagic larval duration and abundance of tropical fishes on temperate coasts ofJapan. J Fish Biol 80:346–357. https://doi.org/10.1111/j.1095-8649.2011.03175.x

Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am Nat 133:240–256. https://doi.org/10.1086/284913

Su JL, Guan BX, Jiang JZ (1990) The Kuroshio. Part I. Physical features. Oceonogr Mar Biol Annu Rev 28:11–71

Tabachnick BG, Fidell LS (2013) Using multivariate statistics (6th ed). Pearson, Upper Saddle River, NJ

Tanaka K, Taino S, Haraguchi H, Prendergast G, Hiraoka M (2012) Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. Ecol Evol 2:2854–2865. https://doi.org/10.1002/ece3.391

Templeton GF (2011) A two-step approach for transforming continuous variables to normal: implications and recommendations for IS Research. Commun Assoc Inf Syst 28(4):41–58

Tose K, Hirata T, Kotera Y, Kanda M, Nakamura Y (2017) Occurrence and reproduction of tropical fishes in ocean warming hotspots of Japanese temperate reefs. Environ Biol Fish 100:617–630. https://doi.org/10.1007/s10641-017-0590-5

Uchiyama Y, Odani S, Kashima M, Kamidaira Y, Mitarai S (2018) Influences of the Kuroshio on interisland remote connectivity of corals across the Nansei Archipelago in the East China Sea. J Geophys Res Oceans 123(12):9245–9265. https://doi.org/10.1029/2018JC014017

Vehviläinen H, Kause A, Quinton C, Koskinen H, Paananen T (2008) Survival of the currently fittest: genetics of rainbow trout survival across time and space. Genetics 180:507–516. https://doi.org/10.1534/genetics.108.089896

Vergés A, Steinberg PD, Hay ME, Poore AG, Campbell AH, Ballesteros E, Heck KL Jr, 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 Royal Soc B 281:20140846. https://doi.org/10.1098/rspb.2014.0846

Wainwright PC, Bellwood DR (2002) Ecomorphology of feeding in coral reef fishes. In: Sale PS (ed) Coral reef fishes: dynamic and diversity in a complex ecosystem. Elsevier, San Diego, pp 33–55

Ward AJW, Webster MM, Hart PJB (2006) Intraspecific food competition in fishes. Fish Fish 7:231–261. https://doi.org/10.1111/j.1467-2979.2006.00224.x

Wellington GM, Victor BC (1989) Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar Biol 101:557–567. https://doi.org/10.1007/bf00541659

Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Change 3:78–82. https://doi.org/10.1038/nclimate1627

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 353:169–172. https://doi.org/10.1126/science.aad8745

Wilson D, McCormick M (1999) Microstructure of settlement-marks in the otoliths of tropical reef fishes. Mar Biol 134:29–41. https://doi.org/10.1007/s002270050522

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:L04061. https://doi.org/10.1029/2010GL046474

Yara Y, Oshima K, Fujii M, Yamano H, Yamanaka Y, Okada N (2011) Projection and uncertainty of the poleward range expansion of coral habitats in response to sea surface temperature warming: a multiple climate model study. Galaxea JCRS 13:1–11. https://doi.org/10.3755/galaxea.13.11