




Original Article

Convictfish on the move: variation in growth and trophic niche space along a latitudinal gradient

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The range expansion of tropical fish into temperate waters is increasing markedly in response to climate change. Range-expanding fish encounter novel diets and environments, but we know little about how these conditions facilitate or hinder distribution shifts. Here, we quantified relative growth rate, morphometric condition and trophic niche of juvenile *Acanthurus triostegus*, a dominant range-expanding tropical surgeonfish, at four locations across 10° of latitude off eastern Australia. We related these metrics to differences in temperature and nutritional quality of dominant seaweeds and the epilithic algal matrix. Temperate food sources were richer in nitrogen than tropical diets. Stable isotope analysis ($\delta^{13}\text{C}$ carbon and $\delta^{15}\text{N}$ nitrogen) of fish muscle revealed a large trophic niche breadth at the highest latitude indicating a generalist foraging strategy, and more nitrogen-enriched isotopic signatures compared to tropical regions. Fish length was strongly correlated to $\delta^{13}\text{C}$ in all regions, suggesting an ontogenetic shift in diet independent of latitude. Despite temperature differences of 4°C, fish growth and body condition were similar across tropical and temperate regions. These results suggest that more nutritious temperate diets may compensate for the effects of cooler water temperatures. Neither summer water temperatures nor dietary factors appear to limit the success of juvenile tropical vagrants as they continue to expand their range along eastern Australia.

Keywords: Acanthuridae, *Acanthurus triostegus*, climate change, marine ecology, range shifts, tropicalization

Introduction

Marine fishes are among the fastest taxa to shift their distribution in response to environmental change (Poloczanska *et al.*, 2013). This is facilitated by poleward-flowing boundary currents, which transport larvae to higher latitude regions (Feary *et al.*, 2014). Recent studies indicate that warmer waters are permitting vagrants to recruit to higher latitude regions for longer periods of time (Booth *et al.*, 2007; Figueira and Booth, 2010). Around the world, the intensification of boundary currents has played a dominant role in the expansion of tropical vagrants leading to tropicalization—i.e. an increase in the proportion of

tropical species within a given region (Vergés, Steinberg, *et al.*, 2014).

Range expansion and settlement of tropical fish species in temperate waters may be influenced by the biotic and abiotic conditions encountered in the new range, such as differences in temperature, habitat, food, and species interactions such as predation and competition (Figueira and Booth, 2010; Feary *et al.*, 2014). Tropical vagrants generally expatriate during summer periods, when ocean temperatures at higher latitudes are within the thermal range experienced in the tropics. After the autumn period, colder temperatures strongly influence the overwintering success

of juvenile tropical vagrants in temperate reefs (Booth *et al.*, 2018). Temperature, diet composition, and feeding patterns generally affect growth patterns of fish (Van Poorten and Walters, 2016) and general fish condition (Berumen *et al.*, 2005; McLeod *et al.*, 2015). The decreases in temperature generally encountered in higher latitudes, as well as new temperate diets and novel biotic interactions with temperate taxa, may therefore influence both growth and fish condition of range-expanding juveniles. In turn, survival rates are positively correlated with the body condition and growth of juvenile reef fish. For example, vagrants with better body condition and faster growth rates may be better at avoiding predation or exploiting diet sources more efficiently, and this may enhance their persistence in newly invaded ecosystems (Hoey and McCormick, 2004).

Surgeonfish (family Acanthuridae) are ecologically important tropical herbivorous fish that are among the most abundant taxa observed expanding their ranges into temperate reefs (Vergés, Steinberg, *et al.*, 2014; Booth *et al.*, 2018). In their natural tropical habitats, these herbivorous fishes can consume up to 100% of algal productivity (Hay, 1991). They play a very important role in tropical systems by removing algae that can otherwise outcompete corals, thereby maintaining reefs in a coral-dominant state and contributing to their resilience (Hughes *et al.*, 2007).

The majority of surgeonfish species are grazers or detritivores that derive their nutrients primarily from turfing algae and detritus (Choat *et al.*, 2004). This food source is commonly referred to as the “epilithic algal matrix” (EAM; Wilson *et al.*, 2003), and consists of a mixture of filamentous algae, detrital material including dead organic matter and some fauna, inorganic matter, microbes and microalgae, as well as sediments (Crossman *et al.*, 2001). Although EAM-consuming surgeonfish do not target adult seaweeds as their food source, they may nevertheless limit their establishment and cover by consuming seaweed recruits. In healthy tropical systems grazers, detritivores and scrapers coexist with browsing species that feed on adult seaweeds, and the feeding complementarity of these fishes is critical in maintaining high coral and low algal cover in tropical regions (Burkepile and Hay, 2008). Recent studies show that the range expansion of tropical, functionally diverse herbivorous fishes can cause dramatic community shifts in temperate systems (Vergés, Tomas, *et al.*, 2014; Bennett *et al.*, 2015). In particular, while the range expansion of browsers can contribute to the overgrazing of dominant habitat-forming kelps, the range expansion of grazers contributes to keeping alternate turf-dominated communities in a cropped state (Bennett *et al.*, 2015; Vergés *et al.*, 2016).

Nitrogen is an important limiting nutrient for many herbivores, including fish, because plants contain much lower levels of nitrogen than animals, and carbohydrate-rich cell walls need to be digested to assimilate plant cell content (Mattson, 1980). Amino acids and proteins are the primary dietary source of nitrogen in both macroalgae and detritus. These compounds are positively related to growth rates of fishes (Fris and Horn, 1993) and are often the primary nutritional constraint to the growth of herbivorous and detritivorous fish (Bowen, 1987). Since nitrogen content tends to increase with latitude in both marine and terrestrial plants (Borer *et al.*, 2013), it has been proposed that this higher quality food in relation to nitrogen content may facilitate the range expansion of tropical herbivorous fishes into temperate areas (Vergés, Steinberg, *et al.*, 2014), but this hypothesis remains untested.

In this study, we hypothesize that higher quality food in temperate regions may be facilitating the range expansion of the tropical surgeonfish grazer *Acanthurus triostegus* (herein referred to as “convictfish”). This species is commonly found in temperate latitudes outside the tropics during the juvenile growth phase within the austral summer months (Booth *et al.*, 2018). The convictfish is a grazing herbivore that primarily feeds on algal sources found in the EAM (Randall, 1961), and is one of the most abundant juvenile tropical herbivores on temperate reefs of eastern Australia (Basford *et al.*, 2016; Booth *et al.*, 2018). The convictfish is expanding its distribution in both eastern and western Australia, as well as southern Japan (Booth *et al.*, 2007; Feary *et al.*, 2014; Vergés, Steinberg, *et al.*, 2014). We quantified the body condition, growth, and trophic niche breadth of convictfish and related this to algal diet quality (i.e. nitrogen and C:N ratio) and temperature changes with latitude along the tropical to temperate coastline of eastern Australia. Specifically, we asked:

- (1) Is growth and body condition of convictfish higher in warmer tropical sites and do these traits decline with increasing latitude?
- (2) Does the trophic niche space occupied by convictfish change along a latitudinal gradient and are there ontogenetic changes in diet as fish grow?
- (3) Is the nutritional quality of the EAM and dominant seaweeds higher in temperate latitudes than in the tropics?

Material and methods

Study species and sites

Convictfish and samples of potential diet sources were collected along the east coast of Australia, spanning ~1200 km between 23°S and 34°S (Figure 1), from across their natural range as well as their vagrant boundaries. The natural range of the convictfish in eastern Australia is known to extend from the northern Great Barrier Reef to Coffs Harbour in northern New South Wales (Reef Life Survey database, www.reeflifesurvey.com).

Fish were collected at four sites—the northernmost (tropical) site was One Tree Island (23.5°S 152.1°E), in the southern Great Barrier Reef. Subtropical to temperate sites included Coffs Harbour (30.4°S 153.1°E), Forster (32.18°S 152.5°E), and Sydney (34.0°S 151.2°E). Potential diet sources were collected for nutrient analysis at the two latitudinal extremes only, in two tropical sites in the southern Great Barrier Reef: One Tree Island (23.5076°S 152.0916°E) and Heron Island (23.4°S 151.9°E), and two temperate sites in the Sydney region: Little Bay (34.0°S 151.2°E) and Narrabeen (33.7°S 151.3°E).

Satellite-derived daily average sea surface temperatures (SSTs; °C) from the four study sites were sourced from the Australian Ocean Data Network portal, which includes data from the Integrated Marine Observing System and the Australian Bureau of Meteorology. A spatial subset of 10 km² around the collection site was obtained, spanning a temporal period of 3 months prior to capture to estimate average temperatures over the juvenile growth period.

Sample collection and processing

Five samples of EAM and five samples of dominant brown seaweeds (*Lobophora* spp. and *Sargassum* spp.) were obtained between April and June 2014 from shallow tropical and temperate

reefs (<1 m depth) in regions where we observed high densities of convictfish juveniles. Sampling was staggered working from north to south, with tropical and temperate samples collected in April and May–June, respectively, to coincide with the timing when high densities of convictfish are observed in the field. *Lobophora* spp. and *Sargassum* spp. were sampled due to their relative abundance in both the temperate and tropical regions selected, as these were considered to be the most likely brown algal recruits incidentally consumed by the convictfish in these areas (Farrant and King, 2009). EAM was sampled in the same microhabitats and at the same time of the year when juvenile convictfish were observed feeding at each region by collecting boulders and pieces of dead coral or rocks and gently brushing off all turf algae, loose sediment, and detritus particles with a brush. These aqueous EAM samples were allowed to settle for 1–2 h before excess water was decanted, and the samples were subsequently frozen, freeze-dried and ground to a fine powder using a glass rod.

Ten juvenile convictfish were captured at each site between April and June 2016 using clove oil and nets (Munday and Wilson, 1997). Fish sampling was staggered from north to south, with tropical samples collected earlier (in April), and temperate samples later (May and June). All fish were collected from very shallow reefs (<1 m depth) or rock pools. Once sedated, the fish were placed on ice to be euthanized, and dissected within 4 h following capture. For each fish, we measured its standard length (SL) and fresh weight (W). In addition, the white muscle in the dorsal region of the fish was extracted for stable isotope analysis (SIA). White muscle was chosen as it has less variable isotopic signature compared to other tissues (Pinnegar and Polunin, 1999). Although the use of anesthetics such as clove oil can alter the isotope signatures of tissues that are in contact with the water containing the anesthetic (e.g. pectoral fins), it does not affect white muscle tissue samples (Nahon et al., 2017).

The algal diet sources and fish specimens used in this study were collected at the same time of the year in all locations (directly after the austral summer period in April–June; when juvenile convictfish settle in both tropical and temperate reefs), but in different years (2014 and 2016, respectively). We attempted to collect EAM diet sources during the 2016 sampling season but our sampling protocol was compromised. As algal nutritional quality in shallow reefs generally varies most among seasons and/or locations, not among years (Stewart et al., 2009), we are presenting the 2014 data to represent broad regional patterns.

SIA of fish muscle

To assess differences in niche width of juvenile convictfish, carbon and nitrogen SIA was conducted only on fish from the four sites. Fish muscle tissue samples were freeze-dried for 48 h, and then ground to a fine powder using a mortar and pestle. All equipment was washed with Milli-Q water and ethanol between samples to prevent cross contamination. Small amounts (0.5–2.0 mg) of samples were weighed using a microbalance and folded in tin capsules for analysis (Saintilan and Mazumder, 2010). Samples were analysed using a continuous flow isotope ratio mass spectrometer (CF-IRMS; Delta V IRMS) and elemental concentrations of carbon and nitrogen were measured using an element analyser (Flash Elemental Analyser). Data are reported relative to International Atomic Energy Agency secondary standards certified relative to Vienna Pee Dee Belemnite for carbon and air for nitrogen. A two-point calibration was employed to

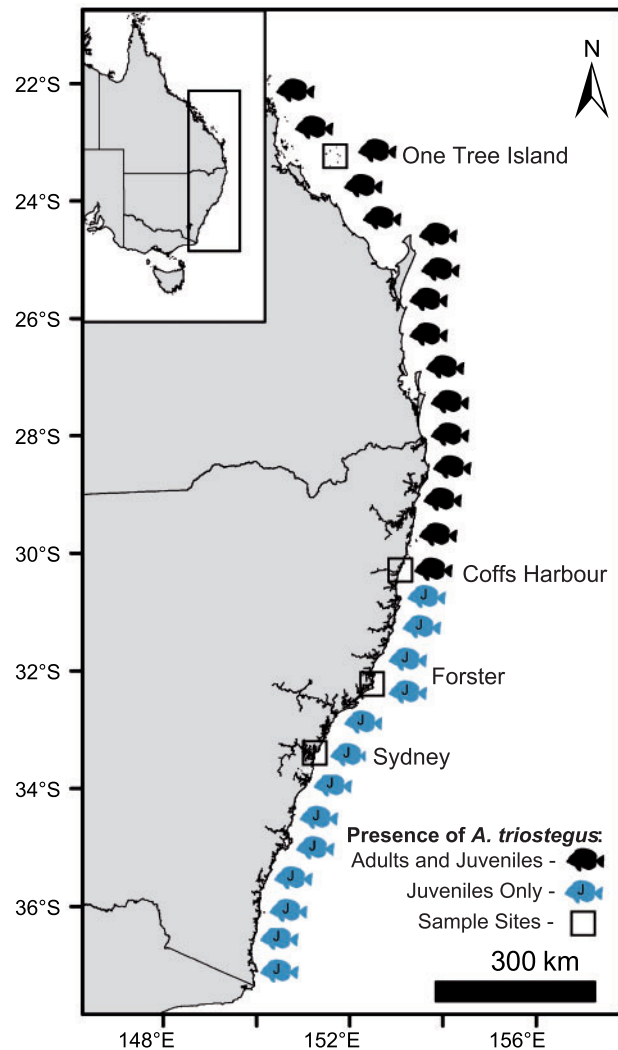


Figure 1. Study sites along the east coast of Australia, spanning a latitudinal range of 23.5°S–34.0°S.

normalize the isotope data, using standards that bracket the samples being analysed. Results are accurate to 1% for both C% and N% and ± 0.3 per mill for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Stable isotope values were reported in delta units in parts per thousand (‰) relative to the international standard and determined as follows:

$$X(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000,$$

where $X = \delta^{13}\text{C}$ or $\delta^{15}\text{N}$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$, respectively.

The carbon to nitrogen molar ratio (C:N) is closely related to the lipid content of tissue (Post et al., 2007). High lipid content in muscle tissue depletes $\delta^{13}\text{C}$ values (DeNiro and Epstein, 1978), so lipid normalization is needed for accurate calculation of trophic relationships (Hoffman et al., 2015). The overall range of C:N values in the fish tissue samples was between 2.8 and 3.6. In the one replicate where C:N was higher than 3.5, normalization adjustments were made for lipid content using the mathematical equation suggested by Post et al. (2007): $\delta^{13}\text{C}:\text{Normalized} = \delta^{13}\text{C}:\text{Untreated} - 3.32 + 0.99 \times \text{C:N}$.

Isotopic niche widths were quantified for each site using the standard ellipse area (SEA, %²), which is the area of an ellipse encompassing ~40% of the isotope data at each site—i.e. a bivariate standard deviation (Jackson *et al.*, 2011). The SEA approach is more robust to small sample sizes (e.g. $n = 10$, in our study) than alternative approaches such as measuring the convex hull area (Jackson *et al.*, 2011; Syväranta *et al.*, 2013). We calculated both the maximum likelihood estimates corrected for small sample sizes (SEAc) and Bayesian estimates (SEA_B) using 10⁴ iterations in the MCMC procedure. The mode of the posterior is reported for SEA_B. SEA was calculated using the “SIBER” R package (Jackson *et al.*, 2011). SEA can also be standardized to niche width of primary producers (Warry *et al.*, 2016) but we could not do this here because the isotopic signature of diet sources was not measured. This means that any differences identified in trophic niche width among sites may be due to differences in the variation in the isotopic diversity of basal resources, as well as differences in diet.

Fish condition and growth

Fish body condition for each individual fish was quantified using Fulton's K , using a modified equation from Suthers (1998):

$$K = \frac{W}{L^x}$$

where W is the weight (g), L is the standard length (mm), and x is the slope of the regression, fitted to all fish:

$$\log(W) = x\log(L) + b.$$

Growth rate was estimated using otolith growth increments as a proxy for age (Choat and Robertson, 2002), given that the daily formation of increments has not been validated for convictfish. Sagittal otoliths were mounted in thermoplastic resin (Crystal Bond™), and polished using fine lapping paper until a transverse section of the otolith nucleus was obtained (Wilson and McCormick, 1997). Otolith sections were then viewed and counted by the same person (HTS) under a compound microscope at $\times 200$ magnification. The mean number of increment counts was determined as the average of blind triplicate, non-successive counts for each otolith, requiring counts to fall within 10% of the mean. If this condition was not met a fourth count was conducted, and if the fourth count still differed >10% from the mean, that otolith was excluded from analyses (Callihan *et al.*, 2008). Only one otolith was excluded based on this criterion.

Otolith weight and length parameters were also used as age proxies alongside increment counts (Pawson, 1990). Growth rate and condition was calculated using standard fish length divided by either increment counts (mm increment⁻¹) or otolith weight (mm mg⁻¹) as slower growing fish have proportionally larger otoliths (Reznick *et al.*, 1989). Growth rates using otolith counts (mm increment⁻¹) were considered relative growth rates because daily increment deposition in otoliths has not been validated for this species. To support the use of otolith increments as an age proxy, the correlations (Pearson's r) between otolith increment counts and fish SL as well as otolith increment count and otolith weight were calculated.

Statistical analysis

Prior to analysis, response variables were examined for normality and homogeneity of variances, using the Shapiro–Wilk and

Levene tests, respectively (Briand *et al.*, 2016). As a result, no transformations were conducted on the data.

Differences in nitrogen content and C:N ratio of the EAM and dominant seaweeds were tested at the regional and site level at the two latitudinal extremes of our study region using a two factor nested analysis of variance (ANOVA), with Region as a fixed factor and site as a random factor nested within region. Region had two levels (tropical or temperate), and there were two sites in each region (One Tree Island and Heron Island in the tropics; Little Bay and Narrabeen in the temperate region).

Differences in SST, fish condition, and growth rates among the four latitudinal sites (One Tree Island, Coffs Harbour, Forster, and Sydney) were tested using a single factor ANOVA. Tukey's Honest Significant Difference (HSD) test was used a posteriori to discern specific differences among sites. Multivariate analysis of covariance (MANCOVA) was used to examine the effect of site on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using standard fish length as a covariate, with significance tested with a Pillai test. Univariate ANCOVA were examined to help interpret the MANCOVA results. All analyses were performed in R version 3.5.2 (R Core Team, 2013).

Results

Temperature, condition, and growth

SST varied significantly among sites during the 3 months prior to sampling (ANOVA, $F_{3,32} = 243.4$, $p < 0.001$), with significant differences between all sites except between Coffs Harbour and Forster. One Tree Island exhibited the highest average daily temperature ($27^\circ\text{C} \pm \text{s.e.}$), which was around 4°C warmer in comparison to the most temperate site in Sydney (Figure 2a).

SL of juvenile convictfish collected (ranging between 25 and 70 mm) was not significantly different among sites (ANOVA, $F_{3,44} = 1.56$, $p = 0.212$), indicating that there was no sampling bias in the capture of fish across sites. There were no significant differences in fish body condition (Fulton's K) among sites (ANOVA, $F_{3,44} = 0.981$, $p = 0.411$) (Figure 2b).

Increment counts of fish ranged between 50 and 130 counts. Relative growth rates were similar across all sites, regardless of whether we used increment counts (ANOVA, $F_{3,35} = 2.087$, $p = 0.12$) (Figure 2c) or otolith weight (ANOVA, $F_{3,27} = 0.326$, $p = 0.0807$) as the age metric. Increment count was correlated with both fish SL ($r = 0.836$) and otolith weight ($r = 0.858$).

Nutritional quality

Total nitrogen content of all temperate diet sources was significantly higher than that of tropical diet sources (nested ANOVA, $F_{1,111} = 30.125$, $p < 0.001$; Figure 3a), and there were no significant differences among sites within each region ($p = 0.468$). Specifically, total nitrogen content of the EAM was three times higher in temperate reefs than in the tropics (nested ANOVA, $F_{1,18} = 63.63$, $p < 0.001$; Figure 3a), nitrogen in *Sargassum* was twice as high in temperate reefs (nested ANOVA, $F_{1,16} = 110.84$, $p < 0.001$; Figure 3a), and similarly *Lobophora* exhibited twice as much total nitrogen in the temperate region (nested ANOVA, $F_{1,15} = 96.57$, $p < 0.001$; Figure 3a).

Carbon to nitrogen ratios (C:N) of tropical diet sources were twice as high as temperate diet sources (nested ANOVA, $F_{1,111} = 19.188$, $p < 0.001$; Figure 3b), with no significant differences among sites within each region ($p = 0.282$). Specifically, C:N ratios of EAM were six times higher in the tropics than in temperate reefs (ANOVA, $F_{3,18} = 23.28$, $p < 0.001$; Figure 3b), however there

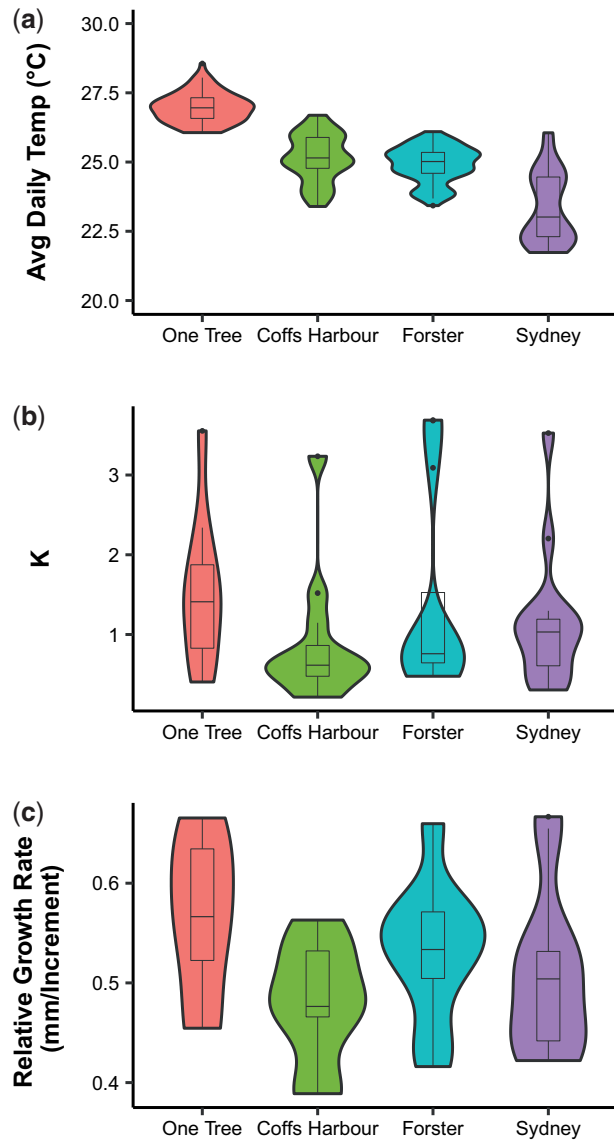


Figure 2. Violin plots of (a) average daily SSTs of study sites, spanning 3 months prior to sampling; (b) fish body condition (Fulton's K) of fish across study sites ($n = 10$ fish per site); (c) growth rates using otolith increments as a measure of relative growth rate. Rates (mm increment^{-1}) are computed using fish SL divided by the number of otolith increments. In all subplots, the width of the "violin" is proportional to the sample density along the y -axis. The area of each "violin" (in each subplot) is the same so the widths represent the proportions within each "violin" and not of the total dataset. The boxplots show the median, 25th and 75th percentiles with the whiskers extending 1.5 times the interquartile range.

were differences among sites within each region ($p = 0.046$). Similarly, C:N was higher in the tropics for both *Sargassum* (nested ANOVA, $F_{1,16} = 13.87$, $p = 0.001$; Figure 3b) and *Lobophora* (nested ANOVA, $F_{1,15} = 90.76$, $p < 0.001$; Figure 3b).

Trophic niche breadth and isotopic signatures

The trophic niche width, as estimated using SEA (Figure 4) was greater for One Tree Island and Sydney compared to Coffs

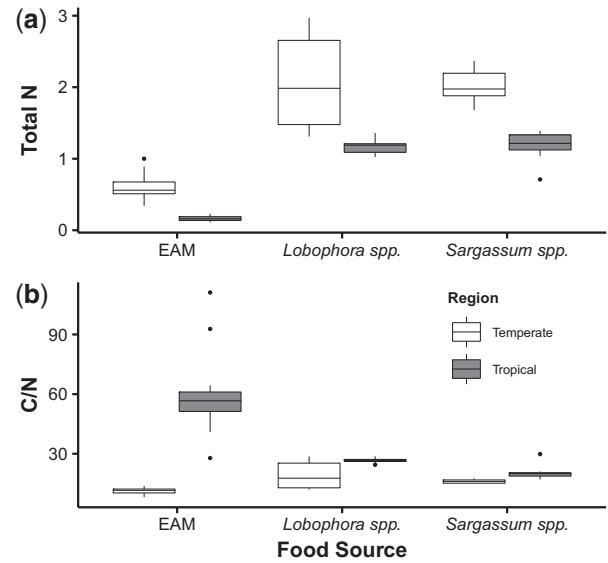


Figure 3. Boxplots showing (a) total nitrogen (% of dry weight) and (b) C:N ratio of food sources across the two study regions (two tropical sites at 23°S and two temperate sites at 34°S). The boxplots show the median, 25th and 75th percentiles with the whiskers extending 1.5 times the interquartile range.

Harbour and Forster (SEA_C, SEA_B: One Tree Island: 3.43, 3.00, Coffs Harbour: 1.11, 1.44, Forster: 1.67, 1.43, Sydney: 4.67, 4.53). The posterior distributions of the Bayesian SEA_B are broad for all sites (Supplementary Figure S1), probably due to low sample sizes (Syväranta et al., 2013), but the lack of overlap provides strong evidence that the niche widths of the Sydney and One Tree Island fish are larger than the niche widths at Coffs Harbour and Forster.

The variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fish isotopic signature among sites was dependent on body size (Figure 5), with a significant interaction between site and SL (MANCOVA, $F_{6,88} = 3.72$, $p = 0.002$). A univariate test of each isotope show that this is largely due to $\delta^{15}\text{N}$, which also showed a significant interaction between site and size ($\delta^{15}\text{N}$: ANCOVA, $F_{3,44} = 5.88$, $p = 0.002$), with One Tree Island fish consistently displaying a lower $\delta^{15}\text{N}$ value than fish from all other sites and not following an increasing trend with fish length (Figure 5). In contrast, fish $\delta^{13}\text{C}$ values increased linearly with fish length at all sites (ANCOVA, $F_{1,44} = 77.92$, $p < 0.001$) and also differed significantly among sites (Figure 5a; $F_{3,44} = 3.13$, $p = 0.035$), with Coffs Harbour displaying lower values than all other sites (Tukey HSD, $p < 0.01$). There was a marginally non-significant interaction between site and fish length ($F_{3,44} = 2.34$, $p = 0.086$), with $\delta^{13}\text{C}$ values of Coffs Harbour fish tending to increase less with body size than at other sites.

Discussion

Our results show that tropical juvenile convictfish are able to sustain similar levels of growth and overall body condition across a wide latitudinal gradient encompassing over 1200 km and 10° of latitude, despite differences in water temperature of up to 4°C among the studied regions. Although temperature can be a dominant constraint for tropical reef fish in their juvenile stages (Booth et al., 2018), our study reveals that the summer temperatures experienced by tropical convictfish during their early juvenile stage in

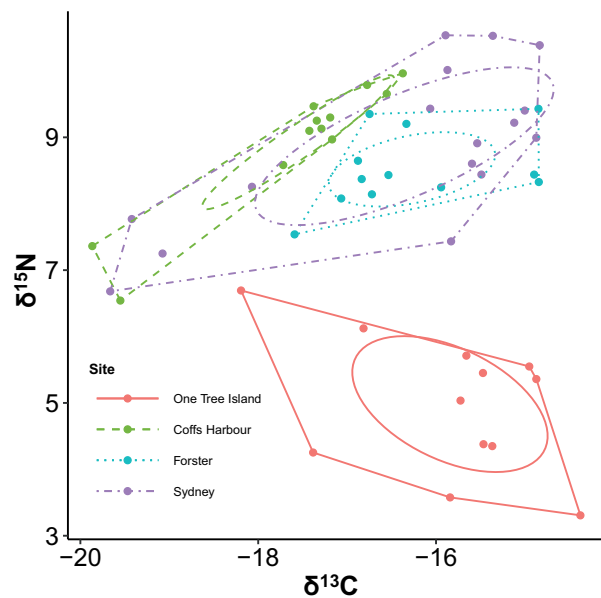


Figure 4. $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ niche space. Each point represents an individual fish, straight lines are convex hulls, and ovals are standard ellipses. All units are ‰. Line types and colours represent the different sites.

temperate reefs as far south as Sydney are not limiting growth or body condition for this species. Diet sources were potentially more nutritious in temperate reefs than in tropical coral-dominated habitats, as suggested by higher nitrogen levels and lower C:N ratios (Atkinson and Smith, 1983). This suggests the possibility that enhanced diet nutritional quality may be compensating for lower water temperatures in higher latitude sites, i.e. overall growth patterns may potentially be maintained as vagrants shift poleward because of greater diet quality in cooler reefs.

Typically, fish growth rates tend to increase with warming temperatures (Hoar and Randall, 1971). Studies on coral reef fishes have demonstrated positive correlations between growth parameters and temperatures (Takahashi *et al.*, 2012), demonstrating a generally linear relationship until a species' thermal threshold is reached. In contrast, here we found no difference in growth and condition indices across a latitudinal gradient revealing on average a 15–20 mm monthly growth rate for fish from all sites. Somewhat similarly, McLeod *et al.* (2015) found an overall decrease in growth rates of larval fish at warmer latitudes.

Although SST generally correlates with *in situ* logger-recorded temperatures, these satellite-derived metrics fail to detect important small-scale variability typical of shallow water reefs (Smale and Wernberg, 2009). In this study, we collected convictfish juveniles in coastal rock pools and shallow reefs, systems that can experience local temperatures $>10^\circ\text{C}$ than nearby open waters during much of the day (Kain, 2008). If latitudinal differences in local microclimates exist, this could potentially dampen the differences in temperature observed using SST data, so that the total difference in temperature between the tropical and the temperate sites would be not as great as revealed using SST. However, we collected convictfish from sites with similar depth profiles at all latitudes (i.e. very shallow reefs <1 m), and we expect that any microclimate effect would be consistent among sites.

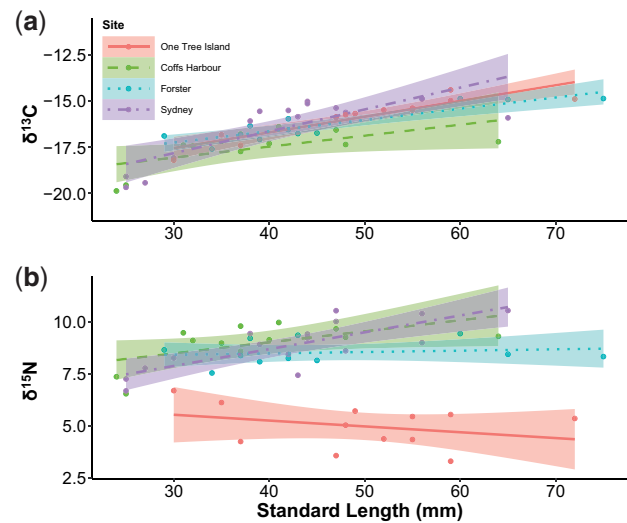


Figure 5. Relationship between fish SL and (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$. Colours and line types represent Sites, and shaded areas represent 95% confidence intervals.

There are major biotic and abiotic differences between the tropical reefs where convictfish typically reside (e.g. One Tree Island and Heron Island in this study) and the temperate reefs studied, where typically only vagrant convictfish juveniles are observed (although some individuals are starting to overwinter; Booth *et al.*, 2018). In addition to substantial differences in temperature, the dominant habitat formers in shallow reefs shift from corals to canopy-forming seaweeds as fish move outside the tropics, with major accompanying changes in overall benthic community composition and available diet sources. It is surprising that despite this variation in both biotic and abiotic summer conditions among sites spanning over 1200 km, there were no regional differences in body condition and growth rate among convictfish populations. Previous studies have indicated that fish condition can influence long-term survivorship (Berumen *et al.*, 2005), which may have significant implications on range expanding populations as they settle and eventually overwinter in higher latitude reefs. Despite being subject to different biotic interactions in a new habitat, vagrant populations in higher latitudes did not show a reduction in overall body condition contrary to suggestions that changes in interspecific competition can impact physiological condition (Berumen *et al.*, 2005).

The greater isotopic niche breadth exhibited by One Tree Island and Sydney fish populations are an indicator of a generalist foraging strategy at the population level, which can be attributed to a potentially greater variety of food sources available to and consumed by these populations (Mazumder *et al.*, 2016). This strategy increases their adaptable capacity and facilitates a greater chance of survival during periods of resource limitation (Helaouët and Beaugrand, 2009). High niche space exhibited by One Tree Island may also potentially coincide with lower food quality in the tropics (Figure 3), as this population may need to ingest larger varieties of food sources to assimilate an adequate proportion of nutrients. The highest niche area was observed in Sydney, which may indicate that this species is a generalist able to adapt to local trophic resources (Azzurro *et al.*, 2007). Invasive populations are often generalists, and thus higher niche space in

Sydney may be a good indicator of the potential for these vagrants to broaden their niche space as they intrude into newer habitats (Machovsky-Capuska *et al.*, 2016). What is less clear is why trophic niche space may have been reduced in the two subtropical sites (Forster and Coffs Harbour). Limited niche space may be attributed to a selective population, which preferentially feeds on higher quality diet sources (Goecker *et al.*, 2005). The diversity in the niche space of all four sites suggests that each population is subject to different local biotic interactions and environmental conditions (Dromard *et al.*, 2015). The niche overlap exhibited between subtropical to temperate sites indicates some similarity in patterns of both diet sources and feeding regimes of fish, in comparison to One Tree Island which appears to be distinct from all other sites. This could be due to differences in coastal oceanography (Suthers *et al.*, 2011), and enhanced urbanization in temperate sites (Gaston and Suthers, 2004) compared to the undeveloped area encompassing One Tree Island.

A positive correlation between $\delta^{13}\text{C}$ and lengths of individual fish from all sites provides important information relating to dietary shifts of this species as individuals grow (Figure 5). This $\delta^{13}\text{C}$ -size relationship indicates an ontogenetic shift in diet, a pattern that is consistent with other studies that have also observed ontogenetic shifts during the early juvenile growth period for this species (McCormick and Makey, 1997; Fr  d  rich *et al.*, 2009). Combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic data from Fr  d  rich *et al.* (2009) demonstrated a rapid shift from zooplanktivory to herbivory in early settled individuals, occurring only a few days post-settlement and roughly once SL is above 25–30 mm. The size-related variation of $\delta^{13}\text{C}$ observed both in this study and in Fr  d  rich *et al.* (2009) is therefore likely reflecting tissue turnover, as it takes some time for isotopic equilibrium to be reached once juveniles start feeding exclusively on EAM/filamentous algae. This provides sound evidence that vagrant populations undergo ontogenetic shifts during their juvenile growth period (McCormick and Makey, 1997), and potentially switch diet sources as they grow. Generally, foraging and predation risk trade-offs, novel diet sources and habitats, as well as physiological changes (i.e. increased mobility with body size) drive many shifts in the ontogenetic niche (Hammerschlag-Peyer *et al.*, 2011).

The $\delta^{15}\text{N}$ value of One Tree Island fish coincides with values from other tropical studies, which exhibited $\delta^{15}\text{N}$ values around 5‰ (Fr  d  rich *et al.*, 2009; Lamb *et al.*, 2012). However, results of this study suggest that independent of size, the One Tree Island fish population have a significantly lower $\delta^{15}\text{N}$ when compared to the three higher latitude sites. This could be potentially due to differences in accessing food from different trophic level (i.e. convictfish feeding on more animal matter in higher latitudes). Alternatively, the higher $\delta^{15}\text{N}$ levels exhibited by temperate sites may be attributed to the presence of food with higher $\delta^{15}\text{N}$ values (Azzurro *et al.*, 2007). Possible explanations for the elevated $\delta^{15}\text{N}$ values of the temperate fish are increased urbanization and associated wastewater pollution, which is known to enrich $\delta^{15}\text{N}$ values of primary producers (McClelland *et al.*, 1997), bivalves (Oczkowski *et al.*, 2008) and fish (Gaston and Suthers, 2004), and upwelling of deep shelf water, which is also enriched in $\delta^{15}\text{N}$ (Suthers *et al.*, 2011).

Carbon to nitrogen ratio (C:N) is a broad measure of food quality, because nitrogen correlates with protein content in the diet (Hill and McQuaid, 2009). Diets with a low C:N ratio (<6) contain a higher proportion of protein and are considered better quality diets compared to diets with a high C:N ratio (Fantle

et al., 1999). The nutritional quality of food sources measured here (C:N and total N) was much greater in temperate reefs across all food types measured (EAM and seaweeds). This supports findings from a large meta-analysis study, which showed that macrophytes from higher latitudes generally exhibit a higher nitrogen concentration than lower latitude macrophytes across terrestrial, freshwater, and marine biomes potentially to maintain metabolic functioning across regions with different insolation and growing season regimes (Borer *et al.*, 2013).

This study has shown that juvenile convictfish are able to maintain similar growth rates and general body condition as they expand their range polewards from their native tropical reefs towards temperate reefs during the austral summer–autumn period. Although some caution needs to be exercised when interpreting our results given the relatively low sample size of all fish measures ($n = 10$), our results suggest that convictfish juvenile growth and feeding habits are not being compromised in temperate regions during summer. Seemingly, the tropicalization of temperate rocky reefs is facilitated not only by ocean transport and coastal warming, but also, potentially, by access to more nutritious resources. Summer conditions of temperate environments are not limiting the extension of juvenile convictfish. Instead, the survival of tropical juveniles, and subsequent establishment as adults, are strongly affected by temperature drops in winter (Booth *et al.*, 2018), and may also be affected by challenges in foraging and competition as juveniles grow and move throughout temperate reefs. The continued expansion of tropical species like convictfish into temperate reefs can lead to increased herbivory as a result of both higher herbivore abundance and greater per-capita consumption rates, as these range-shifters consume more turf algae than local warm-temperate herbivores even at the juvenile stage (Basford *et al.*, 2016). In turn, these increases in herbivory can have major cascading effects in temperate reefs as they can lead to the decline of habitat-forming seaweeds (Verg  s, Steinberg, *et al.*, 2014). Determining what makes tropical vagrants successful in novel environments is therefore key to understanding the changing dynamics of our oceans, as warmer oceans result in more species shifting their distribution polewards.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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References

- Atkinson, M. J., and Smith, S. V. 1983. C:N:P ratios of benthic marine plants 1. *Limnology and Oceanography*, 28: 568–574.
- Azzurro, E., Fanelli, E., Mostarda, E., Catra, M., and Andaloro, F. 2007. Resource partitioning among early colonizing *Siganus luridus* and native herbivorous fish in the Mediterranean: an integrated study based on gut-content analysis and stable isotope signatures. *Journal of the Marine Biological Association*, 87: 991–998.
- Basford, A. J., Feary, D. A., Truong, G., Steinberg, P. D., Marzinelli, E. M., and Vergés, A. 2016. Feeding habits of range-shifting herbivores: tropical surgeonfishes in a temperate environment. *Marine and Freshwater Research*, 67: 75–79.
- Bennett, S., Wernberg, T., Harvey, E. S., Santana-Garcon, J., and Saunders, B. J. 2015. Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs (D. Bellwood, Ed.). *Ecology Letters*, 18: 714–723.
- Berumen, M. L., Pratchett, M. S., and McCormick, M. I. 2005. Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Marine Ecology Progress Series*, 287: 217–227.
- Booth, D. J., Beretta, G. A., Brown, L., and Figueira, W. F. 2018. Predicting success of range-expanding coral reef fish in temperate habitats using temperature–abundance relationships. *Frontiers in Marine Science*, 5: 31. doi: 10.3389/fmars.2018.00031.
- Booth, D. J., Figueira, W. F., Gregson, M. A., Brown, L., and Beretta, G. 2007. Occurrence of tropical fishes in temperate southeastern Australia: role of the East Australian Current. *Estuarine, Coastal and Shelf Science*, 72: 102–114.
- Borer, E. T., Bracken, M. E. S., Seabloom, E. W., Smith, J. E., Cebrian, J., Cleland, E. E., Elser, J. J. *et al.* 2013. Global biogeography of autotroph chemistry: is insolation a driving force? *Oikos*, 122: 1121–1130.
- Bowen, S. H. 1987. Composition and nutritional value of detritus. *In Detritus and Microbial Ecology in Aquaculture ICLARM Conference Proceedings*, pp. 192–216.
- Briand, M. J., Bonnet, X., Guillou, G., and Letourneur, Y. 2016. Complex food webs in highly diversified coral reefs: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes. *Food Webs*, 8: 12–22.
- Burkpile, D. E., and Hay, M. E. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences*, 105: 16201–16206.
- Callihan, J. L., Takata, L. T., Woodland, R. J., and Secor, D. H. 2008. Cohort splitting in bluefish, *Pomatomus saltatrix*, in the US Mid-Atlantic Bight. *Fisheries Oceanography*, 17: 191–205.
- Choat, J. H., Robbins, W. D., and Clements, K. D. 2004. The trophic status of herbivorous fishes on coral reefs. *Marine Biology*, 145: 445–454.
- Choat, J. H., and Robertson, D. R. 2002. Age-based studies. *In Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, pp. 57–80. Ed. by P. F. Sale. Academic Press, San Diego, CA.
- Crossman, D. J., Choat, H. J., Clements, K. D., Hardy, T., and McConochie, J. 2001. Detritus as food for grazing fishes on coral reefs. *Limnology and Oceanography*, 46: 1596–1605.
- DeNiro, M. J., and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42: 495–506.
- Dromard, C. R., Bouchon-Navaro, Y., Harmelin-Vivien, M., and Bouchon, C. 2015. Diversity of trophic niches among herbivorous fishes on a Caribbean reef (Guadeloupe, Lesser Antilles), evidenced by stable isotope and gut content analyses. *Journal of Sea Research*, 95: 124–131.
- Fantle, M. S., Dittel, A. I., Schwalm, S. M., Epifanio, C. E., and Fogel, M. L. 1999. A food web analysis of the juvenile blue crab, *Callinectes sapidus*, using stable isotopes in whole animals and individual amino acids. *Oecologia*, 120: 416–426.
- Farrant, P. A., and King, R. J. 2009. The subtidal seaweed communities of the Sydney region. *Wetlands Australia Journal*, 2: 51.
- Feary, D. A., Pratchett, M. S., Emslie, M., Fowler, A. M., Figueira, W. F., Luiz, O. J., Nakamura, Y. *et al.* 2014. Latitudinal shifts in coral reef fishes: why some species do and others do not shift. *Fish and Fisheries*, 15: 593–615.
- Figueira, W. F., and Booth, D. J. 2010. Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Global Change Biology*, 16: 506–516.
- Frédérich, B., Fabri, G., Lepoint, G., Vandewalle, P., and Parmentier, E. 2009. Trophic niches of thirteen damselfishes (Pomacentridae) at the Grand Récif of Toliara, Madagascar. *Ichthyological Research*, 56: 10–17.
- Fris, M. B., and Horn, M. H. 1993. Effects of diets of different protein content on food consumption, gut retention, protein conversion, and growth of *Cebidichthys violaceus* (Girard), an herbivorous fish of temperate zone marine waters. *Journal of Experimental Marine Biology and Ecology*, 166: 185–202.
- Gaston, T. F., and Suthers, I. M. 2004. Spatial variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of liver, muscle and bone in a rocky reef planktivorous fish: the relative contribution of sewage. *Journal of Experimental Marine Biology and Ecology*, 304: 17–33.
- Goecker, M. E., Heck, Jr, K. L., and Valentine, J. F. 2005. Effects of nitrogen concentrations in turtlegrass *Thalassia testudinum* on consumption by the bucktooth parrotfish *Sparisoma radians*. *Marine Ecology Progress Series*, 286: 239–248.
- Hammerschlag-Peyer, C. M., Yeager, L. A., Araújo, M. S., and Layman, C. A. 2011. A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. *PLoS One*, 6: e27104.
- Hay, M. 1991. Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. *In The Ecology of Fishes on Coral Reefs*, pp. 96–119. Ed. by P. F. Sale. Academic Press, San Diego, CA.
- Helaouët, P., and Beaugrand, G. 2009. Physiology, ecological niches and species distribution. *Ecosystems*, 12: 1235–1245.
- Hill, J., and McQuaid, C. 2009. Effects of food quality on tissue-specific isotope ratios in the mussel *Perna perna*. *Hydrobiologia*, 635: 81–94.
- Hoar, W. S., and Randall, D. J. (1971). *Fish Physiology*, Vol. VI: Environmental Relations and Behavior, pp. 559. Academic Press, New York, London.
- Hoey, A. S., and McCormick, M. I. 2004. Selective predation for low body condition at the larval–juvenile transition of a coral reef fish. *Oecologia*, 139: 23–29.
- Hoffman, J. C., Sierszen, M. E., and Cotter, A. M. 2015. Fish tissue lipid–C:N relationships for correcting $\delta^{13}\text{C}$ values and estimating lipid content in aquatic food-web studies. *Rapid Communications in Mass Spectrometry*, 29: 2069–2077.
- Hughes, T. P., Bellwood, D. R., Folke, C. S., McCook, L. J., and Pandolfi, J. M. 2007. No-take areas, herbivory and coral reef resilience. *Trends in Ecology & Evolution (Amsterdam)*, 22: 1–3.
- Jackson, A. L., Inger, R., Parnell, A. C., and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80: 595–602.
- Kain, J. M. 2008. Winter favours growth and survival of *Ralfsia verrucosa* (Phaeophyceae) in high intertidal rockpools in southeast Australia. *Phycologia*, 47: 498–509.
- Lamb, K., Swart, P. K., and Altabet, M. A. 2012. Nitrogen and carbon isotopic systematics of the Florida Reef Tract. *BMS*, 88: 119–146.
- Machovsky-Capuska, G. E., Senior, A. M., Simpson, S. J., and Raubenheimer, D. 2016. The multidimensional nutritional niche. *Trends in Ecology & Evolution*, 31: 355–365.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, 11: 119–161.

- Mazumder, D., Williams, R. J., Wen, L., Saintilan, N., and Walsh, C. T. 2016. Impoundment constraint of niche diversity of fishes at a south-eastern Australian river. *Hydrobiologia*, 771: 195–206.
- McClelland, J. W., Valiela, I., and Michener, R. H. 1997. Nitrogen-stable isotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. *Limnology and Oceanography*, 42: 930–937.
- McCormick, M. I., and Makey, L. J. 1997. Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. *Marine Ecology Progress Series*, 153: 247–257.
- McLeod, I. M., McCormick, M. I., Munday, P. L., Clark, T. D., Wenger, A. S., Brooker, R. M., Takahashi, M. *et al.* 2015. Latitudinal variation in larval development of coral reef fishes: implications of a warming ocean. *Marine Ecology Progress Series*, 521: 129–141.
- Munday, P. L., and Wilson, S. 1997. Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. *Journal of Fish Biology*, 51: 931–938.
- Nahon, S., Séité, S., Kolasinski, J., Aguirre, P., and Geurden, I. 2017. Effects of euthanasia methods on stable carbon ($\delta^{13}\text{C}$ value) and nitrogen ($\delta^{15}\text{N}$ value) isotopic compositions of fry and juvenile rainbow trout *Oncorhynchus mykiss*. *Rapid Communications in Mass Spectrometry*, 31: 1742–1748.
- Oczkowski, A., Nixon, S., Henry, K., DiMilla, P., Pilson, M., Granger, S., Buckley, B. *et al.* 2008. Distribution and trophic importance of anthropogenic nitrogen in Narragansett Bay: an assessment using stable isotopes. *Estuaries and Coasts*, 31: 53–69.
- Pawson, M. G. 1990. Using otolith weight to age fish. *Journal of Fish Biology*, 36: 521–531.
- Pinnegar, J. K., and Polunin, N. V. C. 1999. Differential fractionation of delta ^{13}C and delta ^{15}N among fish tissues: implications for the study of trophic interactions. *Functional Ecology*, 13: 225–231.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K. *et al.* 2013. Global imprint of climate change on marine life. *Nature Climate Change*, 3: 919–925.
- Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., and Montaña, C. G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, 152: 179–189.
- Randall, J. E. 1961. A contribution to the biology of the convia surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. *Pacific Science*, 15: 215–272.
- R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reznick, D., Lindbeck, E., and Bryga, H. 1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 108–112.
- Saintilan, N., and Mazumder, D. 2010. Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. *Marine and Freshwater Research*, 61: 615–616.
- Smale, D. A., and Wernberg, T. 2009. Satellite-derived SST data as a proxy for water temperature in nearshore benthic ecology. *Marine Ecology Progress Series*, 387: 27–37.
- Stewart, H., Fram, J., Reed, D., Williams, S., Brzezinski, M., MacIntyre, S., and Gaylord, B. 2009. Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA. *Marine Ecology Progress Series*, 375: 101–112.
- Suthers, I. M. 1998. Bigger? Fatter? Or is faster growth better? Considerations on condition in larval and juvenile coral-reef fish. *Austral Ecology*, 23: 265–273.
- Suthers, I. M., Young, J. W., Baird, M. E., Roughan, M., Everett, J. D., Brassington, G. B., Byrne, M. *et al.* 2011. The strengthening East Australian Current, its eddies and biological effects—an introduction and overview. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58: 538–546.
- Syväranta, J., Lensu, A., Marjomäki, T. J., Oksanen, S., and Jones, R. I. 2013. An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. *PLoS One*, 8: e56094.
- Takahashi, M., McCormick, M. I., Munday, P. L., and Jones, G. P. 2012. Influence of seasonal and latitudinal temperature variation on early life-history traits of a coral reef fish. *Marine and Freshwater Research*, 63: 856–864.
- Van Poorten, B. T., and Walters, C. J. 2016. How can bioenergetics help us predict changes in fish growth patterns? *Fisheries Research*, 180: 23–30.
- Vergés, A., Doropoulos, C., Malcolm, H. A., Skye, M., Garcia-Pizá, M., Marzinelli, E. M., Campbell, A. H. *et al.* 2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proceedings of the National Academy of Sciences*, 113: 13791–13796.
- Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L. *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, 281: 20140846.
- Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z., Dendrinis, P., Karamanlidis, A. A. *et al.* 2014. Tropical rabbitfish and the deforestation of a warming temperate sea (Y. Buckley, Ed.). *Journal of Ecology*, 102: 1518–1527.
- Warry, F. Y., Reich, P., Cook, P. L., Mac Nally, R., Thomson, J. R., and Woodland, R. J. 2016. Nitrogen loads influence trophic organization of estuarine fish assemblages. *Functional Ecology*, 30: 1723–1733.
- Wilson, D., and McCormick, M. 1997. Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. *Marine Ecology Progress Series*, 153: 259–271.
- Wilson, S. K., Bellwood, D. R., Choat, J. H. and Furnas, M. J. 2003. Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology: An Annual Review*, 41: 279–309.

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