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ORIGINAL PAPER

Early life history traits and elevated growth trajectories associated with survival into winter in range-expanding coral reef fish

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Abstract
Climate change is driving the poleward range expansion of sub-tropical and tropical marine species into temperate ecosystems, with ocean-warming hotspots experiencing rapid shifts in species distributions. While recruitment to temperate waters by expatriating tropical vagrant fish is increasing, surviving through the cooler winters remains a significant barrier to their establishment. This study investigates the links between early life history traits and survival into winter in the Sergeant Major (*Abudefduf vaigiensis*), a tropical damselfish expanding its range into temperate southeastern Australia. Using otolith microstructure analysis, we reconstructed the early life histories of 122 individuals collected from rocky reefs in Sydney (33.8ºS) Australia in 2022 and 2023 and assessed their early life history traits. Our results demonstrate that individuals sampled during winter (hereafter "wintered fish") had a larger size at hatching, longer pelagic larval duration, and higher body condition than fish collected before winter. Lower settlement water temperatures were positively associated with winter survival, indicating that a settlement date closer to the onset of winter was favourable. Additionally, wintered fish, exhibited higher growth rates in early life compared to fish sampled prior to winter onset. These findings suggest that some early life history traits are selected for survival into winter, potentially mediating the physiological impacts of declining water temperature. If such traits increase overwinter survival they may facilitate the establishment of this range-expanding species in temperate rocky reef environments.

Keywords Climate change · Early life history · Growth rates · Otolith analysis · Overwintering · Range expansion · Tropical fish

Introduction

Climate change is altering marine ecosystems globally, with one significant impact being the poleward range expansion of tropical species into temperate waters (Munday et al. 2008; Pecl et al. 2017; Sunday et al. 2015). Over the past century, ocean temperatures have risen significantly, with the global mean sea surface temperature increasing by approximately 0.13°C per decade since 1900 (Intergovernmental Panel on Climate 2023). The warming trend is particularly pronounced in certain regions, known as ocean warming hotspots. These areas, including the southeast coast of Australia (Suthers et al. 2011), the Mediterranean Sea (Nykjaer 2009), and waters off Japan (Wu et al. 2012) are experiencing temperature increases at two to four times faster than the global average. Such rapid warming is facilitated by the increase in the flow of Western Boundary Currents, increasing incursions of tropical species into traditionally temperate ecosystems (Pecl et al. 2017), and

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as a result altering ecological dynamics and community structures in these regions (Kingsbury, Gillanders, Booth, & Nagelkerken 2020a, b; Nakamura et al. 2013).

The range expansion process in tropical vagrant fishes can be conceptualised using the invasion pathway model, which involves distinct stages: transport, colonisation, establishment, and landscape spread (Hellmann et al. 2008). As global temperatures rise, more tropical fish species appear in temperate waters, far beyond their usual range (Figueira & Booth 2010; Fowler et al. 2018). Vagrant fishes are transported as larvae by strengthening ocean currents, such as the East Australian Current, which has shown increased southward penetration over the past 60 years (Booth et al. 2011; Ridgway 2007; Suthers et al. 2011). While this model provides a useful framework, it is important to note that the establishment and colonisation stages are currently bottlenecked by winter ocean temperatures in temperate waters (Booth et al. 2018). Seasonal mortality rates of vagrant fish approach 99% due to low water temperatures (Figueira & Booth 2010), with most individuals only surviving the arrival season, although a small fraction persists. The high mortality represents a barrier to these species establishing in temperate locations. However, as ocean temperatures continue to rise, the potential for successful overwintering will likely increase, removing a key barrier in the invasion pathway model. Our understanding of individual traits that may enhance survival near thermal limits remains limited, particularly for range-expanding marine species.

Early life histories potentially play a significant role in individuals persisting near their lower thermal limits. The growth mortality hypothesis posits that faster-growing individuals experience enhanced survival due to their ability to avoid selective predation and environmental stressors (Robert et al. 2023). This framework has been extensively validated in tropical fish within their natal environments, where early life history traits (ELHTs), such as growth rates, pelagic larval duration (PLD), and size at key early life milestones, are well-established factors influencing post-settlement survivorship.(Monica Gagliano et al. 2007; Rankin & Sponaugle 2011; Sponaugle & Grorud-Colvert 2006; Sponaugle et al. 2006; Vigliola & Meekan 2002). However, their specific role in facilitating survival to and through winter for range-expanding marine species in temperate ecosystems remains poorly understood.

Fish may have undergone a selective process during their pelagic larval phase, with certain phenotypes persisting through high mortality events such as hatching, PLD, and settlement (M. Gagliano et al. 2007; Garrido et al. 2015). The surviving subset of fish may already possess traits that favour survival in general, but whether these traits are advantageous for overwintering in a temperate environment remains an open question. Studies on tropical reef fishes in their native ranges have identified several ELHTs affecting survivorship, including size at hatching, PLD, growth, and size at settlement (Rankin & Sponaugle 2011; Sponaugle et al. 2006) and thus it is plausible that they also influence persistence in cooler temperate environments.

The period between settlement, usually in warmer ocean temperatures, and the onset of winter ocean temperatures is likely crucial for the survival of vagrant fish through the winter months. As larvae arrive in cohorts throughout the austral summer and autumn, the duration of this window varies for each group. During this time, fish can grow rapidly and build energy reserves before water temperatures decline. Rapid growth during early life stages is frequently associated with increased survival in fish, particularly for species with high early-life mortality rates (Monica Gagliano et al. 2007; Vigliola & Meekan 2002). Faster growth leads to larger body size, which confers several advantages. Larger individuals are often better equipped to compete for resources, avoid predators, and withstand environmental stressors (Dingeldein & White 2016; Garrido et al. 2015; Meekan & Fortier 1996). However, for tropical vagrants, this period of rapid growth coincides with their arrival in temperate waters and adaption to different environmental conditions, such as food and habitat, may differ substantially from their native ranges, potentially affecting their growth trajectories and subsequent survival.

This study investigates the links between early life history traits and survival into winter for the Sergeant Major (*Abudefduf vaigiensis*), a tropical damselfish expanding its range into temperate waters of Southeast Australia. This species was selected due to its documented range expansion into temperate waters, driven by warming ocean temperatures (Beck et al. 2016; Booth et al. 2018; Figueira et al. 2009). The relatively high seasonal recruitment and seasonal mortality in temperate waters provide an ideal context for investigating the ELHTs that influence survival at the poleward thermal limits. Our objectives were:

(1) To determine which early life history traits, such as size at hatching, pelagic larval duration (PLD), and size at settlement, are associated with survival into winter in temperate ecosystems, and
(2) To evaluate how growth trajectories during early life stages affect the likelihood of survival into winter in a vagrant tropical fish in temperate waters

Methods

Permits and ethics

This investigation was conducted following the University of Technology Sydney's Animal Ethics Committee Approval (ETH-6609) and under the NSW DPI permit (F94/696(A)-9.0).

Sample collection

Abudefduf vaigiensis (n=122) samples were collected from shallow rocky reefs in Sydney, Australia, at four sites: Little Manly (33.8067° S, 151.2870° E), Malabar (33.9679° S, 151.2511° E), Little Bay (33.9817° S, 151.2403° E), and Freshwater Beach (33.7813° S, 151.2906° E). These locations were chosen to provide a broader spatial representation of the species within temperate waters. Sampling was conducted between January and August of 2022 and 2023, with a monthly sampling regimen employed to obtain a variety of size classes (Fig. 1). While a multitude of factors, such as lunar cycles, ocean currents and temperature, can influence settlement patterns in pomacentrids (Feary et al. 2014), this study focused on capturing broader temporal trends of recruitment. The collected samples were approximately representative of the body length distribution of wild conspecifics (Supp. Tab.1).

Fish were sedated and immobilised using a clove oil dilution protocol (1:4 ethanol) and then captured using hand nets (Fernandes et al. 2017). They were euthanised by placing them in an ice bath. All captured fish were transported to the University of Technology Sydney, where they were

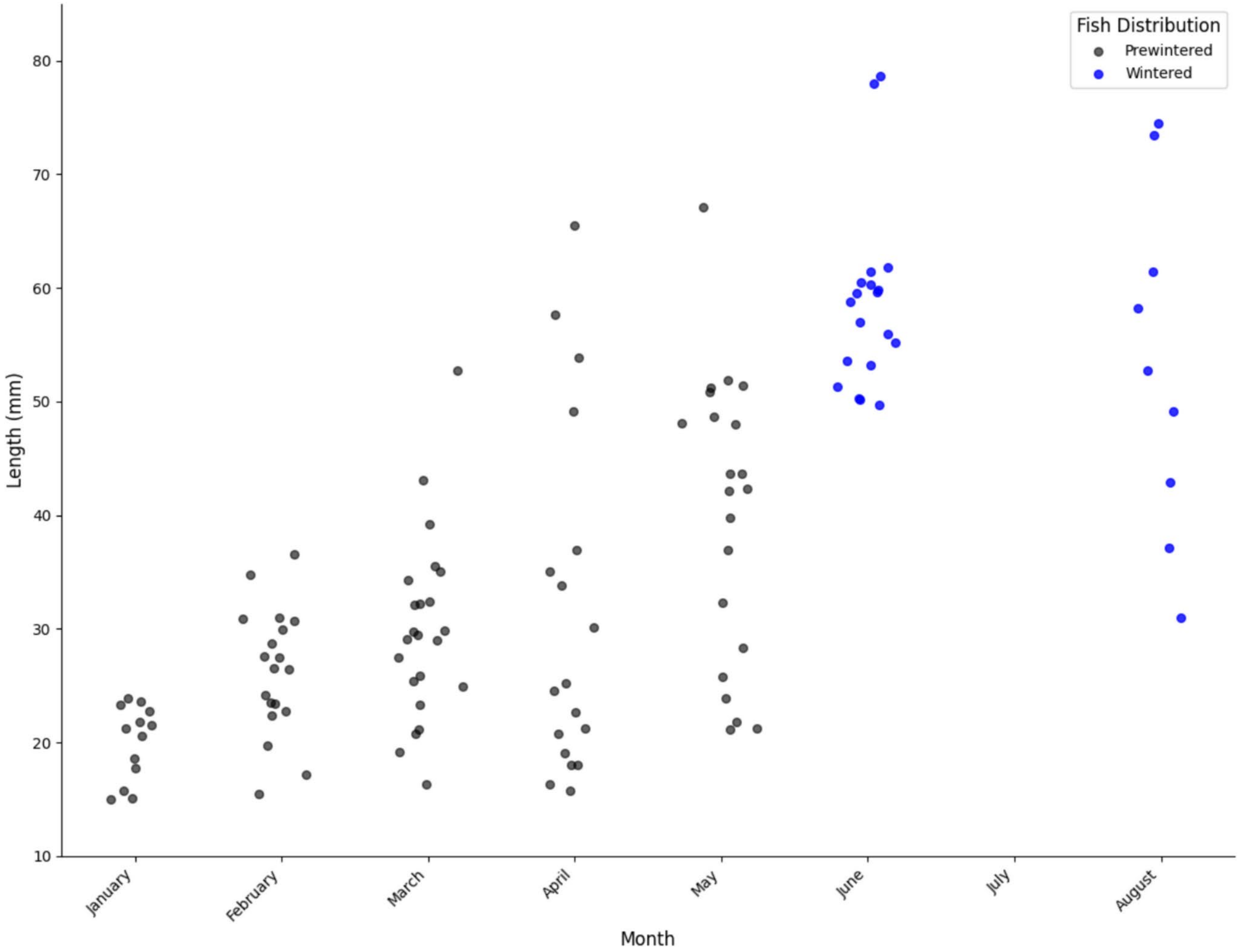

Fig. 1 Distribution of Fish Size Across Months. Each data point represents the length of a single fish in millimetres (mm). Sample sizes per month were January (n = 12), February (n = 19), March (n = 23), April (n = 18), May (n = 21), June (n = 19), and August (n = 9). Fish were pooled across the four sampling locations and over two years (2022 and 2023). Data are grouped by month to illustrate temporal variations in fish size distributions. Fish are categorised into 'Prewintered' (black) and 'Wintered' (blue) groups based on their survival classification: Prewintered fish were collected before the winter temperature threshold, while Wintered fish were collected after this threshold. Note that these data reflect collected samples and may not represent an unbiased survey of the population

weighted (to the nearest 0.001g) and measured with callipers (to the nearest 0.1mm), then stored at -4°C until otolith analysis.

Otolith analysis

Otoliths, the calcified structures found in the inner ears of fish, were used to collect information on ELHTs. The validity of using otoliths for such purposes has been well-documented in previous studies (Panfili et al., 2009), and a validation study has been conducted specifically for this species (Rigg et al. 2023). In Rigg et al. (2023) daily deposition of visible micro-increments (light and dark banding) was confirmed, meaning the number of increments in an otolith could be counted to determine the time elapsed in days and allow daily growth rates to be estimated. Fish were dissected under a stereomicroscope using a probing tool and scalpel to extract the lapillus otoliths. The otoliths were then mounted on microscope slides with the dorsal side facing up, using Crystalbond™ (509-1A) as the mounting medium. The samples were polished using 3-µm lapping paper to obtain a flat surface for the measurements. The lapilli were chosen for increment width measurements due to their distinct and clear increment banding (Rigg et al. 2023).

Several precautions were taken to ensure the accuracy and reliability of otolith readings. Fish were randomly selected and analysed without knowledge of their size or collection date to minimise potential reader biases. Each otolith was read twice by a single experienced reader, and if the two readings differed by more than 10%, a third reading was performed. The reading closest to the third reading was considered the most reliable (Wilson et al. 2009). Consultation with another experienced researcher was undertaken to reach a consensus on identifying key otolith markings, such as the hatch check, settlement mark, and daily growth increments. The methods employed adhered to the guidelines outlined by Panfili et al. (2009).

A Nikon Upright NI Series microscope was used, and measurements were taken using Nikon NIS-elements Advanced Research software (V5.02.02), spanning from the centre of the primordium to the furthest point on the anterior-posterior axis. The radius of the hatch check, daily increment width, settlement mark, and total otolith radius were recorded for each fish.

Key ELHTs examined using otolith microstructure included size at hatch, early life growth rates, PLD, body condition at capture, and size at settlement (Tab. 1). The analysis involved identifying and measuring specific otolith structures: the primordium, hatch check, daily growth increments, and settlement mark (Fig 2). Settlement marks were identified by an abrupt change in increment width, characteristic of a Type I settlement mark (Wilson and McCormick 1999). The position of this mark relative to the otolith edge varied predictably with fish size, appearing close to the edge in small, recent settlers and further from the edge in larger, older fish. This pattern was consistent with a settlement mark of similar size and duration among individuals. Increment width measurements and counts of these structures provided identification of individual growth histories and key life history transitions.

Body condition at capture

Body condition at capture was calculated using Fulton's K formula ($K = \text{weight (g)}/\text{length (cm)}^3) \times 100$) (Fulton, 1904) (Tab. 1). The measure is frequently used to assess body condition, providing a standardised measure of the fish's condition at capture (Bolger & Connolly 1989; Hamilton 2008; Kingsbury, Gillanders, Booth, Coni, et al., 2020). It is important to note that body condition at capture may reflect recent environmental influences, such as temperature stress and behaviours that are not directly measured in this study. As such, condition may shift seasonally due to external pressures, and its interpretation requires caution. To account

Table 1 Summary of life history traits used to assess the impact of wintering in vagrant tropical fish. Traits, including hatch radius, daily increment width, pelagic larval duration (PLD), size at settlement, ocean temperature at settlement, and Fulton's K Body Condition. The raw otolith values were used in the size-at-age model to approximate fish size in millimetres at hatch radius, daily increment width, and size at settlement

Early Life History Trait	Description
Hatch Radius (µm)	The distance from the centre of the otolith primordium (core) to the hatch check mark (Fig 2). Provides an estimate of the size of the fish at hatching
Daily Increment Width (µm)	The distance between two consecutive daily growth rings on the otolith. The values were used to model growth trajectories of the fish
Pelagic Larval Duration (days)	The number of daily increments between the hatch check and the settlement mark on the otolith (Fig. 2). This represents the fish's total days in its pelagic (open-water) larval stage before settling into a benthic habitat
Otolith Radius at Settlement (µm)	The distance from the centre of the otolith primordium to the settlement mark (Fig.2). This serves as an indicator of the fish's size when it transitioned from the pelagic larval stage to the benthic juvenile stage
Condition (Fulton's K) at Capture	A measure of the fish's overall condition, calculated as $K=W/L^3\times100$, where W is the fish's weight (g) and L is the fish's length (cm). This index reflects the robustness or fatness of the fish
Temperature at Settlement (°C)	The ocean temperature at settlement was determined by backcalculating the time interval from the otolith microstructure (from the date of settlement to the date of capture) and using satellite data to estimate the temperature (see methods, *Water Temperature*)

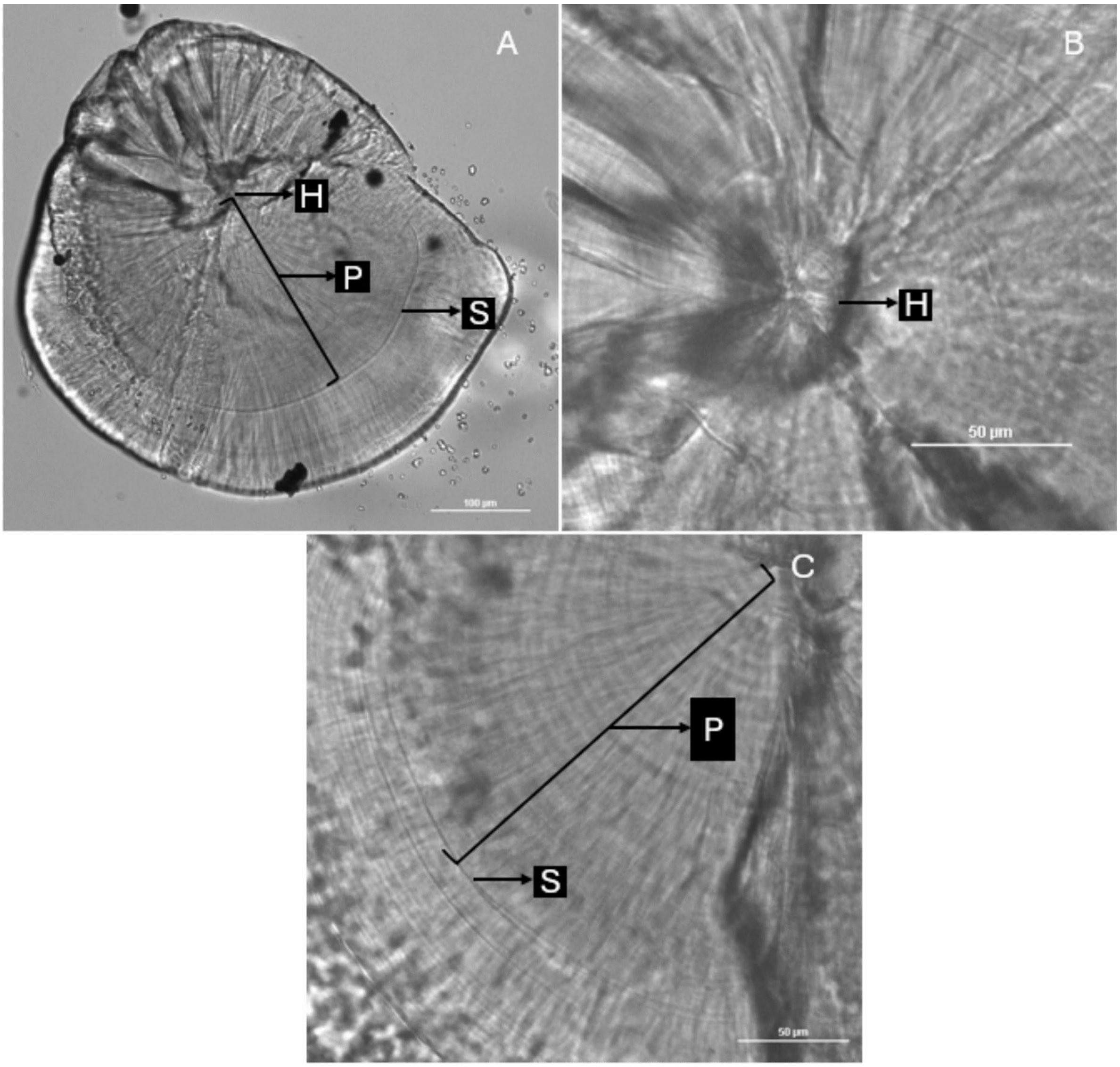

Fig. 2 Microstructure of a lapillus otolith from *Abudefduf vaigiensis*. (**A**) Whole otolith view showing key developmental markers: H - hatch check, P - pelagic larval duration (PLD), and S - settlement mark. (**B**) Magnified view of the otolith core region, highlighting the hatch check (H). (**C**) Close-up of the otolith edge region, showing the transition from pelagic (P) to post-settlement (S) growth. Scale bars: 100μm (**A**), 50μm (**B**, **C**). These structures allow for accurate aging and reconstruction of early life history events in this vagrant tropical fish species

for potential biases in K caused by allometry (the relationship between body length and plumpness) (Froese 2006), we examined the relationship between K and body length. Allometry was not a significant factor within the size range we examined in this species, as indicated by a regression analysis (R2 = 0.012, P = 0.228).

Size-at-age model

Following otolith microstructure analysis, size at each age was estimated using the Biological Intercept Model (BI model; Campana, 1990). The BI Model assumes a linear relationship between otolith and somatic growth, which was subsequently validated for *A. vaigiensis* during the early growth phase (r2 = 0.97, Supp Fig. 1). For each fish, otolith intervals (distances between daily increments) were measured, and back-calculated body lengths (Lt) for each age were calculated using:

$$L_t = L_c - \left(\frac{R_c - R_t}{R_c}\right) \times (L_c - L_0)$$

where L_t is the length at age t, L_c is the capture length, R_c is the capture radius, R_t is the radius at time t, and L_0 is the initial length.

Water temperature to determine winter onset and settlement temperature

Sea surface temperature (SST) data for Sydney during 2022 and 2023 were obtained from the NOAA OISST V2 High-Resolution dataset (Huang et al. 2021). Shelly Beach (33.7992° S, 151.2983° E) was selected as the representative site for SST measurements across all four sampling locations. To justify the use of Shelly Beach data as representative for all sites, we assumed that SST patterns are broadly similar across the relatively small geographic range (~16km) of our study area due to the proximity of the locations. However, it is important to note that local variations may exist and were not directly measured in this study. The SST data were extracted and processed using Python with the *xarray* library, resampled to obtain daily mean temperatures, and compiled for further analysis.

Winter onset definition and fish survival classification

The onset of winter conditions was defined using a sea surface temperature (SST) threshold of approximately 20°C, derived from synthesising physiological studies on tropical damselfish in temperate environments and satellite temperature data (as above). This threshold estimates the critical temperature at which *A. vaigiensis* begins to experience physiological stress. It delineated two groups of fish:'prewintered' (those collected before winter onset) and'wintered' (those that were collected after winter onset). Importantly, the prewintered group likely includes individuals with traits that could have allowed them to survive into winter had they not been sampled, meaning these groups are not fully independent but represent trait distributions shaped by environmental selectivity. Several key studies informed this threshold: Djurichkovic et al. (2019) demonstrated significant physiological effects below 22°C in tropical *Abudefduf* species; Eme and Bennett (2008) reported mean minimum acclimation temperatures of 19.3°C for Indo-Pacific damselfishes; Figueira and Booth (2010) estimated 17.1°C as the overwinter survival threshold for *A. vaigiensis*; and Booth et al. (2018) identified 15.6-19.8°C as overwintering temperatures for *Abudefduf* species. The 50th percentile of observed temperature distributions for 2022 (20.21°C) and 2023 (20.76°C) coincided with the onset of sustained cooler conditions, with winter onset identified as June 8th, 2022, and May 27th, 2023 (Supp. Fig. 2). This threshold closely mirrors our 2023 in situ temperature logger data collected at Shelly Beach (Unpublished data, 2023 only). The defined threshold captures the beginning of the rapid seasonal environmental changes wintering fish face, after which winter mortality increases due to the physiological thresholds of *A. vaigensis*.

Statistical analysis

Early life history traits at settlement

We conducted a logistic regression analysis to investigate the factors influencing fish survival. The response variable was Survivorship (binary: wintered or prewintered), and the predictor variables included size at hatching (mm), pelagic larval duration (PLD, days), size at settlement (mm), body condition at capture (Fulton's K), and ocean temperature at settlement (°C). All continuous predictor variables were standardised prior to analysis. A generalised linear model (GLM) with a binomial error distribution and logit link function was employed. The initial full model included all predictor variables. Manual backward elimination was performed using the Akaike Information Criterion (AIC) to select the most parsimonious model.

Given the small sample size of wintered fish in the 2023 data, including year as a random effect was not feasible. The 2023 model exhibited traits of overfitting, with extreme standard errors and unreliable coefficients. As a result, we pooled data from both 2022 and 2023 to strengthen the statistical power and reliability of the analysis. To examine whether data from different years might affect model outcomes, we compared the pooled model (2022 + 2023) with a model using only the 2022 data. Key predictors such as size at hatching, condition at capture, and temperature at settlement were consistent in both models, supporting the decision to pool the data.

The final model specification was:

$$\begin{aligned}&\text{logit}(\text{P}(\text{Survivorship}))\\&=\beta_0+\beta_1*\ \text{Size at Hatch}\ +\beta_2*\ \text{PLD}\\&\quad+\beta_3*\ \text{Size at Settlement}+\beta_4*\ \text{Condition}\\&\quad+\beta_5*\ \text{Settlement Temp}\end{aligned}$$

Where Logit(P(survivorship)) is the logit function of the probability of survivorship, β_0 is the intercept term, and β_1–β_5 are coefficients that quantify the relationship between each predictor variable and the log odds of survivorship.

Model diagnostics were performed using the DHARMa package (Hartig 2018) to assess logistic regression assumptions. Variance Inflation Factors (VIF) were calculated to check for multicollinearity. The log odds ratios and their 95% confidence intervals were computed to interpret the effects of the predictor variables. All analyses were conducted in R version 4.2.

Early growth trajectories

We used Generalised Additive Models (GAMs) to investigate growth trajectories between fish that survived into winter and prewintered fish. The decision to use GAMs over Generalised Linear Models (GLMs) was driven by the potential for complex, non-linear relationships between fish size and day of observation, which could not be adequately captured by a standard linear model. GAMs allowed for more flexibility in modelling the non-linear growth patterns, that are typical of early growth in tropical fish with a PLD.

The models were fitted using the *mgcv* package in R (v4.2). Initially, we tested multiple models with different distributions, link functions, and interactions to account for non-linear growth patterns, heteroscedasticity, and non-normality in the data. The response variable was fish size (mm), and the predictor was day of observation (Day), with separate smooth functions (splines) for each group (wintered, prewintered).

Model selection was based on Akaike Information Criterion (AIC) values. The Gamma distribution with a log link function provided the best fit with the lowest AIC. We also ensured that overfitting was minimised using the Restricted Maximum Likelihood (REML) method for smooth parameter selection. Model diagnostics, including Q-Q plots, residuals versus fitted values plots, and histograms of residuals, confirmed an adequate fit of the final model.

We incorporated random effects in all models to account for variability between individual fish and the repeated growth measures. Random intercepts and random slopes were fitted for each fish to capture individual deviations in growth rates and starting sizes. These random effects were nested within the survival group (Survivorship), allowing each fish to have its own growth trajectory while accounting for the influence of survival status.

The final model specification was:

$$\begin{aligned}&\mathrm{Size(mm)} \sim \mathrm{s(Day, by = Survivorship, K = -1, bs = ``cs")}\\&\quad + \mathrm{Survivorship} + \mathrm{s(FishNumber,\ by = Survivorship,\ bs = ``re")}\\&\quad + \mathrm{s(Day,\ FishNumber,\ by = Survivorship = ``fs")}\end{aligned}$$

where s(Day, by = Survivorship, bs = "cs") represented a cubic spline fitted to the day of observation, allowing for an interaction between Day and Survivorship. This interaction enabled the model to fit separate growth trajectories for each group, accounting for differences in the relationship between Day and Size in pre-winter and wintered fish. The term s(FishNumber, by = Survivorship, bs = "re") captured the random intercepts for each fish, accounting for individual differences in the initial size within each survival group. The term s(Day, FishNumber, by = Survivorship, bs = "re") modelled the random slopes for each fish, allowing individual growth rates to vary over time within survival groups. The k parameter (number of knots, K=-1) was evaluated to ensure the smooth term was adequately flexible without overfitting.

Results

Early life history traits in wintered vagrant fish

We conducted backward elimination using the Akaike Information Criterion (AIC) to select the most parsimonious model. All terms initially included in the full model—size at hatch, pelagic larval duration (PLD), size at settlement, condition at capture, and temperature at settlement—were retained based on the AIC selection process. The logistic regression analysis identified several significant predictors of surviving into winter (Fig. 3). Size at hatch was a strong positive predictor (OR = 8.03, 95% CI: 2.34–27.55, p < 0.001), indicating that larger hatch sizes substantially increase the odds of surviving into winter. Similarly, size at settlement (OR = 2.92, 95% CI: 1.06–8.05, p = 0.038) and condition at capture (OR = 3.07, 95% CI: 1.18–7.99, p = 0.021) were significant positive predictors. Conversely, temperature at settlement was a significant negative predictor (OR = 0.24, 95% CI: 0.09–0.68, p = 0.003), suggesting that higher temperatures at settlement reduce the odds of surviving into winter. Pelagic larval duration did not significantly predict surviving into winter (p = 0.146).

Early growth rate

The model incorporating group-specific splines (wintered and prewintered) had a lower Akaike Information Criterion (AIC) value (27793.11) compared to the model without group-specific splines (AIC = 27856.20, Fig. 4). The reduction in AIC indicated that the growth trajectories between fish that survived into winter and prewintered fish differed, justifying the use of separate growth curves for each group. The parametric coefficient for survivorship in the model was positive and significant (estimate = 0.329, p < 0.001). This result suggests that, on average, fish that survived into winter had a larger body size than prewintered fish. Both groups exhibited non-linear growth patterns over time, as evidenced by the significant smooth terms for day (p < 0.001). The effective degrees of freedom (edf) for the smooth terms indicated moderately complex growth patterns, with edf = 8.77 for fish that did not survive and edf = 8.27 for fish that survived into winter. The random effects for individual fish were significant in both groups (prewintered: p = 0.026; wintered: p = 0.098). This finding indicated significant individual variability in growth among the fish

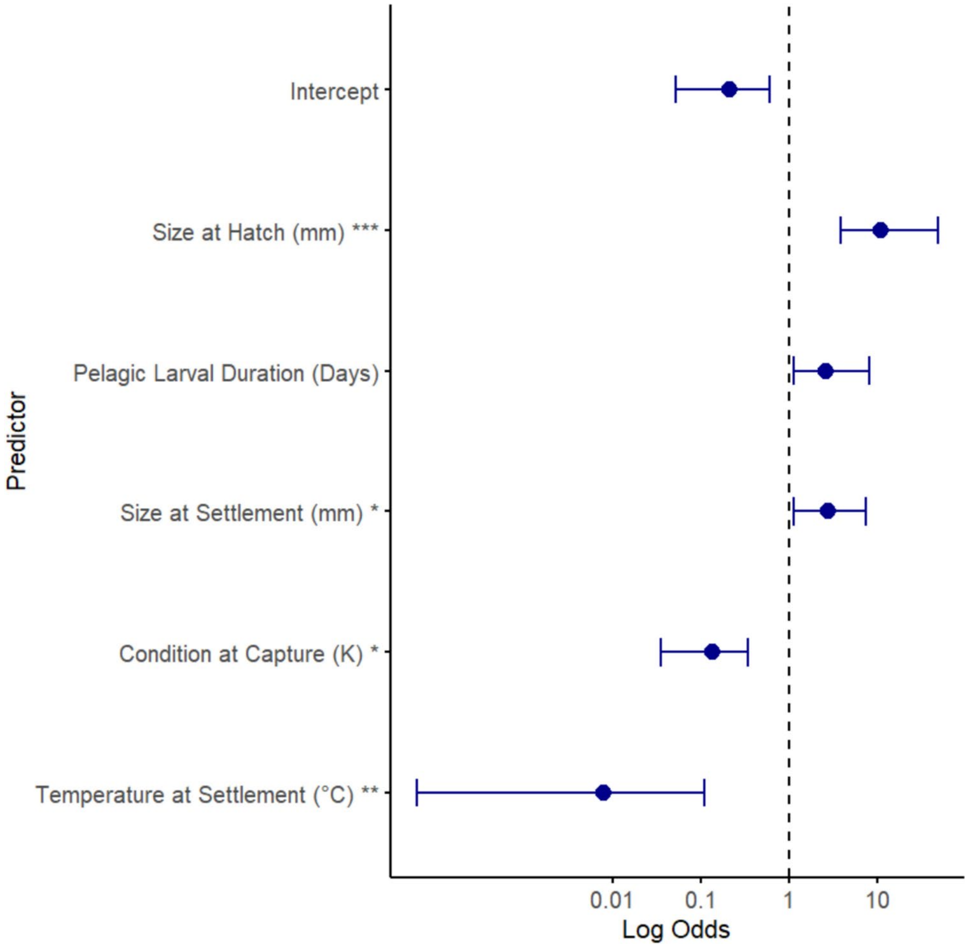

Fig. 3 Forest plot showing the effect log odds (with 95% confidence intervals) from a Logistic Generalized Linear Model assessing the influence of five predictors on fish survival (wintered vs prewintered). Positive estimates indicate traits or conditions associated with increased odds of survival, while negative estimates suggest decreased odds of survival. The vertical dashed line at 0 represents no effect. Significance levels are indicated by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$)

within each group. Notably, the interaction between individual fish and time was significant for fish that survived into winter ($p = 0.038$) but not for the prewintered group ($p = 0.261$), indicating a higher degree of variability in growth patterns in the wintered group.

Discussion

Understanding the early life history traits (ELHTs) that enable tropical fish to survive into winter in temperate regions is crucial for predicting how range-shifting marine species will respond to climate change. Our study used a novel approach to investigate these traits, classifying fish into 'prewintered' and 'wintered' groups based on a temperature threshold marking the onset of winter conditions. This allowed us to explore potential trait-based survival advantages in the range-expanding tropical fish, *A. vaigiensis*, in temperate southeastern Australia.

We found that larger size at hatching and settlement, along with higher body condition at capture, significantly increased the odds of surviving into winter. Conversely, higher settlement temperatures were associated with decreased survival odds. These findings highlight the importance of selective pressures in shaping trait distributions, where survival is linked to traits that may provide physiological advantages in colder waters.

Our study identified size at both hatch and settlement as potentially influential factors for winter survival in tropical vagrant fish within temperate environments. This finding aligns with broader patterns observed in tropical fish in their natal environments, where larger individuals at hatch consistently demonstrate faster growth and development across numerous coral reef fish species (Vigliola & Meekan 2002). The relationship we observed between early size advantages and winter survival in vagrant *A. vaigiensis* potentially stems from one or several well-documented mechanisms that become particularly critical in temperate environments. While larger hatchlings generally possess more substantial yolk reserves (Coleman & Galvani 1998) and better-developed sensory and swimming capabilities (Peck et al. 2012), these advantages may be especially important for vagrant fish facing novel environmental challenges. Enhanced swimming capabilities and sensory development could help vagrant fish better cope with cooler temperatures and unfamiliar predator-prey dynamics in temperate waters.

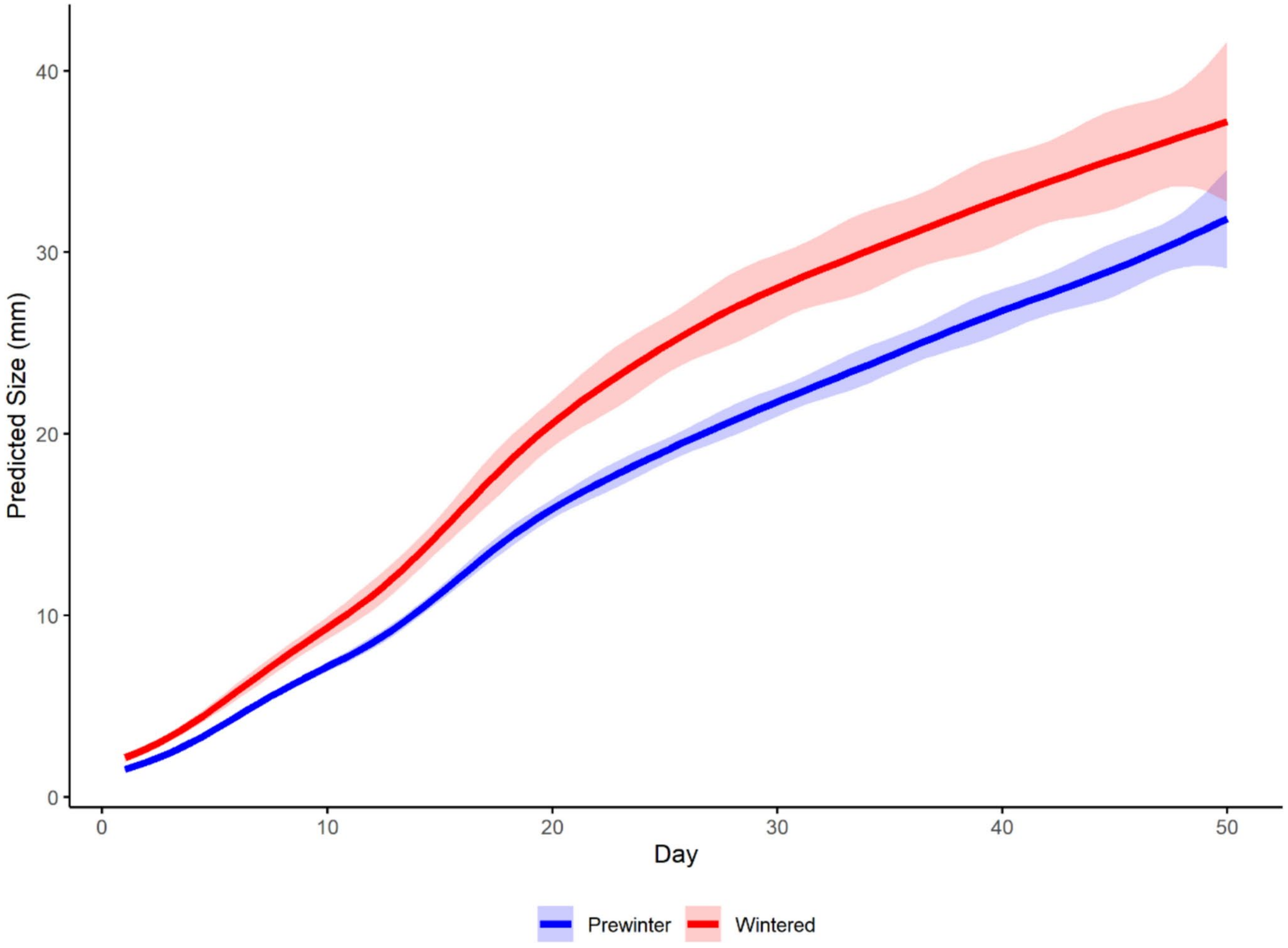

Fig. 4 Growth trajectories predicted by the Generalised Additive Model, comparing wintered fish (red) and prewinter fish (blue). The x-axis represents time in days from hatching, and the y-axis represents the predicted size of fish in millimetres (mm). Shaded regions denote 95% confidence intervals of fixed effects, highlighting the divergence between the two groups' growth trajectories

Previous studies in tropical environments have shown that these traits lead to higher growth rates and improved predator evasion (Cowan Jr & Houde, 1992; Monica Gagliano et al. 2007), with larger hatchlings experiencing lower mortality during critical post-hatching periods (McCormick & Hoey 2004). For vagrant fish, these early survival advantages appear particularly important for winter survival, as they may help individuals build the physiological reserves needed to endure thermal stress.

The advantages of larger size appear to compound throughout development in this study, creating cumulative benefits that extend into settlement. Larger individuals often exhibit higher metabolism (Giguère et al. 1988) and demonstrate more efficient foraging behaviours (Brown et al. 2007), enabling them to secure better nutrition during critical growth periods and before winter's reduced food availability (Dingeldein & White 2016). While size-selective predation typically targets smaller individuals in temperate waters (Almany & Webster 2006; Cowen & Sponaugle 1997), research from tropical environments offers an intriguing contrast– whereby larger and bolder individuals can face heightened predation risk post-settlement (Hulthén et al. 2017; Rodgers et al. 2015). We observed a size advantage in our study, which could suggest that the physiological benefits of larger size might outweigh typical predation costs. The persistence of larger individuals thus represents a subset of the population that has already passed significant mortality filters before winter arrives, implying that winter survival depends on traits selected earlier in development. While size advantage likely reflects multiple beneficial traits, their relative importance may shift between tropical and temperate environments.

Our study associated higher body condition at capture with winter presence, but this relationship may be influenced by complex interactions between physiological traits and environmental pressures, and interpreting this relationship requires consideration of our sampling design. The observed differences in condition between prewintered and wintered fish could reflect two distinct possibilities: either that better body condition enhanced survival chances, or that the entire distribution of body condition values shifted in response to dropping temperatures. Since all sampled fish experienced temperature stress, the body condition could not be measured before the temperature drop and we cannot definitively determine whether body condition influenced survival or simply responded to seasonal changes.

Regardless of which possibility explains our observations, the uncertainty in interpreting body condition patterns is further highlighted by previous research. Kingsbury et al. (2020a, b) found that tropical fishes maintained their body condition in temperate environments despite reduced activity and feeding in cooler waters, suggesting a potential trade-off between growth and condition maintenance. However, our results did not demonstrate such a trade-off, as we observed higher growth rates and better body conditions in wintered fish. While our study did not follow fish through the entire winter season, survivors are typically very rare and difficult to capture later in winter. Mitchell et al. (2023) proposed that some tropical species exhibit physiological plasticity in temperate winter conditions, potentially reallocating energy resources for long-term survival. While we did not directly measure physiological changes, we observed that growth and condition were maintained in wintered fish, suggesting that *A. vaigiensis* may have adaptive strategies to survive the cooler waters. It is important to note that our body condition measurements were taken at capture and that we were unable to measure body condition before the drop in ocean temperature. Since we did not track individual fish through the temperature transition, we cannot determine whether the better condition of wintered fish represents a selective advantage or a physiological response to cooling waters. Future studies that measure body condition before and after winter are thus needed to more accurately assess the role of body condition in winter survivorship.

The subset of vagrant fish that survived into winter grew faster and were substantially larger (39% on average) than those sampled prewintered, demonstrating that these growth advantages persist and compound throughout early life history stages. The larger size at each life stage reflects their ability to capitalise on available resources and avoid predation during the pelagic larval duration (PLD) phase. The complex, non-linear growth patterns observed in both groups suggest that growth trajectories are highly responsive to environmental conditions and ontogenetic transitions. Notably, the faster growth rates in wintered fish highlight the importance of achieving a size threshold before winter, giving them a significant advantage in surviving into cooler winter waters.

The significant individual variation in growth among survivors, indicated by the random effects and fish-by-day interactions, suggests there may be a broad range of viable growth trajectories in novel temperate environments. Rather than specific growth strategies being favoured, this variation suggests flexibility in the growth patterns that can lead to winter survival. Selection for higher growth in early life histories is documented in other tropical species (Bergenius et al. 2002; Monica Gagliano et al. 2007; McCormick & Hoey 2004), but our results indicate that multiple growth trajectories may be compatible with winter survival. This flexibility in growth patterns could be advantageous for tropical vagrants establishing in temperate ecosystems, potentially supporting their range expansion under climate change.

Sampling the same cohort of fish before and after a winter temperature cutoff potentially introduced some dependence into our dataset, because some'prewintered' individuals might have otherwise survived into the'wintered' group if they were not removed during sampling. This may have increased the likelihood of Type II error in our survival analysis, i.e. not detecting a true effect, because trait distributions may have overlapped to some degree across the two groups. While this may have contributed to the lack of an effect detected for PLD trait, it did not prevent detection of effects for size at hatch and settlement, condition at caption and temperature at settlement. We therefore do not consider our fundamental conclusions regarding the latter effects to be influenced by the potential sampling dependence, but cannot exclude the possibility that effect sizes may be underestimated to some extent.

Our results suggest a complex relationship between settlement timing, water temperature, and overwintering success in *A. vaigiensis*. The link between settlement temperature and time of year suggests that settlement timing could be a factor in interpreting this result. Specifically, fish settling at higher temperatures, typically earlier in the recruitment season, faced reduced survival odds in our study. This suggests that while warmer temperatures are common in their tropical range, settling in warm periods further from winter might be disadvantageous in temperate waters. Wintered fish, on average, settled approximately 50 days before the winter temperature drop, which may facilitate acclimation to the sudden drop in temperature change at the onset of winter. This is supported by the speed of temperature decline, not just the temperature itself, likely affects acclimation to cooler water temperatures (Reid et al. 2022). Fish therefore settling during cooling periods may cope better with environmental changes than those arriving in warmer summer conditions (Stewart et al. 2023). Later settlers in turn face fewer threats from predators and competitors, potentially saving energy for winter. They also settle in cooler water, which may require less physiological adjustment.

As ocean warming continues to facilitate the range expansion of tropical species into temperate waters, understanding the mechanisms behind their survival in these marginal environments becomes increasingly important. Our in-depth study provides a critical foundation for understanding the factors contributing to the winter survival of tropical fish in temperate environments. *A. vaigiensis* is one of the most common tropical vagrants, exhibiting some of the highest survival in temperate regions through winter (although it is still low), and further research is needed to determine how representative our results are of other species. Comparative studies with other range-expanding species, and multi-year studies that account for inter-annual variability in environmental conditions and capture fully overwintered specimens will thus be an important next step in assessing the generality of the observed patterns. Notably, our results highlight that due to their growth advantages and physiological resilience, larger individuals are better equipped to withstand the selective pressures imposed by cooler climates. By identifying these critical periods of vulnerability and understanding the growth dynamics, we can therefore more accurately predict not only the persistence of these species but also their competitive interactions and ecological impacts within temperate marine ecosystems.

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Author contributions All authors contributed to the study's conception and design. AR conducted the fieldwork, dissections, otolith analysis, statistical analysis, and manuscript writing. AF and BS provided feedback and guidance on manuscript structure, statistical analysis, and discussion. DB supervised the project and provided feedback and guidance across all aspects. All authors read and approved the final manuscript.

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References

Almany GR, Webster MS (2006) The predation gauntlet: early post-settlement mortality in reef fishes. Coral reefs 25(1):19–22. https://doi.org/10.1007/s00338-005-0044-y

Beck HJ, Feary DA, Fowler AM, Madin EMP, Booth DJ (2016) Temperate predators and seasonal water temperatures impact feeding of a range expanding tropical fish. Marine biology 163(4):1–14. https://doi.org/10.1007/s00227-016-2844-8

Bergenius MAJ, Meekan MG, Robertson R, McCormick MI (2002) Larval growth predicts the recruitment success of a coral reef fish. Oecologia 131:521–525

Bolger T, Connolly PL (1989). The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology*, *34*(2), 171-182. https://doi.org/10.1111/j.1095-8649.1989.tb03300.x

Booth DJ, Beretta GA, Brown L, Figueira WF (2018). Predicting Success of Range-Expanding Coral Reef Fish in Temperate Habitats Using Temperature-Abundance Relationships [Original Research]. *Frontiers in Marine Science*, *5*(31). https://doi.org/10.3389/fmars.2018.00031

Booth DJ, Bond N, Macreadie P (2011) Detecting range shifts among Australian fishes in response to climate change: Climate Change and Australian Aquatic Environments, Fish and Fisheries. Marine and Freshwater Research 62(9):1027–1042

Brown C, Jones F, Braithwaite VA (2007). Correlation between boldness and body mass in natural populations of the poeciliid Brachyrhaphis episcopi. *Journal of Fish Biology*, *71*(6), 1590-1601. https://doi.org/10.1111/j.1095-8649.2007.01627.x

Coleman RM, Galvani AP (1998) Egg Size Determines Offspring Size in Neotropical Cichlid Fishes (Teleostei: Cichlidae). Copeia 1998:209–213

Cowan JH Jr, Houde ED (1992) Size-dependent predation on marine fish larvae by Ctenophores, Scyphomedusae, and Planktivorous fish. Fisheries Oceanography 1(2):113–126. https://doi.org/10.1111/j.1365-2419.1992.tb00030.x

Cowen RK, Sponaugle S. (1997). Relationships between early life history traits and recruitment among coral reef fishes. In R. C. Chambers & E. A. Trippel (Eds.), *Early Life History and Recruitment in Fish Populations* (pp. 423-449). Springer Netherlands. https://doi.org/10.1007/978-94-009-1439-1_15

Dingeldein AL, White JW (2016). Larval traits carry over to affect post-settlement behaviour in a common coral reef fish [https://doi.org/10.1111/1365-2656.12506]. *Journal of Animal Ecology*, *85*(4), 903-914. https://doi.org/10.1111/1365-2656.12506

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. Scientific reports 9(1):13937–13939. https://doi.org/10.1038/s41598-019-50303-z

Eme J, Bennett WA (2008) Low temperature as a limiting factor for introduction and distribution of Indo-Pacific damselfishes in the eastern United States. Journal of thermal biology 33(1):62–66. https://doi.org/10.1016/j.jtherbio.2007.10.003

Feary DA, Pratchett MS, Emslie J, M., Fowler, A. M., Figueira, W. F., Luiz, O. J., Nakamura, Y., & Booth, D. J. (2014) Latitudinal shifts in coral reef fishes: why some species do and others do not shift. Fish and fisheries (Oxford, England) 15(4):593–615. https://doi.org/10.1111/faf.12036

Fernandes IM, Bastos YF, Barreto DS, Lourenço LS, Penha JM (2017) The efficacy of clove oil as an anaesthetic and in euthanasia procedure for small-sized tropical fishes. Braz J Biol 77(3):444–450. https://doi.org/10.1590/1519-6984.15015

Figueira WF, Biro P, Booth DJ, Valenzuela VC (2009) Performance of tropical fish recruiting to temperate habitats: role of ambient temperature and implications of climate change. Marine ecology. Progress series (Halstenbek) 384:231–239. https://doi.org/10.3354/meps08057

Figueira WF, Booth DJ (2010). Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Global Change Biology*, *16*(2), 506-516. https://doi.org/10.1111/j.1365-2486.2009.01934.x

Fowler AM, Fowler AM, Parkinson K, Parkinson K, Booth DJ, Booth DJ (2018) New poleward observations of 30 tropical reef fishes in temperate southeastern Australia. Marine biodiversity 48(4):2249–2254. https://doi.org/10.1007/s12526-017-0748-6

Froese R (2006). Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*, *22*(4), 241-253. https://doi.org/10.1111/j.1439-0426.2006.00805.x

Gagliano M, McCormick MI, Meekan MG (2007) Survival against the odds: ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. Proceedings. Biological sciences 274(1618):1575–1582. https://doi.org/10.1098/rspb.2007.0242

Garrido S, Ben-Hamadou R, Santos AMP, Ferreira S, Teodósio MA, Cotano U, Irigoien X, Peck MA, Saiz E, Ré P (2015) Born small, die young: Intrinsic, size-selective mortality in marine larval fish. Scientific reports 5(1):17065. https://doi.org/10.1038/srep17065

Giguère LA, Côté B, St-Pierre JF (1988) Metabolic rates scale isometrically in larval fishes. Marine ecology. Progress series (Halstenbek) 50(1/2):13–19. https://doi.org/10.3354/meps050013

Hamilton SL (2008) Larval history influences post-metamorphic condition in a coral-reef fish. Oecologia 158(3):449–461. https://doi.org/10.1007/s00442-008-1153-4

Hartig F (2018). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. In *R Packag version 020*.

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five Potential Consequences of Climate Change for Invasive Species. Conservation biology 22(3):534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Huang B, Liu C, Banzon V, Freeman E, Graham G, Hankins B, Smith T, Zhang H-M (2021). Improvements of the Daily Optimum Interpolation Sea Surface Temperature (SST) Version 2.1. *Journal of Climate*, *34*(8), 2923-2939. https://doi.org/10.1175/JCLI-D-20-0166.1

Hulthén K, Chapman B, Nilsson A, Hansson L-A., Skov C, Brodersen J, Vinterstare J, Brönmark C (2017). A predation cost to bold fish in the wild. *Scientific reports*, *7*. https://doi.org/10.1038/s41598-017-01270-w

Intergovernmental Panel on Climate C (2023). *Climate Change 2021–The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. https://doi.org/10.1017/9781009157896

Kingsbury KM, Gillanders BM, Booth DJ, Coni EOC, Nagelkerken I (2020). Range-extending coral reef fishes trade-off growth for maintenance of body condition in cooler waters. *Science of The Total Environment*, *703*, 134598. https://doi.org/10.1016/j.scitotenv.2019.134598

Kingsbury KM, Gillanders BM, Booth DJ, Nagelkerken I (2020) Trophic niche segregation allows range-extending coral reef fishes to co-exist with temperate species under climate change. Global Change Biology 26(2):721–733. https://doi.org/10.1111/gcb.14898

McCormick MI, Hoey AS (2004). Larval Growth History Determines Juvenile Growth and Survival in a Tropical Marine Fish. *Oikos*, *106*(2), 225-242. http://www.jstor.org/stable/3548108

Meekan MG, Fortier L (1996). Selection for fast growth during the larval life of Atlantic cod Gadus morhua on the Scotian Shelf. *Marine Ecology Progress Series*, *137*, 25-37. https://www.int-res.com/abstracts/meps/v137/p25-37/

Mitchell A, Hayes C, Booth DJ, Nagelkerken I (2023) Projected ocean acidification and seasonal temperature alter the behaviour and growth of a range extending tropical fish. Coral reefs 42(4):919–929. https://doi.org/10.1007/s00338-023-02396-2

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008). Climate change and the future for coral reef fishes. *Fish and Fisheries*, *9*(3), 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(12):e81107–e81107. https://doi.org/10.1371/journal.pone.0081107

Nykjaer L (2009) Mediterranean Sea surface warming 1985–2006. Climate Research - CLIMATE RES 39:11–17. https://doi.org/10.3354/cr00794

Peck MA, Huebert KB, Llopiz JK (2012). Chapter 3 - Intrinsic and Extrinsic Factors Driving Match–Mismatch Dynamics During the Early Life History of Marine Fishes. In G. Woodward, U. Jacob, & E. J. O'Gorman (Eds.), *Advances in Ecological Research* (Vol. 47, pp. 177-302). Academic Press. https://doi.org/10.1016/B978-0-12-398315-2.00003-X

Pecl, GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I C, Clark TD, Colwell RK, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S, Williams SE (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Rankin TL, Sponaugle S (2011) Temperature influences selective mortality during the early life stages of a coral reef fish. PLOS ONE 6(5):e16814. https://doi.org/10.1371/journal.pone.0016814

Reid CH, Patrick PH, Rytwinski T, Taylor JJ, Willmore WG, Reesor B, Cooke SJ (2022) An updated review of cold shock and cold stress in fish. Journal of Fish Biology 100(5):1102–1137. https://doi.org/10.1111/jfb.15037

Ridgway KR (2007). Long-term trend and decadal variability of the southward penetration of the East Australian Current [https://doi.org/10.1029/2007GL030393]. *Geophysical Research Letters*, *34*(13). https://doi.org/10.1029/2007GL030393

Rigg AL, Bellotto C, Fowler AM, Booth DJ (2023) Staining protocols affect use of otolith to estimate the demography of the damselfish sergeant major (Abudefduf vaigiensis). J Fish Biol. https://doi.org/10.1111/jfb.15601

Robert D, Shoji J, Sirois P, Takasuka A, Catalán IA, Folkvord A, Ludsin SA, Peck MA, Sponaugle S, Ayón PM, Brodeur RD, Campbell EY, D'Alessandro, EK, Dower JF, Fortier L, García AG, Huebert KB, Hufnagl M, Ito S-i, Pepin P (2023). Life in the fast lane: Revisiting the fast growth—High survival paradigm during the early life stages of fishes. *Fish and Fisheries*, *24*(5), 863-888. https://doi.org/10.1111/faf.12774

Rodgers GM, Downing B, Morrell LJ (2015) Prey body size mediates the predation risk associated with being "odd." Behavioral Ecology 26(1):242–246. https://doi.org/10.1093/beheco/aru185

Sponaugle S, Grorud-Colvert K (2006) Environmental variability, early life-history traits, and survival of new coral reef fish recruits. Integrative and Comparative Biology 46(5):623–633. https://doi.org/10.1093/icb/icl014

Sponaugle S, Grorud-Colvert K, Pinkard D (2006) Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish Thalassoma bifasciatum in the Florida Keys. Marine ecology. Progress series (Halstenbek) 308:1–15. https://doi.org/10.3354/meps308001

Stewart EMC., Frasca VR., Wilson CC, Raby GD (2023). Short-term acclimation dynamics in a coldwater fish. *Journal of thermal biology*, *112*, 103482. https://doi.org/10.1016/j.jtherbio.2023.103482

Sunday JM, Pecl GT, Frusher S, Hobday AJ, Hill N, Holbrook NJ, Edgar GJ, Stuart-Smith R, Barrett N, Wernberg T, Watson RA, Smale DA, Fulton EA, Slawinski D, Feng M, Radford BT, Thompson PA, Bates AE, Worm B (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. Ecology letters 18(9):944–953. https://doi.org/10.1111/ele.12474

Suthers IM, Young JW, Baird ME, Roughan M, Everett JD, Brassington GB, Byrne M, Condie SA, Hartog JR, Hassler CS, Hobday AJ, Holbrook NJ, Malcolm HA, Oke PR, Thompson PA, Ridgway K (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(5):538–546. https://doi.org/10.1016/j.dsr2.2010.09.029

Vigliola L, Meekan MG (2002) Size at Hatching and Planktonic Growth Determine Post-Settlement Survivorship of a Coral Reef Fish. Oecologia 131(1):89–93. https://doi.org/10.1007/s00442-001-0866-4

Wilson JA., Vigliola L, Meekan MG (2009). The back-calculation of size and growth from otoliths: Validation and comparison of models at an individual level. *Journal of Experimental Marine Biology and Ecology*, *368*(1), 9-21. https://doi.org/10.1016/j.jembe.2008.09.005

Wu L, Cai W, Zhang L, Nakamura H, Timmermann A, Joyce T, McPhaden MJ, Alexander M, Qiu B, Visbeck M, Chang P, Giese B (2012) Enhanced warming over the global subtropical western boundary currents. Nature Climate Change 2(3):161–166. https://doi.org/10.1038/nclimate1353