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Faster larval growth and shorter pelagic duration enhance the post-settlement persistence of a common range-extending coral-reef fish in a temperate ecosystem

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Abstract Climate-induced ocean warming facilitates the poleward range expansion of tropical marine species into temperate waters. Such tropicalisation is reshaping marine ecosystems globally and has ecological implications. Our understanding of the factors influencing the establishment and persistence of vagrant tropical species in temperate waters remains limited. To address this knowledge gap, we examined which early life history traits affect the post-settlement persistence of a vagrant tropical fish, the sergeant major damselfish Abudefduf vaigiensis, in temperate waters off southeast Australia. Over an 8-week period, fish were collected, and otolith microstructure analysis indicated that early post-settlement persistence was linked to fast larval growth in the week prior to settlement and to shorter pelagic larval duration, but not body size at hatching or body size at settlement. We conclude that successful invasions of temperate ecosystems by this vagrant tropical fish is likely mediated by demographic advantages these fish gain as early-stage larvae.

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Introduction

Climate-induced ocean warming is transforming marine ecosystems worldwide, with temperate regions experiencing an influx of expatriated tropical fish species (referred to as 'vagrant' fish) (Figueira and Booth 2010; Fowler et al. 2018; Nakamura et al. 2013). This phenomenon is particularly evident in climate change hotspots (Hobday and Pecl 2014), where strengthening poleward currents facilitate the transport of tropical larvae to temperate habitats (Suthers et al. 2011). As a result, these regions serve as natural laboratories for studying the early life history dynamics and survival of vagrant fish species in novel environments.

One such hotspot is the southeastern coast of Australia, where the strengthening of the East Australian Current (EAC) has increased the presence of vagrant tropical fish (Booth et al. 2018). However, this phenomenon is not unique to southeast Australia; similar observations have been made on the temperate west coast of Australia (Pearce et al. 2016) and in other temperate regions globally, such as Japan (Beck et al. 2016, 2017), the Mediterranean Sea (Azzurro et al. 2011), and the western North Atlantic (Zarzyczny et al. 2024). These temperate ecosystems are gradually shifting towards tropical conditions, with the establishment of vagrant fish populations currently limited by their ability to survive the critical settlement phase and the cooler temperatures of winter to the next season (overwintering) (Figueira and Booth 2010).

The settlement phase is a crucial period for reef fishes, particularly vagrant fish species arriving in temperate

regions, as they transition from pelagic larval stages to benthic juvenile stages and face novel challenges in terms of diet, habitat preference, and growth rates (Kimirei et al. 2013). Early life history traits (ELHTs), such as size at hatching, size at settlement, pelagic larval duration (PLD), and growth rates, are common metrics linked to the survival and success of individual fish during this critical phase (Bergenius et al. 2005, 2002; Vigliola and Meekan 2002). A larger settlement size is often considered advantageous, as it can confer benefits in resource competition and predator avoidance (Hoey and McCormick 2004). However, the relationship between ELHT and post-settlement survivorship is complex, with studies suggesting a decreasing risk of predation and rapid growth (Dingeldein and White 2016).

In the context of vagrant tropical fish species settling in temperate environments, the importance of ELHT may be heightened due to the novel challenges they face in these non-native habitats. Factors such as thermal stress, novel habitats and ecological interactions may result in a shift in or strengthening of, the selective pressures acting on ELHT compared to those in their native range (Coni et al. 2022; Kingsbury et al. 2020; Rankin and Sponaugle 2011). Temporal studies following individual cohorts offer a unique opportunity to investigate which factors influence the survival of vagrant fish species during settlement. This approach is particularly valuable for understanding the challenges faced by vagrant fish species in temperate environments, as the settling fish persistence is often limited to the warmer seasons, with few individuals successfully overwintering (Figueira et al. 2009).

Fish otoliths are small, calcified structures in fish's inner ears that grow in concentric rings, typically representing daily growth (Panella 1971). The size and microstructure of these rings provide a historical timeline (proxy) of a fish's age, growth rate, and settlement timing. The validity of otolith analysis has been well-established (Panfili et al. 2009a), including for the species reported here, the sergeant major damselfish *A. vaigiensis* (Rigg et al. 2023). Temporal studies using otolith analysis offer a unique opportunity to investigate demographic factors influencing the growth and survival of vagrant fish species during settlement, as they allow for a focussed examination of the relationship between ELHT and post-settlement persistence.

Here, we examine the relationship between ELHTs and early post-settlement persistence in the vagrant tropical damselfish, *Abudefduf vaigiensis*, to understand the traits that contribute to its successful settlement in temperate waters. We employed a site-specific temporal approach, tracking newly settled fish over 56 d at a single location throughout a high recruitment period in an ocean warming hotspot off southeastern Australia. By analysing hatch size, pelagic larval duration (PLD), size at settlement, and growth rates, we identified ELHTs that could enhance post-settlement persistence. Understanding the factors that mediate the survival of a vagrant tropical fish during settlement is crucial for better predicting potential poleward range expansions and the establishment of warm-water populations in temperate regions.

Methods

Abudefduf vaigiensis was chosen as a model species because it is a common vagrant fish that often arrives in high numbers in temperate waters during summer–autumn recruitment seasons (Beck 2014; Beck et al. 2014). Additionally, the ELHTs of *A. vaigiensis* have been previously validated through otolith analysis (Rigg et al. 2023) making it suitable for investigating the relationship between these traits and post-settlement persistence in a vagrant tropical fish.

The study was carried out on a shallow subtidal rocky reef at Little Manly, Sydney, Australia, over 56 d from the 4th of March 2021 to the 29th of April 2021 (coordinates: 33.8068°S, 151.2867°E). During this time, there was a significant influx of *A. vaigiensis* larvae which led to the establishment of several shoals in the area. Fish were collected during seven sampling events over 8-weeks using hand nets, with each sampling event targeting randomly selected individuals from these shoals. The shoals consisted of fish of approximately the same size class during each event, ensuring a consistent sample in terms of size across the study period. Prior to sampling, fish were immobilised using a clove oil solution (1:5 dilution in ethanol). Following collection, specimens were euthanised using an ice bath.

The total length of each fish was measured to the nearest 0.1 cm using callipers, and mass was measured to the nearest 0.001 g. The lapillus otoliths were extracted and mounted because the lapillus was found to be flatter and resulted in clearer depositions and markings for analysis (Rigg et al. 2023). The mediolateral axis was oriented for analysis (Online Resource 3). To achieve a flat surface, samples were polished using lapping paper (3 μ m) and water to minimise marks generated during grinding. Measurements spanned from the primordium's centre to the furthest point on the anterior–posterior axis (Online Resource 3).

A Nikon Eclipse Ni-E microscope was used at $200 \times mag$ nification, with Nikon NIS-elements Advanced Research software (V5.02.02) for measurements. Cedarwood oil was applied during microscopy to improve clarity for reading otoliths.

A strong positive relationship between otolith radius and fish total length was established ($R^2 = 0.8668$, Online Resource 1), validating this study's use of otolith measurements as proxies for fish size and growth. Based on this relationship, the hatch radius, used as a proxy for size at hatch, was determined by measuring the distance from the centre of the primordium to the edge of the hatch check mark, expressed in micrometres (μ m). Daily increment width was determined by measuring the distance between the edges of two consecutive increments. The settlement mark corresponds to the settlement day and was used to calculate the PLD by counting the increments between the hatch check and the settlement mark. The otolith radius at the settlement mark, measured from the hatch check, was used as a proxy for size at settlement. The growth rate immediately prior to settlement was calculated by averaging the increment widths for each fish 7 d before settlement and was expressed in μ m/ day. To characterise the dependent variables, we examined their distributions. These histograms, coupled with density plots, highlighted the range, central tendency, and spread of the data for each trait (Online Resource 3).

Otolith microstructure analysis methods followed the guidelines provided by Panfili et al. (2009b) to ensure the reliability of the readings. Fish were randomised and read blind to avoid potential biases. Otoliths were read twice; if counts of daily increments in those readings differed by more than 10%, a third reading was done. The reading closest to the third reading was considered more reliable. If the two readings were similar, they were likely correct and accepted. Discussions with another researcher on the otolith markings (i.e. hatch, PLD, etc.) were conducted to reach a consensus.

To investigate the relationship between ELHTs and post-settlement persistence, we conducted linear regression analyses using age (days post-settlement) as the independent variable and each of the following traits as dependent variables: size at hatch, pelagic larval duration (PLD), size at settlement, and pre-settlement growth rate. We also tested the relationship between PLD and growth rates using the same process. The average otolith increment width over 7 d prior to settlement was used as a proxy for immediate presettlement somatic growth. This approach is commonly used to estimate growth and development during the early life stages of fish and has been employed in numerous studies exploring ELHTs (Searcy and Sponaugle 2000; Sponaugle and Grorud-Colvert 2006; Wilson and McCormick 1999).

The regression models were evaluated using the coefficient of determination (R^2) to assess the proportion of variance explained by the relationship. A p < 0.05 was considered significant. Assumptions of linearity, homoscedasticity, independence, and normality of residuals were checked. Linearity and homoscedasticity were assessed visually using residual plots. The Breusch–Pagan test was used to statistically test for homoscedasticity, with p > 0.05 indicating homoscedastic residuals. The normality of residuals was assessed by visually inspecting Q-Q plots.

All statistical analyses were performed using Python (version 3.11.5) with the *statsmodels* and *scipy* libraries. Visualisations of the regression analyses were created using the *matplotlib* and *seaborn* libraries.

Results and discussion

Early life history dynamics have been shown to drive subsequent post-settlement population dynamics of reef fishes (Doherty and Fowler 1994). However, this has rarely been assessed for vagrant range-extending species. Here, we examined a suite of ELHTs using an 8-week sampling approach to understand which ELHTs influenced the postsettlement persistence of *A. vaigiensis* at a temperate site. We defined post-settlement persistence as the duration an individual remained at the site after settlement, using days post-settlement as a proxy for this measure.

We found a significant negative relationship between PLD and days post-settlement ($R^2 = 0.24$, p = 0.0005, Fig. 1a), indicating that individuals with shorter PLDs persisted longer after settlement. The PLDs we observed (21–29 d, Table 1) were longer than those reported for *A. vaigiensis* in its native tropical eastern Pacific range (17–20 d, n=3) (Wellington and Victor 1989). This finding suggests that the sampled individuals may have experienced extended duration in the plankton.

While the relationship between PLD and dispersal distance is complex and often inconsistent across larval marine species (Feary et al. 2014; Shanks 2009), our findings suggest that individuals with PLDs closer to those observed in the species' native tropical range may have an advantage when extending into temperate environments. This advantage in post-settlement persistence might stem from these individuals retaining more energy reserves for postsettlement survival, possibly due to spending less time in the plankton. Additionally, these energy reserves could potentially support faster growth rates, which may contribute to better survival in the new environment. Alternatively, these results could indicate a mixed cohort from different origins, with fish from populations closer to the study site having shorter PLDs and better survival. Future studies using analysis of elemental isotopes in otoliths could reveal if fish had a common origin (Gillanders 2005; Trueman et al. 2012). Similarly, LA-ICPMS could provide finer-scale insights into natal origins by analysing otolith microchemistry (Fairclough et al. 2011); while, genomic approaches could assess genetic connectivity among populations (Gajdzik et al. 2021).

We found a significant positive relationship between pre-settlement growth rate and persistence ($R^2 = 0.13$, p = 0.0121, Fig. 1b). Fish with faster pre-settlement growth rates also tended to have shorter PLDs ($R^2 = 0.12$, p = 0.0167, Fig. 2). This aligns with the "growth-mortality hypothesis" (Anderson 1988; Searcy and Sponaugle 2001), which states that faster-growing larvae can achieve the minimum size required for settlement more quickly, potentially reducing their exposure to high mortality rates in the pelagic environment. Our results extend this concept to vagrant populations,



Fig. 1 Relationships between days post-settlement of *A. vaigiensis* and **a** Pelagic larval duration (days), **b** Pre-settlement growth rate (μ m/day), **c** Size at settlement (μ m), and **d** Size at hatch (μ m). Dots represent individual fish and colours represent one of seven collection

Table 1 Descriptive statistics for *A. vaigiensis* samples (n=47), showing the range and mean (with standard deviation) for age, length, hatch size, Pelagic larval duration, size at settlement and pre-settlement growth rate

Variable	Range	Mean \pm SD
Age (days)	33–77	56.9 ± 14.3
Total body length (mm)	13.5-50.0	31.7 ± 9.7
Hatch size (µm)	7.5–16.9	11.4 ± 1.8
PLD (days)	21.0-29.0	26.0 ± 1.6
Total length at settlement (µm)	158.9–248.7	199.6 ± 22.1
Pre-settlement growth rate (μ m/day)	4.4–13.3	7.7 ± 1.8

SD=1 standard deviation

suggesting that the ability to grow quickly and settle earlier might be an important factor for the successful establishment of this tropical species in temperate waters.

Surprisingly, we did not find a significant relationship between days post-settlement and size at settlement $(R^2=0.00, p=0.7989, Fig. 1c)$, suggesting that while fastergrowing individuals settled earlier, they did not necessarily settle at a larger size. Slower growers may need to stay in the plankton for longer to reach the larger sizes required for successful settlement (Searcy and Sponaugle 2001). This dynamic may explain our finding of lower persistence in fish with longer PLDs, as these individuals likely represent

groups. The dashed lines indicate linear regression fits and the shaded area represents the CI 95% interval. R^2 values show the coefficient of determination, and *p*-values indicate the statistical significance of each relationship

slower growers that remained in the plankton longer and possibly entered the settlement phase in a weaker condition compared to their faster-growing counterparts. This suggests that this range-extending tropical fish is subject to trade-offs in their novel ranges like their normal ranges, where body size at settlement is not a crucial mediator of their persistence, but growth rate and PLD are key factors influencing post-settlement survival (Gagliano et al. 2007).

Our analysis revealed no significant relationship between days post-settlement and size at hatch ($R^2 = 0.05$, p = 0.1518, Fig. 1a), contrasting with previous studies on other species within natal ranges where size at hatch influences early life survival and recruitment success (Gagliano et al. 2007; Vigliola and Meekan 2002). However, our findings suggest that the relationship between size at hatch and early settlement may not hold for range-extending tropical fish in temperate waters for this species. The lack of correlation between size at hatch and post-settlement persistence in our study indicates that the factors influencing the survival of this vagrant species in novel environments may differ from those in their native ranges.

In conclusion, our study provides evidence that early life history traits, particularly shorter pelagic larval duration and faster pre-settlement growth rates, may confer advantages for individuals of *A vaigiensis* and possibly other vagrant tropical fish early persistence in temperate environments.



Fig. 2 Relationship between pelagic larval duration (PLD) and presettlement growth rate. The x-axis shows pre-settlement growth rate (μ m/day) and the y-axis shows pelagic larval duration (days). Each dot represents an individual fish. The dashed line indicates the linear

As ocean warming continues to facilitate range expansions, understanding these traits amongst other species could help better predict which individuals and populations are more likely to successfully establish in new environments, with implications for ecosystem changes in temperate regions.

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Author contribution AR performed data collection and analysis, and wrote the initial draft of the manuscript. DB, AF, and IN provided critical feedback, contributed to the interpretation of results, and assisted with manuscript revision. All authors reviewed and approved the final version of the manuscript.

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regression fit and the shaded grey area represents the 95% confidence interval. R^2 value shows the coefficient of determination (0.12), and the *p* value (0.0167) indicates the statistical significance of the relationship between PLD and pre-settlement growth rate

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare that they have no competing interests, financial or non-financial, that are directly or indirectly related to the work submitted for publication.

Ethical approval 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).

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