

Opposing life stage-specific effects of ocean warming at source and sink populations of range-shifting coral-reef fishes

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Funding information

Australian Research Council, Grant/Award Number: DP170101722; The Environment Institute (The University of Adelaide)

Handling Editor: Greta Bocedi

Abstract

1. Climate change is altering the latitudinal distributions of species, with their capacity to keep pace with a shifting climate depending on the stochastic expression of population growth rates, and the influence of compensatory density feedback on age-specific survival rates. We use population-abundance time series at the leading edge of an expanding species' range to quantify the contribution of stochastic environmental drivers and density feedbacks to the dynamics of life stage-specific population growth.
2. Using a tropical, range-shifting Indo-Pacific damselfish (*Abudefduf vaigiensis*) as a model organism, we applied variants of the phenomenological Gompertz-logistic model to a 14-year dataset to quantify the relative importance of density feedback and stochastic environmental drivers on the separate and aggregated population growth rates of settler and juvenile life stages.
3. The top-ranked models indicated that density feedback negatively affected the growth of tropical settlers and juveniles. Rates of settlement were negatively linked to temperatures experienced by parents at potential source populations in the tropics, but their subsequent survival and that of juveniles increased with the temperatures experienced at the temperate sink. Including these stochastic effects doubled the deviance explained by the models, corroborating an important role of temperature. By incorporating sea-surface temperature projections for the remainder of this century into these models, we anticipate improved conditions for the population growth of juvenile coral-reef fishes, but not for settlers in temperate ecosystems.
4. Previous research has highlighted the association between temperature and the redistribution of species. Our analyses reveal the contrasting roles of different life stages in the dynamics of range-shifting species responding to climate change, as they transition from vagrancy to residency in their novel ranges.

KEYWORDS

climate change, coral reefs, global warming, marine fishes, range shifts, species distribution, temperate ecosystems, transient population dynamics

1 | INTRODUCTION

Climate change is driving the redistribution of many species globally, threatening the structure and functioning of recipient communities (Griffith et al., 2018; Pecl et al., 2017). Most studies documenting shifts in distributions along latitudinal, depth or elevation gradients identify temperature change as the main driver of this reshuffling (Chen et al., 2011; Dulvy et al., 2008; Parmesan & Yohe, 2003). However, the processes underlying species redistributions combine environmental forcings, interspecific interactions, species traits and intrinsic population dynamics (Forchhammer et al., 1998; Poloczanska et al., 2016; Sunday et al., 2015). Together, these factors influence how much climate velocity (i.e. the rate and direction of climate isoclines) affects a species' realized rate of redistribution (Pinsky et al., 2019; Sunday et al., 2015). Additionally, although responses to environmental drivers can vary across life stages (Levy et al., 2015; Monaco et al., 2015), this has not been examined in the context of species redistributions driven by modern climate change. Robust predictions of rates of spread and site-specific probability of establishment require mechanistic frameworks to describe how population dynamics respond to this complex and variable set of potential drivers.

Modelling the characteristics of a species' population dynamics at the leading edge of its distribution provides a unique opportunity to examine the influence of both exogenous (e.g. environmental drivers) and endogenous (e.g. density feedback) mechanisms influencing its probability of establishing in a new region (Hobday & Pecl, 2014). However, previous research has focused on environmental drivers of demographic variability, with little empirical attention given to potentially important constraints imposed by intrinsic density feedback, due to the inherent complexity of separating the two drivers (Forchhammer et al., 1998; Poloczanska et al., 2016; Sunday et al., 2015). Density feedbacks resulting from intraspecific competition for resources can modify a species' response to its environmental conditions (Turchin, 2003; Yang et al., 2008). Explicitly considering both endogenous and exogenous elements is therefore essential to resolve the relative contribution of direct and indirect effects to a species' propensity to establish and spread as a consequence of global change (Boggs & Inouye, 2012; Turchin, 2003).

One approach to disentangle the endogenous and exogenous processes operating on the population dynamics at the leading edges of a species' distribution is to apply discrete-time density-feedback models within the phenomenological theta-logistic family (Brook & Bradshaw, 2006). Linear simplifications of the theta-logistic model, such as the Ricker or Gompertz-logistic (GL) models (Boggs & Inouye, 2012; Yang et al., 2008), have effectively distinguished the temporal variability of population growth arising from compensatory density feedbacks from the process error generated by environmental stochasticity (Turchin, 2003). These models are thus strong candidates to describe the complex, boom/bust-cycle characteristics of transient populations at the redistribution front (Bates et al., 2014; Strayer et al., 2017).

As a global-warming hotspot (Hobday & Pecl, 2014), the south-eastern coast of Australia is receiving an increasing frequency and

diversity of tropical and subtropical marine vagrant species (Booth et al., 2007; Fowler et al., 2017; Sunday et al., 2015). This process is facilitated by the ongoing strengthening of the poleward-flowing East Australian Current (Ridgway, 2007), enhancing the dispersal potential of animals with pelagic larval stages. This southward transport of propagules occurs predominantly early in the year. Upon settlement in temperate latitudes, many of these vagrants ultimately succumb to low winter temperatures that exceed their lower thermal tolerance thresholds (Booth et al., 2018), yet recent long-term studies observe that some species appear to be profiting from warmer winters by reaching juvenile and occasionally, adult stages (Fowler et al., 2017; Pearce et al., 2016). The role of major environmental drivers on the redistribution process of tropical vagrants has been explored (Feary et al., 2014; Monaco, Bradshaw, et al., 2020), but the mechanistic understanding of the establishment process remains limited.

We applied a series of variants of the GL model that consider compensatory density feedback in concert with relevant environmental variables, within a multi-model inference framework (Burnham & Anderson, 2002; Link & Barker, 2006; Turchin, 2003). We first tested the hypothesis that compensatory density feedbacks can explain some of the variability in population growth rates of the most conspicuous tropical vagrant fish on the temperate southeast Australian coast—the Indo-Pacific damselfish *Abudefduf vaigiensis* (Pomacentridae), hereafter *Abudefduf*. Second, we compared a suite of models that included several potentially important environmental drivers (i.e. strength of the East Australian Current, sea-surface temperature and chlorophyll *a* concentration as an index of productivity) to examine the importance of environmental stochasticity on population growth rates (Figure 1). We initially tested the influence of these drivers on the dynamics of settlers and juveniles aggregated, but inconclusive models suggested that alternative mechanisms could affect these size classes differently. We then treated these effects as either contributing to the facilitation of the species' settlement (i.e. colonization) or subsequent establishment (i.e. survival; Bates et al., 2014) by analysing settlers and juveniles separately.

We hypothesized that the population growth of settlers would be favoured by periods when the East Australian Current is strong (Booth et al., 2007; Pearce et al., 2016) due to its effect on larval transport from source populations while the dynamics of juveniles should depend more on the higher mortality rates caused by cold winter temperatures at the sink (Booth et al., 2018; Figueira & Booth, 2010; McBride & Able, 1998). We also tested the hypothesis that warmer temperatures experienced by parent fish in potential tropical source populations negatively affect the population growth of vagrant recruits in the temperate zone via decreased reproductive performance (Donelson et al., 2012, 2014). Finally, we examined whether variation in ocean productivity (chlorophyll *a* concentration) at the sink population influenced vagrant dynamics by modifying the physiological condition of individual fish (Booth et al., 2011; Donelson et al., 2012). As tropical vagrants move from inherently oligotrophic tropical environments to relatively productive temperate inshore waters, we hypothesized that greater food availability in the temperate zone could enhance the establishment potential

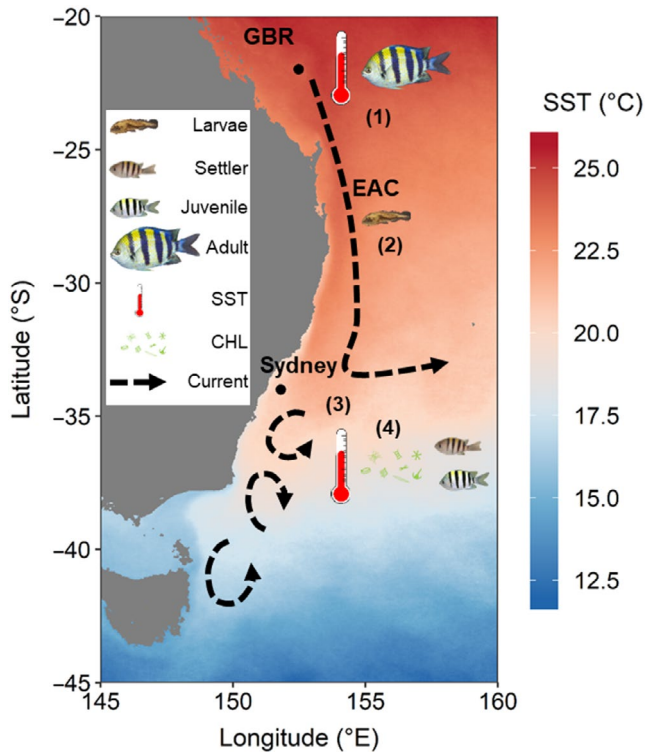


FIGURE 1 Environmental variables hypothesized to drive the numerical responses of vagrant populations of *Abudefduf vaigiensis* in temperate Australian waters. Hypotheses: (1) warmer sea-surface temperature (SST) at a potential source population (southern Great Barrier Reef, GBR) increases reproductive output, (2) stronger East Australian Current (EAC) disperses more larvae southwards, (3) warmer SST at temperate sink sites (Sydney and surroundings) increases winter survival of early recruits and juveniles and (4) increased chlorophyll *a* (CHL) enhances physiological condition and improves survival. Arrows represent main flows of the EAC and associated eddies. Colours illustrate long-term (14 years) averages of SST across the study region (downloaded from the Integrated Marine Observing System repositories)

of tropical vagrant fishes (Booth et al., 2011; Donelson et al., 2012). Alternatively, stresses associated with a novel environment (e.g. sub-optimal temperatures, novel predators, novel competitors) could offset any benefits accrued from higher relative productivity at the sink.

2 | MATERIALS AND METHODS

2.1 | Fish abundance

Abudefduf abundance data were collected as part of a long-term project to monitor the demographics of tropical vagrant fishes along the east Australian coast (Booth et al., 2007, 2018). We used data from the most intensively sampled site, Cabbage Tree Bay, Sydney (33°48'00"S, 151°17'50"E), from January 2004 to December 2017. Sampling was done across the year but more frequently during the first semester (Figure S1), when the arrival of vagrant fishes to temperate sites is strongest due to intensified

ocean currents (Booth et al., 2018) and a seasonal reproduction (Wilson et al., 2018). Depending on the year, the sampling frequency varied between 0 and 5 surveys/month (Figure S1). We calculated monthly averages from these surveys to maintain consistency across the entire time series, treating months with no surveys as non-available data.

Surveys were done by snorkelling, using the roaming underwater visual census method at two locations (240 m² each) on the east and west sides of Cabbage Tree Bay. The habitat is characterized by cobble rocks, with areas covered by kelp or turf, and interspersed barren sections. Divers recorded every individual encountered, discriminating early settlers, and small and large juveniles. The larvae of *Abudefduf* settle on reefs after 20–30 days of planktonic transport (Pearce et al., 2016). At our sites, early settlers were usually ~10–20 mm long and had transparent fins—they tended to congregate in groups within crevices. Small and large juveniles were ~20–50 mm and ~50–80 mm in length respectively. All juveniles were young-of-the-year and the species does not migrate post settlement. To avoid potentially assigning fish of intermediate sizes to the wrong stage, we used data only for settlers and large juveniles in the population-dynamics models. We converted counts to densities (1,000 m⁻²) and averaged densities from each transect, sampling event and stage (Figure 2).

2.2 | Life stage-specific population-growth models

We applied the GL model to describe the dynamics of intrinsic population growth rate (r_t) in relation to $\log_e(x + 0.1)$ -transformed population density (D_t), that includes a mean long-term carrying capacity parameter (K) (Brook & Bradshaw, 2006; Turchin, 2003). Because the instantaneous carrying capacity of range-shifting populations is uncertain, K represents a temporally averaged approximation of carrying capacity. To calculate r_t , we used only survey data collected across at least 2 consecutive months within a year. We formalized the additive effect of relevant environmental drivers by including specific additive terms (Env_t) in the model (Equation 1). We also included season (S_t , coded as consecutive quarters) as an additive variable with a linear effect on r_t (Figure S3):

$$\log_e \left(\frac{D_{t+1}}{D_t} \right) = r_t = r_m \left\{ 1 - \left[\frac{\log_e(D_t)}{\log_e(K)} \right] \right\} + \beta Env_t + \gamma S_t + \epsilon_t, \quad (1)$$

where r_m and $\epsilon_t = N(0, \sigma^2)$ represent the maximum intrinsic population growth rate (relative to K) and the model's unexplained residual error respectively. We estimated the parameters r_m , K , β , γ and σ^2 using maximum likelihood from the *bbmle* library in *R* (Bolker & R Development Core Team, 2017). To test the model support for the hypothesis of compensatory density feedback, we contrasted the base GL model (no environmental or seasonal terms) with a random-walk and an exponential-growth model, both lacking an endogenous component. To examine the influence of the four environmental drivers on r , we compared the base GL model with those also including each putative environmental driver and a full model including all terms.

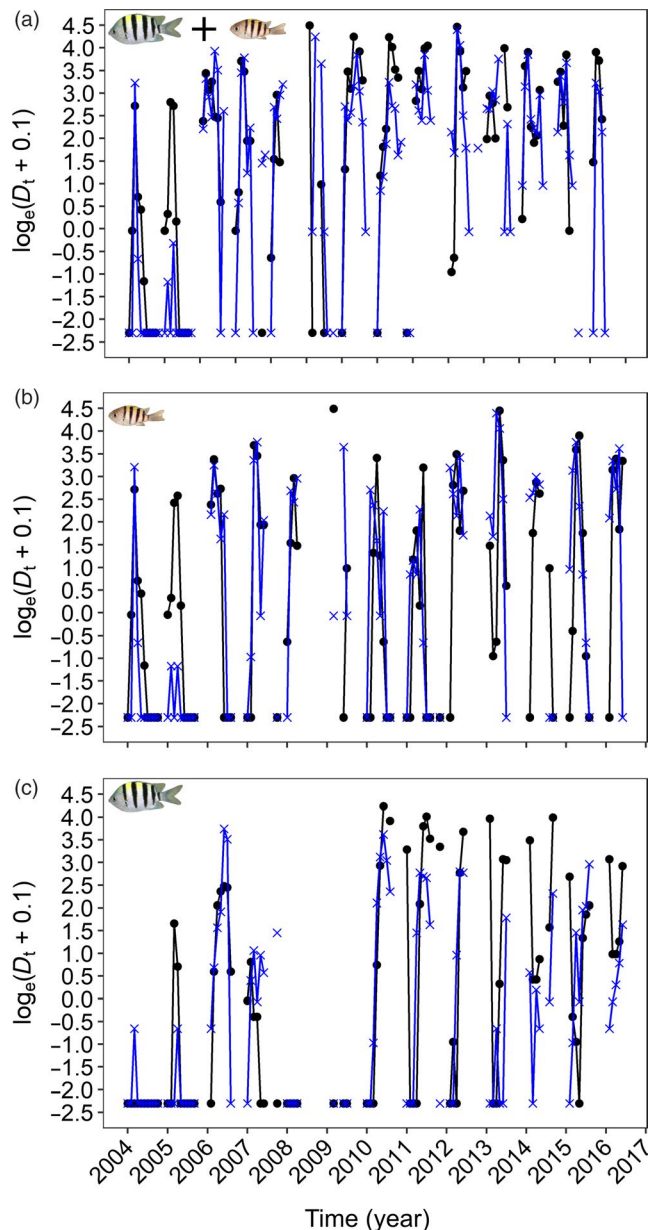


FIGURE 2 Temporal dynamics of *Abudedefduf vaigiensis* (a) aggregated settlers and juveniles, (b) settlers and (c) juveniles surveyed at Shelly Beach, Sydney (temperate sink population). Points depict $\log_e(x + 0.1)$ -transformed density observed at each sampling event ($n = 86$). Lines connect sampling events occurring on consecutive months used to derive population growth. Data from Cabbage Tree Bay east (blue crosses) and west (black dots) are overlaid, revealing the similar dynamics observed in both locations

To determine the relative support of each model considered, we followed a multi-model-inference approach based on the information-theoretic paradigm (Burnham & Anderson, 2002; Link & Barker, 2006; Turchin, 2003). For each model, we calculated Akaike's information criterion corrected for small sample sizes (AIC_c) and the Bayesian information criterion (BIC) and their weights ($wAIC_c$, $wBIC$) to provide a relative probability of model 'truth', assuming that the true model is included in the model set (Link & Barker, 2006). BIC

generally highlights the models comprising the most influential parameters in dynamical models, whereas AIC_c performs better when tapering effects exist, and is therefore most suitable when predicting values from fitted models (Burnham & Anderson, 2002; Link & Barker, 2006). We also calculated the percent deviance explained (%DE) by each model (relative to the intercept-only model) as a measure of goodness-of-fit. We built and compared all models using population growth data (r) calculated using either settlers and late juveniles aggregated, only settlers or only juveniles. We favoured this approach over stage-structured models because the temporal resolution of our survey data were insufficient for model convergence—we are therefore obliged to treat these two life stages essentially as different *populations*. While these life stages must in some way be linked, we cannot yet infer the functional shape of that relationship based on our surveys alone. We also tested the ability of our data to separate the relative contributions of survival and stage transitions to the population growth by examining the relationship between the dynamics of settlers and juveniles. A negative association would indicate a high probability of transition between size classes. However, we found no evidence for a relationship (linear model vs. intercept-only model: evidence ratio = 1.02, effect size $\eta^2 = 0.02$). We additionally tested for the link between stages by including the population growth rate of one stage as an additional driver in the top-ranked model identified for the other stage. These new models performed worse than the top-ranked models for both settlers (evidence ratio = 1.44) and juveniles (evidence ratio = 1.63). These tests therefore confirmed the inadequacy of this dataset for modelling the structured-population dynamics mechanistically.

2.3 | Environmental variation

Our models examined the potential effects of the strength of the East Australian Current (EAC_s) and the average sea-surface temperature experienced by the focal population in the temperate sink area—that is, Sydney (SST_{SYD}). We estimated EAC_s based on the near-surface (~12 m water depth), southward velocity component derived from Bluelink ReANalysis (BRAN3.5) products (Oke et al., 2013). The long-term BRAN hydrodynamics dataset is produced by integrating the Ocean Forecasting Australian Model and the Bluelink Ocean Data Assimilation System, and is validated against empirical observations along eastern Australia. Daily data are available at a spatial resolution of 1.5 km (Oke et al., 2013). The EAC originates in the South Coral Sea (15–24°S), flows south along the continental shelf and diverges east before reaching Sydney (~32°S), giving rise to unstable eddies (Ridgway & Dunn, 2003). To capture the EAC_s (v -component, in m/s) along the region of larval fish advection, we extracted data from pixels on the 200-m isobath between latitudes 25° and 37°S at 0.1° latitude intervals, and averaged them monthly from 2004 to 2017.

We also examined the potential influence of average sea-surface temperatures experienced by potential parent populations in the southern Great Barrier Reef (SST_{GBR}) on vagrant population growth rates. Based on *Abudedefduf*'s ontogeny, we included lags of 3 months for

SST_{GBR} , and 1 month for all other environmental variables. The lags considered for SST_{GBR} include a 1-month plankton larval duration, and the preceding breeding period (i.e. parental reef environment), which can extend for 2–8 weeks in damselfishes (Wittenrich, 2007). We downloaded SST_{GBR} and SST_{SYD} data from the Integrated Marine Observing System repositories (imos.org.au). Estimates are derived from satellite imaging (NOAA—Polar orbiting Operational Environmental Satellites) and have been extensively validated based on buoy measurements (Griffith et al., 2018). We used 'skin' sea-surface temperature estimates (day–night composites) available daily at a horizontal resolution of 1.1 km. To avoid errors due to poor satellite imaging on shallow coastal waters (Darecki & Stramski, 2004), we extracted pixels 10-km offshore (with a 2-km circular buffer) in Sydney (33°49'58.296"S, 151°23'53.88"E) and off the Swain sector, on the south section of the Great Barrier Reef (21°58'54.62"S, 152°28'23.62"E). We chose the latter region to represent a putative parent source population on the southern edge of the Great Barrier Reef, because earlier studies have demonstrated this area to be a potential origin for tropical vagrants in temperate south-eastern Australia (Feary et al., 2014).

We tested the hypothesis that greater food availability in temperate waters could also favour the establishment of tropical vagrants (Booth et al., 2011; Donelson et al., 2012) by including chlorophyll *a* concentration (*CHL*, in mg/m³) data, a proxy for ocean productivity, as an additional driver influencing the survival of settlers and juveniles. We worked with estimates derived from NASA's Aqua/MODIS (Moderate Resolution Imaging Spectrometer) satellite imaging, which have been validated for the region (Schroeder et al., 2016). We downloaded the rasters at a temporal resolution of 1 day and a spatial resolution of 4 km from the Integrated Marine Observing System repositories. We extracted the data for the sink population (Sydney) 10-km offshore (with a 2-km circular buffer), and averaged them monthly for analysis.

We used the *R* package *raster* (Hijmans, 2017) to extract the environmental data from netCDF files, for the dates and pixels corresponding to our fish dataset. Although some data were missing due to masking cloud cover, averaging monthly resolved this and no imputations were necessary. Monthly averages can also help smooth errors in satellite-derived estimates that would manifest at higher temporal resolutions of sampling (Pearce et al., 2016). Figure S2 shows monthly anomalies to illustrate both long-term trends and month-specific departures from the means. All variables except for *CHL* show a positive trend, consistent with a signal of anthropogenic climate change (Pearce et al., 2016; Ridgway, 2007). We z-transformed the environmental variables before including them in the population-dynamics models to standardize parameters for direct comparison in the linear models.

2.4 | Life stage-specific population growth under climate-change scenarios

To explore the potential influence of increases in sea-surface temperature due to climate change on the numerical response of future settler and juvenile *Abudefduf*, we followed a model-averaging approach using Akaike's information criterion weights ($wAIC_c$) of the

models including sea-surface temperatures. Because *Abudefduf* does not yet survive until breeding age at our study locations, and the size and productivity of their exact larval source areas are unknown, we lack the appropriate data to parameterize a closed population-dynamics model. Hence, we focused solely on how temperature will extend the growth season of recruit and juvenile life stages in the temperate sink environment. We simulated population-growth dynamics for settlers and juveniles between 2006 and 2100 under two Representative Concentration Pathway (RCP) emission scenarios: RCP4.5 and RCP8.5. RCP4.5 assumes moderate mitigation of greenhouse gas emissions, resulting in an initial increase in radiative forcing, followed by stabilization at 4.5 W/m² by 2100. RCP8.5 assumes no mitigation (i.e. a reference case), reaching 8.5 W/m² in 2100. Global air temperature projections for the end of the century relative to 1990 are 1.0–2.6°C and 2.6–4.8°C for RCP4.5 and RCP8.5 respectively (Harris et al., 2014). We used monthly sea-surface temperature projections derived from the ACCESS1.0 general circulation model archived by the Coupled Model-Inter-comparison Project, phase 5 (Taylor et al., 2012). We extracted estimates using bilinear interpolation for the 1 × 1° pixels offshore of our two sites: Sydney (sink population) and Swain sector at the Great Barrier Reef (potential source population). We z-transformed these data according to the scaling attributes of the sea-surface temperature time series used to build the population-growth models, and incorporated these predicted sea-surface temperatures into the top-ranked models to project future population growth of settlers and juveniles. To assess change across time, we recorded the number of months per year when population growth rates (*r*) were positive (i.e. increasing populations).

3 | RESULTS

3.1 | Density feedback and environmental drivers

Regardless of the life stage analysed, or whether we aggregated life stages, our model comparisons revealed most support for the compensatory *GL* model relative to those ignoring density-feedbacks (Table 1; Table S1). Note however that the deviance explained by the *GL* models was relatively low, the models for aggregated settlers and juveniles, and for settlers and juveniles tested separately explained 4.91%, 4.06% and 4.12% more of the deviance—relative to the random-walk models respectively (Table 1; Table S1). The density feedback occurred for juveniles at a lag of 2 months, but there was no non-random lag apparent for settlers or the aggregated settlers and juveniles (partial autocorrelation function, Hyndman & Khandakar, 2008; Figure S4). For the top-ranked models, the *GL* parameters r_m and *K* differed between settlers and juveniles. Settlers exhibited higher intrinsic population growth and carrying capacity than juveniles (Table 2).

Incorporating environmental drivers and season in the *GL* model increased the percent deviance explained by more than twofold (Table 1; Table S1). The top-ranked model for the aggregated settlers and juveniles included only season, and none of the environmental

TABLE 1 Model rankings to examine the combined effect of compensatory density feedback and environmental drivers on population dynamics of settler and juvenile *Abudefduf vaigiensis* recorded in temperate, sink population (Sydney). The two top-ranked, Gompertz-logistic, exponential and random-walk models are given. See Table S1 for complete information. GL = Gompertz-logistic compensatory density feedback, SST_{GBR} = sea-surface temperature recorded at the source population (Great Barrier Reef) with lag of 3 ($t-3$) months; EAC_s = strength of the East Australia Current, SST_{SYD} = sea-surface temperature recorded in Sydney, CHL = chlorophyll *a* concentration recorded in Sydney; *full* = all variables considered; *S* = season. LL = log-likelihood; *k* = number of model parameters; ΔAIC_c = difference in Akaike's information criterion (corrected for small sample size) between the current and top-ranked models; $wAIC_c$ = AIC_c weight (~model relative probability); ΔBIC = difference in Bayesian information criterion between the current and top-ranked models; $wBIC$ = BIC weight (~model relative probability); %DE = percent deviance explained

	LL	<i>k</i>	ΔAIC_c	$wAIC_c$	ΔBIC	$wBIC$	%DE
Settlers and juveniles aggregated							
GL.S	-143.087	4	0.000	0.187	0.000	0.505	12.157
GL.CHL.S	-142.027	5	0.140	0.174	2.335	0.157	12.807
GL	-154.896	3	21.415	0.000	19.165	0.000	4.907
Random walk	-162.889	1	33.153	0.000	26.241	0.000	–
Exponential	-162.709	2	34.891	0.000	30.336	0.000	0.110
Settlers							
GL. SST_{SYD} . $SST_{GBR(t-3)}$.S	-152.449	6	0.000	0.363	0.586	0.235	16.216
GL. EAC_s . SST_{SYD} . $SST_{GBR(t-3)}$.S	-152.032	7	1.543	0.168	4.206	0.038	16.445
GL	-174.566	3	37.454	0.000	31.458	0.000	4.060
Random walk	-181.954	1	47.981	0.000	37.325	0.000	–
Exponential	-181.454	2	49.080	0.000	40.779	0.000	0.275
Juveniles							
GL. SST_{SYD} .S	-129.311	5	0.000	0.336	0.000	0.546	9.311
GL.CHL. SST_{SYD} .S	-128.867	6	1.430	0.165	3.566	0.092	9.622
GL	-136.713	3	10.340	0.002	5.895	0.029	4.120
Exponential	-140.667	2	16.099	0.000	9.350	0.005	1.347
Random walk	-142.588	1	17.841	0.000	8.735	0.007	–

drivers considered. However, the support for this model was relatively weak ($wAIC_c = 0.19$) and poorly resolved compared to that of the alternative models (Table 1; Table S1). Furthermore, the second-ranked model highlighted the negligible effect of chlorophyll *a*, a variable that predicted the population growth rate of aggregated settlers and juveniles poorly (Table 1; Table S1). For settlers, the top-ranked model ($wAIC_c = 0.36$) included the positive effect of local temperatures in the sink area (SST_{SYD} ; Figure 3a; Table 2), and the temperature experienced by individuals at the potential source population ($SST_{GBR(t-3)}$) which negatively affected their intrinsic growth rates (Figure 3b; Table 2). In contrast, in the top-ranked model for juveniles ($wBIC = 0.34$), growth responded more to local temperatures in the sink area (SST_{SYD}), which promoted survival (Figure 3c) and positive population growth in temperate areas. The models considering the strength of the East Australian Current or ocean productivity had substantially less support (Table 1; Table S1).

3.2 | Life stage-specific population growth under climate-change scenarios

The strong influences of sea-surface temperature on both settlers and juveniles were evident across the top-ranked models (Table 1; Table

S1). For settlers, the three top-ranked models included the combined effects of SST_{SYD} and $SST_{GBR(t-3)}$, with substantial empirical support ($\sum wAICs = 0.66$). For juveniles, the three top-ranked models, which also received considerable support ($\sum wAICs = 0.65$; Table S1), included SST_{SYD} , but not $SST_{GBR(t-3)}$. We explicitly considered these top three-ranked models in the model-average predictions of future population growth rates.

Future climate-driven increase in sea-surface temperatures at temperate and tropical sites forced unequal dynamics for settlers and juveniles (Figure 4). We projected that the net population growth of settlers in temperate areas will increase moderately for both emissions scenarios until ~2060, when growth tends to stabilize under RCP4.5 and accelerate under RCP8.5 (Figure 4c–e). This was explained by a strongly negative effect of temperature at the potential source population on fish replenishment, as opposed to the positive effect of local temperature on the survival of settlers (Figure 3; Table 1; Table S2). This model predicts that the number of months per year with positive growth will remain between two and four until ~2060, and increase to eight by 2,100 assuming the reference climate-change scenario (Figure 4e). In contrast, because juvenile growth depends on only the positive effect of local temperature (Figure 3; Table 1), the warming projected for this century led to

TABLE 2 Stochastic Gompertz-logistic model parameters estimated using maximum likelihood to examine the combined effect of compensatory density feedback and environmental drivers on population dynamics of settlers and juveniles aggregated, and settlers and juveniles separated for *Abudedefduf vaigiensis* recorded in Sydney. The two top-ranked, Gompertz-logistic, exponential and random-walk models are given. The values for all models computed are in Table S2. GL = Gompertz-logistic compensatory density-feedback, SST_{GBR} = sea-surface temperature recorded at the southern Great Barrier Reef with lag of 3 ($t-3$) months; EAC_s = strength of the East Australia Current, SST_{SYD} = sea-surface temperature recorded in Sydney, CHL = chlorophyll *a* concentration recorded in Sydney; S = season; SE = standard error; z = z-score; p = p -value

	Estimate	SE	z	p
Settlers and juveniles aggregated				
GL.S				
r_m	2.35	0.38	6.23	<0.001
$\log_e K$	6.37	1.19	5.35	<0.001
S	-0.87	0.17	-5.21	<0.001
σ	1.28	0.10	13.11	<0.001
GL.CHL.S				
r_m	2.47	0.38	6.47	<0.001
$\log_e K$	6.99	1.38	5.08	<0.001
CHL	0.21	0.15	1.47	0.143
S	-0.94	0.17	-5.48	<0.001
σ	1.26	0.10	13.11	<0.001
GL				
r_m	0.60	0.20	3.03	0.002
$\log_e K$	1.91	0.51	3.76	<0.001
σ	1.47	0.11	13.12	<0.001
Random walk				
σ	1.61	0.12	13.12	<0.001
Exponential				
r_m	0.10	0.17	0.60	0.548
σ	1.60	0.12	13.11	<0.001
Settlers				
GL. SST_{SYD} · $SST_{GBR(t-3)}$ · S				
r_m	2.20	0.56	3.95	<0.001
$\log_e K$	2.96	0.88	3.36	<0.001
SST_{SYD}	0.82	0.36	2.31	0.002
$SST_{GBR(t-3)}$	-0.50	0.20	-2.58	<0.001
S	-1.06	0.28	-3.79	<0.001
σ	1.42	0.11	13.12	<0.001
GL. EAC_s · SST_{SYD} · $SST_{GBR(t-3)}$ · S				
r_m	2.20	0.55	3.97	<0.001
$\log_e K$	3.00	0.89	3.35	<0.001
EAC_s	0.16	0.18	0.92	0.359

TABLE 2 (Continued)

	Estimate	SE	z	p
SST_{SYD}	0.89	0.36	2.47	0.013
$SST_{GBR(t-3)}$	-0.56	0.21	-2.75	<0.001
S	-1.06	0.28	-3.81	<0.001
σ	1.42	0.11	13.12	<0.001
GL				
r_m	-0.04	0.20	-0.19	0.853
$\log_e K$	-0.11	0.57	-0.19	0.853
σ	1.84	0.14	13.12	<0.001
Random walk				
σ	2.01	0.15	13.12	<0.001
Exponential				
r_m	-0.22	0.22	-1.00	0.316
σ	2.00	0.15	13.11	<0.001
Juveniles				
GL. SST_{SYD} · S				
r_m	0.14	0.43	0.33	0.742
$\log_e K$	0.83	2.65	0.31	0.753
SST_{SYD}	0.51	0.18	2.94	0.003
S	0.07	0.22	0.32	0.748
σ	1.09	0.08	13.12	<0.001
GL.CHL. SST_{SYD} · S				
r_m	0.39	0.49	0.78	0.434
$\log_e K$	2.52	4.03	0.63	0.531
SST_{SYD}	0.52	0.20	2.60	0.009
CHL	0.15	0.13	1.15	0.249
S	-0.05	0.25	-0.19	0.848
σ	1.08	0.08	13.05	<0.001
GL				
r_m	0.28	0.13	2.15	0.032
$\log_e K$	1.63	0.93	1.74	0.081
σ	1.19	0.09	13.11	<0.001
Exponential				
r_m	0.27	0.13	1.98	0.048
σ	1.24	0.09	13.11	<0.001
Random walk				
σ	1.27	0.10	13.12	<0.001

an upward trend in their population growth rates in temperate areas (Figure 4d-f). Assuming the reference case (i.e. RCP8.5), we can expect 12 months of growth for juveniles (i.e. enhanced winter survival) by around the year 2070 in their temperate environment, compared to 10 months following an emission-reduction scenario (i.e. RCP4.5; Figure 4f). Currently, juveniles at this temperate site exhibit around 4 months of population growth per year (Figure 4f).

(Continues)

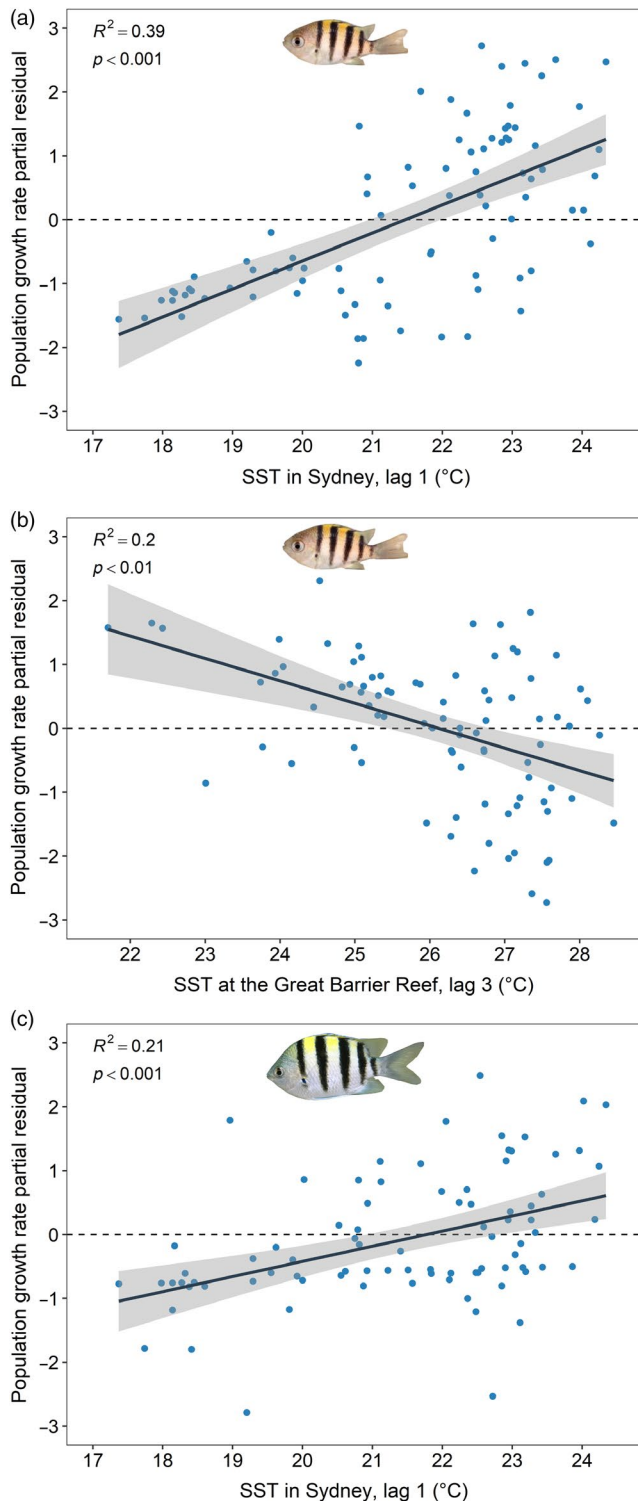


FIGURE 3 Partial residual plots showing the relative effects of the main environmental drivers associated with changes in *Abudefduf vaigiensis* population growth at the sink population. Panels (a) and (b) illustrate the contrasting effects of SST_{SYD} , 1-month lag, and SST_{GBR} , 3-month lag (i.e. potential source population), on settlers. (c) The effect of SST_{SYD} , 1-month lag, on juveniles. SST = sea-surface temperature. Juveniles were not directly affected by the SST at the potential source population. The lines are linear regression fits with 95% confidence bounds shown by grey-shaded areas

4 | DISCUSSION

The speed and direction of ongoing species redistributions already indicate a strong effect of global warming, because species tend to follow the displacement of isotherms to stay within their preferred thermal niches (Payne et al., 2018; Pinsky et al., 2013; Poloczanska et al., 2016). While temperature is obviously the predominant driver, the species' establishment in new regions depends on both endogenous and exogenous factors influencing demographic rates at different spatial and temporal scales (Forchhammer et al., 1998; Poloczanska et al., 2016; Sunday et al., 2015). Using multi-model inference, we were able to quantify the relative contributions of compensatory density feedbacks and relevant environmental drivers to the life stage-specific dynamics of a conspicuous tropical vagrant, *Abudefduf vaigiensis*. While previous studies have examined the importance of isolated drivers to the success of migrant fishes (e.g. Feary et al., 2014), ours is the first to model early life dynamics of population growth quantitatively with an emphasis on life stage-specific processes.

Our assessments indicate that population cycles of *Abudefduf* at the leading edge of its distribution are slightly better explained by compensatory GL models than by the simpler random-walk or exponential models. The relatively low support for the density feedback component, and the boom-bust population cycles could still suggest non-endogenous-control mechanisms that remain unexplored, especially in the context of range-shifting species. The percent deviance explained by the GL model was slightly higher when considering settlers and juveniles together than when treated separately. This could be due to the higher sample size, but also suggests that the endogenous control is present at the whole-population level. However, the inability of this model to capture the signal of environmental forcings indicated that, to elucidate the mechanisms underlying the dynamics further, a life stage-specific analysis is warranted. When discriminating between life stages, we found that density feedback is more important for juveniles than settlers. While empirical evidence suggests that the sensitivity to biotic and abiotic factors varies with ontogeny in a wide range of marine and terrestrial animal taxa (Gaillard et al., 2000; Hazlerigg et al., 2012; Oro et al., 2010), most population-dynamics models for marine fishes have assumed that density feedback operates similarly across life stages (Botsford et al., 2011). Our data clearly show that distinguishing the partial contribution of density feedback across life stages is important. As this species gradually establishes breeding populations in its novel range, the contribution of adults, which can reproduce and thus more strongly influence population growth than juveniles, will become especially relevant for this range-extending species (Bates et al., 2014).

The distinction also matters because of potential ontogenetic differences in sensitivity to environmental drivers and endogenous control, which can identify potential population bottlenecks. The exact mechanisms explaining the greater influence of endogenous process in juveniles than settlers are unclear for *Abudefduf*. Empirical and theoretical studies on other fishes suggest that while density feedback in earlier life stages is driven primarily by predation or parasitism (Hixon & Carr, 1997), resource limitation (e.g. food, refuge)

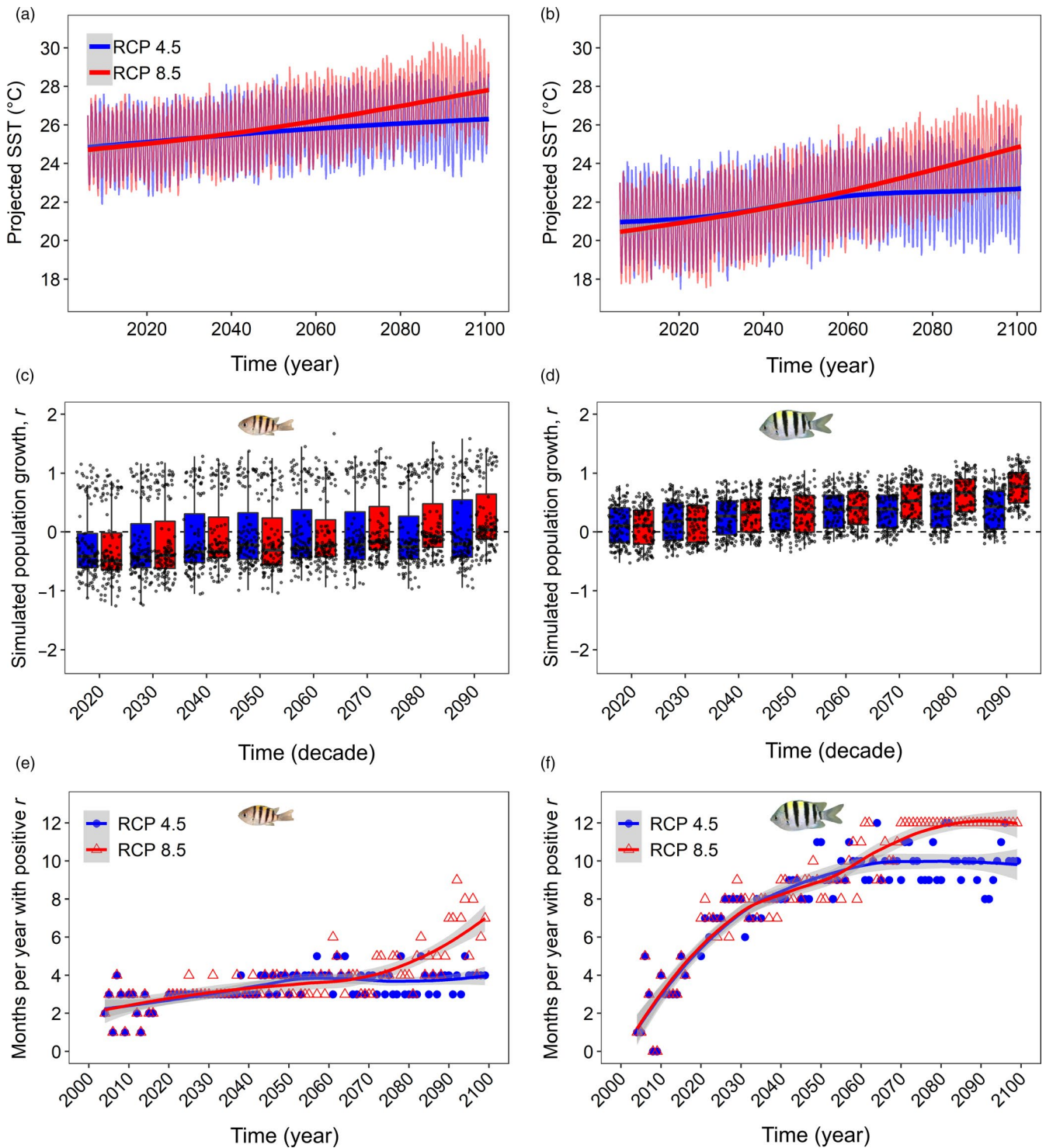


FIGURE 4 Simulated population growth rates as a function of future climate change projections of sea-surface temperature (SST). The two upper panels show the monthly SSTs expected at (a) the southern Great Barrier Reef (potential source population) and (b) Sydney (sink population), assuming climate change scenarios of Representative Concentration Pathways (RCP) 4.5 and 8.5. The two middle panels show 10-year aggregated population growth rates (r) model-averaged predictions for (c) settlers and (d) juveniles for the two RCP scenarios. The two lower panels show the number of months predicted to exhibit positive growth by (e) settlers and (f) juveniles for the two RCP scenarios. The lines in panels a, b, e and f are temporal trends with 95% confidence bounds, calculated as cubic regression splines. The boxplots in panels c and d contain 25th and 75th percentiles of the distribution, with vertical lines denoting $1.5 \times$ the interquartile range. Data are also overlaid

might be more influential at later stages (Lorenzen, 2008; Sandin & Pacala, 2005). However, even if intraspecific resource limitation explains the larger endogenous signal in juveniles, this effect

might be confounded by positive interspecific interactions. Indeed, *Abudefduf* individuals grow larger when shoaling with temperate species (e.g. *Atypichthys strigatus*, *Trachinops taeniatus*), possibly

due to greater access to novel food resources (Paijmans et al., 2019; Smith et al., 2018), on which the diet-generalist *Abudefduf* can capitalize (Monaco, Bradshaw, et al., 2020). Ultimately, despite a species' ability to adjust to novel interactions with others, our findings suggest that the net effect of density feedback is a relevant contributor to the population dynamics of invading marine species in temperate ecosystems.

Environmental variability improved the explanatory power of the *GL* models by more than twofold. As previously reported, ocean warming is the main force behind the poleward redistribution of *Abudefduf* (Fowler et al., 2017; Pearce et al., 2016). We find that while the survival of settlers and juveniles is favoured by warmer temperatures locally, the number of propagules to this temperate region decreases with warmer temperatures experienced by a potential source population at the Great Barrier Reef. Previous investigations provide additional support for both of these processes. First, field and laboratory studies suggest that survival of temperate overwintering *Abudefduf* and other tropical vagrant fishes increases during warmer winters, with a minimum threshold temperature for persistence of $\sim 17.5^{\circ}\text{C}$ (Figueira & Booth, 2010). Second, laboratory experiments show that breeding activity, sperm production and overall reproductive output of another tropical pomacentrid (*Acanthochromis polyacanthus*) can be hindered by high temperatures ($+2.6$ – 4.8°C) expected under a reference case climate-change scenario (Donelson et al., 2014; Donelson et al., 2010)—we suspect that a similar mechanism might explain results for *Abudefduf* at the initial stages of range extensions. Nevertheless, here we reveal that temperature exerts a strong, but opposite effect on the production of propagules (i.e. negative) versus the survival of established settlers and juveniles (i.e. positive), stressing the importance of considering spatially-coupled temperature effects in our models to predict climate range shifts. The inherent complexity of the processes governing these dynamics cautions against silver-bullet statements. Notably, the interplay between lower recruitment rates and higher settler and juvenile survival predicted under climate change, combined with the density feedbacks identified for juveniles would suggest two potential bottlenecks for the long-term establishment of *Abudefduf*: (a) low probability of arrival and (b) endogenous regulation of population growth. Importantly, this assessment ignores possible changes in coastal circulation patterns, and the resulting source population, also driven by climate change. Our focus on large juveniles could also lead to a bias towards healthier individuals. Similarly, because our analysis forcibly ignores dynamics in the probability of transitioning between stages, we assume that the juvenile population operates independently of the presence of settlers, a caveat that deserves further attention when more data become available. Our models can nevertheless serve as heuristic tools to reveal otherwise unnoticed ecological processes regulating early stages of range extension.

Previous efforts characterizing the influence of environmental forces on the establishment of tropical vagrants at higher latitudes have emphasized local population bottlenecks (Figueira et al., 2009; Pearce et al., 2011) and interactions among thermally sensitive species

(Figueira et al., 2019). However, as a species with a dispersive pelagic larval stage, the population growth rate of vagrant *Abudefduf* is inherently subject to many different ecological processes occurring across broader spatial scales. The multi-model inference approach acknowledges that stochastic drivers are not mutually exclusive parameters (Link & Barker, 2006). While our assessments do not negate the recognized contribution of a stronger East Australian Current under climate change (Booth et al., 2007; Pearce et al., 2016), they provide more support for the role of temperature variability. This has implications for forecasting the species' future success across its entire distribution range. Although we did not survey the potential source area, our quantitative models suggest that the persistence of those populations might be increasingly compromised by warmer temperatures, leading to a contraction on the trailing edge of this species' range at some point in the near future (García Molinos et al., 2015). Assuming a reference RCP8.5 climate-change scenario, the apparent negative effect of source-population temperatures might be counterbalanced by the positive effect of warmer local temperatures, allowing for higher net population growth of settlers. For juveniles, and solely given by the influence of local temperature, our models indicated an imminent extension of the leading edge of the distribution of *Abudefduf*, regardless of which scenario of greenhouse gas emissions we assumed. Despite a slight departure around the 2060s, data from model runs for both RCP scenarios 4.5 and 8.5 project positive population growth for >8 months/year by 2050, and for 10–12 months/year by 2070.

We found little evidence for the effects of other, presumably relevant, environmental drivers of the early life dynamics of *Abudefduf* population growth. For both settlers and juveniles, the *GL* models that considered variability in chlorophyll *a* concentration and the strength of the East Australian Current received more support than the null and the exponential-growth models, but substantially less support than the top-ranked models. Although the second-ranked model for settlers and juveniles aggregated included chlorophyll *a*, this model did not convincingly outperform the alternatives, and the role of chlorophyll *a* was not evident when isolating its effect. The percentages of deviance explained by all models considering environmental variation were broadly similar, attesting to the inherent complexity of the survey data to which we fitted our models, or the existence of factors we could not consider here. Although these models outperformed random formulations, they clearly ignored other potentially relevant sources of variability in population growth rates. For instance, while we included an index of the strength of the East Australian Current as a proxy for population replenishment, the realized connectivity between source and sink populations also depends on eddies that can export larvae offshore (Condie et al., 2011). Incorporating this and other potential drivers would increase the local-scale ecological realism captured by these models. However, given our emphasis on the long-term projections of population displacement, for which higher order indicators of environmental pressure generally overwhelm small-scale dynamics (Johnson et al., 2011; Southward et al., 2004), we maintain that our projections of life stage-specific population growth rate are nonetheless revealing.

Our model projections might be subject to uncertainties regarding temperature thresholds of this and other tropical vagrant species. While previous field studies have shown that the minimum winter temperature for survival of *Abudefduf* is ~17.5°C, laboratory trials indicate tolerance of <16°C, suggesting an important role of the interaction landscape on this species' persistence probability (Figueira et al., 2009, 2019). *Abudefduf* is the most conspicuous vagrant tropical fish settling on temperate Australian reefs. Their relatively low abundances at tropical native sites (D. Booth, personal observation) suggests that upon arriving to novel regions, they operate as a *weedy species* by capitalizing on reduced negative interactions, relative to those of the highly biodiverse tropics (Connell, 1978), and greater food availability in the more productive temperate waters (Booth et al., 2011). However, this release from enemies might only be temporary, as the number of tropical vagrant species moving southwards, including predators, continues to increase (Fowler et al., 2017). Studies that characterize the dynamics of vagrant community assemblages are warranted. Nevertheless, the relatively high abundance of vagrant species at the leading edge of their distribution suggests that organismal dispersal and population-level processes might initially overwhelm the influence of novel species interactions during the arrival and early establishment phases of range extensions.

Robust projections of species' redistribution call for models capable of capturing the nonlinear processes emerging from intrinsic and environmental forces. The phenomenological approach we employed provides a means to examine and discriminate main drivers of population dynamics of vagrant species not yet in equilibrium with their new environment (Yang et al., 2008). Models that explicitly treat environmental signals as stochastic processes driving changes in population sizes are particularly well-suited for organisms that disperse via ocean currents, including many marine invertebrates and fishes with planktonic life stages. Using this approach, we demonstrate that different life stages of a vagrant coral-reef fish exhibit opposite responses to global warming, with unexpected knock-on effects that challenge our ability to predict climate change-driven transitions from vagrancy to residency.

ACKNOWLEDGEMENTS

This project was supported by an Australian Research Council Discovery grant (DP170101722) to I.N., D.J.B., D.S.S. and B.M.G. The first draft of this manuscript was produced at the 2018 Coobowie Writing Retreat funded by the University of Adelaide's Environment Institute. H. Beck, G. Beretta and A. Fowler assisted D.J.B. during field surveys. E. Coni, C. Ferreira, A. Jones, K. Kingsbury, M. Sasaki and H. Ullah provided logistic support and constructive comments on the analyses. D. Smith helped improve the manuscript.








AUTHORS' CONTRIBUTIONS

C.J.M. and C.J.A.B. chose the analyses; C.J.M. did the analyses and led the writing. All the authors contributed to the original concept and revision of the manuscript.

DATA AVAILABILITY STATEMENT

All data and code are available at: <https://doi.org/10.5281/zenodo.4248117> (Monaco, Nagelkerken, et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Monaco CJ, Nagelkerken I, Booth DJ, et al. Opposing life stage-specific effects of ocean warming at source and sink populations of range-shifting coral-reef fishes. *J Anim Ecol*. 2021;90:615–627. <https://doi.org/10.1111/1365-2656.13394>