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RESEARCH ARTICLE

Ocean warming and novel species interactions boost growth and persistence of range-extending tropical fishes but challenge that of sympatric temperate species in temperate waters

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Abstract

Aim: Climate change can have a broad range of impacts on the physiology and behaviour of animals. These effects can be mediated by the presence of other species in the community, but current forecasts of species responses to climate change largely ignore biological interactions. This is particularly true for novel interactions between range-extending and native species, as this is often considered as noise and excluded from predictive models. Here we simulate how a tropical range-extending and a local temperate fish species respond to the independent and combined effects of future ocean warming (RCPs 4.5 and 8.5) and novel ecological interactions in temperate ecosystems.

Location: East coast of Australia, along a ~ 2,000 km latitudinal gradient in a global climate warming hotspot.

Taxon: *Abudefduf vaigiensis* (tropical) and *Atypicthys strigatus* (temperate) fishes.

Methods: We use a dynamic energy budget model to simulate the length growth (i.e., increases in body length of individuals over time) and population persistence of juveniles of a tropical and a temperate fish species that form mixed-species shoals, under different climate scenarios with and without the effects of novel ecological interactions.

Results: Our model forecasts that length growth of the juvenile tropical species will increase under ocean warming across subtropical to temperate regions. This increased length growth will be more drastic in temperate regions than in the subtropics, as winter warming will allow the tropical species to overwinter more frequently and show positive growth throughout the year. In contrast, warmer summer temperatures in the subtropics will likely exceed the optimal temperature of the juvenile temperate species at their trailing edge, resulting in reduced length growth under climate warming. Novel species interactions increased length growth of the juvenile tropical species but did not affect its winter or summer survival. In contrast, novel species interactions with tropical species were forecast to reduce length growth of the juvenile temperate species.

Main Conclusions: Our study suggests that for some coastal fish species future warming will likely reverse body size dominance between temperate and tropical fish species, with increased novel interactions in temperate ecosystems (due to range extensions) but decreased novel interactions in the subtropics (due to range contractions). Novel species interactions and warming effects on body size and species survival are likely to reshuffle temperate fish communities and their competitive interactions.

KEYWORDS
climate change, dynamic energy budget, novel species interactions, ocean warming, range shifts, vagrant species

1 | INTRODUCTION

Climate change is reshuffling biological communities, as species track changing environmental temperatures at different rates (Chen et al., 2011; Poloczanska et al., 2013). Notably, warming facilitates the extension of biogeographic ranges of warm-adapted species towards ecosystems and higher latitudes that were previously unsuitable for them. This has resulted in shifts in biodiversity along temperature gradients. For instance, warming-induced range shifts have caused declines in species diversity at lower latitude while leading to increases at higher latitudes, where tropical range-extending species mix with temperate species (Worm & Lotze, 2021).

In the temperate recipient ecosystems where tropical range-shifting species interact with resident temperate species, different fish species will likely respond to ocean temperature changes differently due to each species having its own optimal temperature range. Because fish species originating from warm regions have higher optimal temperatures compared to those in cooler regions (Payne et al., 2016), ocean warming at higher latitudes will likely favour those that are shifting from the tropics to cooler temperate waters compared to those that are resident to higher latitudes. Given that changes in ambient temperature have a strong influence on the metabolic rate of fish species (Sinclair et al., 2016; Volkoff & Rønnestad, 2020), changes in energy demand associated with temperature increases can lead to shifts in energy demand and growth rate of fish species (Volkoff & Rønnestad, 2020). Hence, future ocean warming at higher latitudes will likely enhance growth rate of the range-shifting species but decline that of the residents. In addition to direct impact of climate change on the physiological performance, arrival of range-shifting species can challenge resident species via competition (Zeidberg & Robison, 2007) and predation (Hollebone & Hay, 2008; Vergés et al., 2014), or by modifying local habitat composition (Ling, 2008; Whitney & Gabler, 2008), thus threatening to alter the structure of the communities they occupy (Kordas et al., 2011; Williams & Jackson, 2007). As such, a better understanding of the combined effects of climate change-related stressors and novel species interactions is key to forecasting the ecological consequences of poleward range shifts on recipient communities (Alexander et al., 2015).

The ecological success of species depends both on biotic and abiotic elements of the environment. However, current forecasts of species responses to climate change still largely exclude species interactions (Dolci & Peruzzi, 2022; Gillard et al., 2017; Guisan et al., 2006), and especially competition (Araújo & Luoto, 2007). Some models exist that include predator–prey interactions (e.g., aquatic taxa, Monaco et al., 2016; Moullec et al., 2019, terrestrial taxa, Aryal et al., 2016; Bastille-Rousseau et al., 2018). Although some studies model species' future physiological performance and include competitive interactions, these studies are uncommon and largely limited to species with limited ability to move (e.g., mussels: Monaco & McQuaid, 2019; trees: Caplat et al., 2008; Liang et al., 2017). This leaves a critical knowledge gap concerning aquatic mobile taxa as range extensions by mobile fish species are increasingly documented (Osland et al., 2021; Pinsky et al., 2020; Poloczanska et al., 2013; Vergés et al., 2014). These species have the potential to compete with resident species due to their shared utilization of available resources, which may significantly impact resident species given their susceptibility to environmental change (Manes et al., 2021). Furthermore, warming-related range shifts (Gervais et al., 2021; Hyndes et al., 2016; Johnson et al., 2011) suggest that increasing ocean temperatures will likely accelerate the rate of range expansion. As such, predicting how novel species interactions and future climate will affect the persistence and physiological performance of species is an urgent outstanding question.

A common approach to predicting species responses to a changing climate is the use of correlative niche models, such as species distribution models. These models are mathematical representations of the environmental niche of a species, built based on the conditions (e.g., temperature, salinity, chlorophyll *a*) they experience across their distribution range. These models can provide estimates of the future distribution of the species by modifying the habitat temperatures based on climate change projections. To capture the thermal niche of a species (Peterson & Vieglais, 2001), these correlative models often assume that the distribution range corresponds to its entire native range (Araújo et al., 2005; Araújo & Pearson, 2005; Guisan & Zimmermann, 2000). However, it is not uncommon to remove individuals that occur outside of the species native range ("vagrants") from correlative models because they are considered as a source of error (e.g., Cooper & Soberón, 2017; D'Amen & Azzurro, 2019; Rose et al., 2016). Filtering these individuals consequently removes information regarding the novel interactions occurring between a vagrant and local species as well as their novel climate niche. Although comparing the analyses with a filtered niche across a range of percentiles (e.g., from 75% to 100%) allows researchers to understand the impact of removing novel environments (Guisan et al., 2014), when model calibrations are performed on such data, predictions beyond present-day conditions can consequently be compromised due to calibration ignoring novel conditions (Lee-Yaw et al., 2022; Liu et al., 2020; Zurell et al., 2012). These drawbacks in niche modelling can be accommodated by using either shape-constrained GAMs (Citores et al., 2020) or mechanistic models designed to explicitly account for direct physiological and indirect behavioural responses to climate change-related drivers. For example, the Dynamic Energy Budget (DEB) model framework (Kooijman, 2010) uses an organisms' physiology to identify suitable environmental conditions of the species, instead of reconstructing species niches from their geographical distribution (Kearney et al., 2008). As this mechanistic model uses the species' fundamental niche (as opposed to the realized niche in species distribution models), more robust predictions beyond their native ranges are possible.

DEB theory is a powerful framework to describe an organisms' energy metabolism throughout their life cycle (Marques et al., 2018; Van der Meer, 2006). Variations of the DEB model has been used to model the physiological performance of species across geographical scales, including predictions under future climate change scenarios (bivalves: Thomas & Bacher, 2018; Monaco & McQuaid, 2019). DEB models have been developed to accommodate competitive interactions based on changes in the individual's behaviour (Beale & Lennon, 2012); however, these model variants have not been explored in a context of species range shifts due to climate change.

Here we modelled the physiological performance, based on survival and growth, of a common range-extending coral-reef fish, the Indo-Pacific sergeant major *Abudefduf vaigiensis* (hereafter "tropical species"), and a shoaling local temperate fish, Australian mado *Atypichthys strigatus* (hereafter "temperate species"), in a warming hotspot in temperate SE Australia. *A. vaigiensis* occurs from tropical to warm-temperate waters (from 36°N to 39°S, Froese & Pauly, 2000) and their breeding population has been observed at a latitude as high as 28.7°S based on western Australian records (Pearce et al., 2016). Note that observations of breeding behaviour at such high latitudes in eastern Australia are not available. This tropical species feeds on zooplankton, benthic algae, and small invertebrates (Allen & Erdmann, 2012; Sasaki et al., 2024). *A. strigatus* is endemic to temperate waters of eastern Australia (Bray, 2023). Similar to the tropical species, *A. strigatus* feeds on zooplankton and benthic organisms (e.g., algae and invertebrates) as well as parasitic organisms (e.g., caligoids and monstrilloids) (Glasby & Kingsford, 1994; Sasaki et al., 2024). The tropical *A. vaigiensis* is one of the most abundant vagrant species colonizing climate-warming hotspots (Ridgway, 2007) of temperate Australia during late summer (Booth et al., 2018; Monaco et al., 2020). Juveniles of this tropical species have been observed to school with juveniles of *A. strigatus* (Smith et al., 2017) along with Eastern hula fish (*Trachinops taeniaus*) (Smith et al., 2017) and stripey (*Microcanthus strigatus*, Coni et al., 2021). Previous studies showed mixed types of interaction between *A. vaigiensis* and *A. strigatus*. For instance, the interaction with juveniles of the temperate species in temperate Australia (i.e., novel environment for the tropical species) led to enhanced growth in *A. vaigiensis* towards winter (Smith et al., 2017), showing a positive interaction outcome. By contrast, *A. strigatus* interacted aggressively and prevented *A. vaigiensis* from accessing food during a feeding experiment in the field (Coni et al., 2021), showing a negative interaction. Despite the mixed results, overlaps in diet between *A. vaigiensis* and *A. strigatus* (e.g., calanoids and cyclopoids, Glasby & Kingsford, 1994; Sasaki et al., 2024) make the juveniles of tropical *A. vaigiensis* potential competitors to the juveniles of temperate species. Furthermore, increases in the abundance of range-shifting tropical species may not be favourable to the local species due to a positive relationship between the abundance of range-shifting tropical species and their feeding rate (Coni et al., 2021). As such, we used these two species as model organisms to study the effects of novel species interactions due to climate change.

Currently, vagrant populations of this tropical species in temperate Australia (leading edge of the species distribution) still suffer from very high (10% overwinter ratio based on 18-year survey, Booth et al., 2018) winter mortality because temperatures drop below their thermal minimum. As such, novel interactions between the tropical and the temperate species are restricted to the warmer parts of the year and largely cease in winter before the following summer recruitment event occurs. However, with climate change-driven temperature increases, their survival through winter is expected to increase (Figueira et al., 2009; Figueira & Booth, 2010; Monaco et al., 2020), extending the duration of these novel interactions.

In contrast to tropical range extenders, cool-adapted temperate species, particularly the populations located at their warm range trailing edge, are expected to experience reduced physiological and behavioural performance with increasing and potentially stressful levels of warming (Donelson et al., 2019). As such, cool-adapted species are expected to suffer from either reduced growth or increased mortality, or shift to more suitable habitats as seen in several taxa (terrestrial organisms: Parmesan, 2006; marine organisms: Pinsky et al., 2020). If their populations decline at their trailing edges, this might also reduce the magnitude of novel interactions and possible minimize negative effects on tropical range extenders. Thus, future warming is expected to affect both the physiological condition of temperate fish species and the magnitude of their potential ecological interactions with range extending tropical species.

Here, we modelled the thermal physiological performance of tropical and temperate juvenile fishes in Australia to understand how future warming and novel species interactions might impact communities. We hypothesised that future ocean warming will enhance the growth rate and survival duration of juveniles of tropical species compared to temperate species in temperate regions. Additionally, we hypothesised that the presence of novel interactions has a mediating effect (either positively or negatively) on the physiological responses (i.e., growth rate and survival duration) of our model species. For this, we parameterised the DEB model for a sympatric juvenile tropical and temperate fish species, using life-history traits (e.g., body size, age, and reproductive output (obtained from published data, Table S1)) and species thermal sensitivities. Importantly, we included novel ecological interactions based on food ingestion rates and growth rates in the presence and absence of novel interactions based on controlled aquarium experiments. Our model allowed us to forecast the temporal persistence and growth of the two species under present-day and two future ocean warming scenarios (i.e., RCP 4.5 and RCP 8.5) with and without novel species interactions. Because the DEB model is not spatially explicit, the current simulation was limited to latitudes between 27.5 to 43.3°S along the southeast coast of Australia where two species are known to occur and where novel ecological interactions due to climate warming are currently most common.

2 | MATERIALS AND METHODS

2.1 | Future climate projections

We used a dynamic energy budget (DEB) model to parameterise parameters to simulate the physiological change of juvenile tropical and temperate species in Australia under future warming scenarios with and without novel interactions. The DEB model description including diagrams showing the model differences between non-stressful and stressful conditions (Figure S1), parameterisation, use of individual-based DEB model, and testing for model fit is found in the Appendix.

The simulations were limited to the juvenile stages as we were interested in growth of the tropical species when they recruit in temperate regions during the summer. This means that we excluded the larval period and considered fish performance from settlement stage sizes, i.e., >1.21 and 1.20 cm for the tropical and the temperate species, respectively. We restricted our geographical range for simulation of growth to latitudes 27.5–43.3°S along the southeast coast of Australia, covering the known occurrence range of the vagrant population of the tropical species (Atlas of Living Australia, 2021a) and the known distribution of the temperate species (Atlas of Living Australia, 2021b). The latitudinal ranges used in the simulation cover several climate zones including subtropics (from 27.5 to 30.5°S), warm-temperate (from 31.5 to 34.5°S), mild-temperate (from 35.5 to 38.5°S) and cool temperate (from 39.5 to 43.3°S) areas. The sites used for simulation were chosen at every one degree of latitude from the lowest latitude of 27.5°S to the highest at 43.3°S, resulting in a total of 11 and 16 sites for the tropical and the temperate species, respectively.

Within these settings, we simulated growth in body size and development in maturity of the two species for 1 year, from the first of January to the end of December using the parameters estimated (Table S2) in the DEB_IBM-model version 3.1 (Martin et al., 2012) in NetLogo 6.1 (Wilensky, 1999). Note that we did not account for the density-body size relationship (Cyr, 2000; Cyr et al., 1997). We selected January because both species have been observed to start recruiting during this month in SE Australia (Table S3). Note that January recruitment of two species at the same site does not always occur (Table S3), but we still observed the two species co-occurring at the same site in temperate Australia (Figure S2). At the end of each simulation, we obtained the total number of months in which individuals of each species had sufficient energy to grow ("persistence duration") and the total standard length ("length growth"). Note that persistence duration reflects a temporal duration from the beginning of a simulation (i.e., January) until a month when the level of energy reserves falls below the scaled length (Martin et al., 2010). For the total standard length, we sum length growth of an individual across persistence duration.

Two variables that we used in the simulation were monthly averaged sea-surface temperature (SST) (current and future year 2100) and presence/absence of species interaction. For the SST data, we retrieved satellite-derived SST for the year 2018 from Australia's Integrated Marine Observing System (IMOS) (IMOS, 2019) and projected SST for the year 2100 from WDC CLIMATE (2019). The latter was derived using the Australian Community Climate and Earth System Simulator (ACCESS) under the Coupled Model Intercomparison Project Phase 5 (CIMP5). We used two Representative Concentration Pathways (RCP), the intermediate RCP 4.5 and the high RCP 8.5, representing greenhouse gas emissions leading to radiative forcing in 2100 stabilizing at 4.5 and 8.5 $\mathrm{W\,m^{-2}}$, respectively. On average, the ocean temperatures across all simulated sites increases by 1.10 and 3.42°C in 2100, relative to the annual average ocean temperature in 2018, under RCP 4.5 and RCP 8.5, respectively (Figure S3). Of all simulated latitudes, latitude 28.5°S showed the highest yearly average ocean temperature in all scenarios (Figure S3) and scored the highest summer temperature of 30.63°C in 2100 under RPC 8.5.

We simulated the effect of presence/absence of novel species interactions using the feeding rates of individuals as estimated in the aquarium experiment: *f_paired* (Table S2) and *f_single* (Table S2) were used for the presence and absence of the interaction, respectively. Novel interactions occurred only when the months of persistence overlapped between two species ("duration of the novel interaction"). We did not simulate the effect of species interactions at latitudes ≥37.5°S in the current study as it is uncertain if the tropical species will cross the Bass Strait to reach the island of Tasmania by 2100.

Comparison of persistence duration and length growth between current and future scenarios was used to understand the effect of future warming and species interactions on fish physiological performance.

3 | RESULTS

3.1 | Model fit

We found that the model with interactions predicted the maximum standard length of both species slightly better than the model without interactions, with a mean absolute percentage error of −0.036 (Figure S4b) compared to 0.067 (Figure S4a), respectively. These error rates were slightly worse than the average relative error estimated across 500 DEB models (the median mean relative error of <0.1, Marques et al., 2018). The correlations between predicted and observed maximum standard length improved from 0.524 (Figure S4c) to 0.724 (Figure S4e) for the tropical species and from 0.069 (Figure S4d) to 0.094 (Figure S4f) for the temperate species as species interaction was included in the model. The mean absolute percentage error of model fit further improved to 0.024 (Figure 1a) as we selected the model (with or without the interaction) based on the lowest absolute percentage error between the observed and predicted size. The correlations between predicted and observed maximum standard length improved to 0.901 for the tropical species (Figure 1b) and 0.234 for the temperate species (Figure 1c).

3.2 | The effect of climate change on body length growth (without novel species interactions)

Increasing ocean warming is predicted to boost length growth of the juvenile tropical species by an average 41.5% under RCP 4.5 and 58.4% under RCP 8.5, respectively (Figure 2a). The rate of length growth increase in the juvenile tropical species is more extensive at warm- to mild-temperate (32.5–37.5°S) compared to subtropical to warm-temperate (27.5–31.5°S) latitudes: 70.5% vs 6.7% (RCP 4.5) and 97.8% vs 10.9% (RCP 8.5), respectively (Figure 2a). Nevertheless, largest absolute lengths were still accomplished at subtropical to warm-temperate latitudes (27.5–31.5°S) (Figure 2c).

In contrast, future warming is projected to be less favourable for the juvenile temperate species. Under RCP 4.5, the rate of change in juvenile length growth was on average +3.2, +15.0 and −21.8% at the trailing (i.e., subtropics between 27.5 and 30.5°S), core (i.e., warm- to mild-temperate between 31.5 and 37.5°S) and leading edges (i.e., mild- to cool-temperate between 38.5 and 43.3°S), respectively (Figure 2b). Under RCP 8.5, juvenile length growth is predicted to drop by 36.8% at the trailing edge, but to increase by 14.3% at the core and by 74.4% at the leading edges, respectively (Figure 2b). Under both climate change scenarios, largest fish sizes are forecast to shift in occurrence from the current trailing edge to the core range (Figure 2d).

Under present-day ocean temperatures, average body size of the juvenile tropical species is smaller than that of juvenile temperate species by 8.0%–42.5% at subtropical to mild-temperate latitudes (i.e., 27.5–37.5°S). However, in year 2100 under RCP 8.5, the juvenile

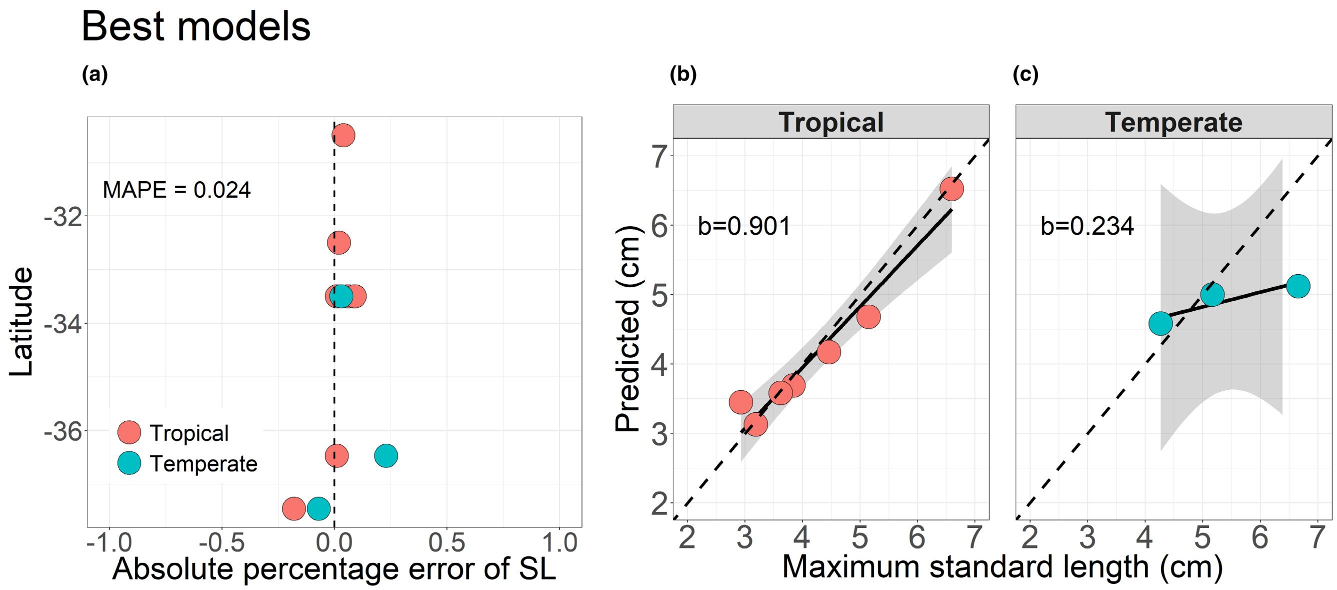


FIGURE 1 Model performance based on absolute percentage error between observed maximum length and predicted length for model with lowest absolute percentage error (i.e., "Best models") (a). Mean absolute percentage error (MAPE) was calculated and shown at top left corner of each plot. Correlations between simulated standard length and observed maximum length for the tropical (b) and temperate species (c). Slope values (*b*) and their significance (*) from a 1:1 relationship (hatched lines) are provided. Shaded areas show 95% confident intervals.

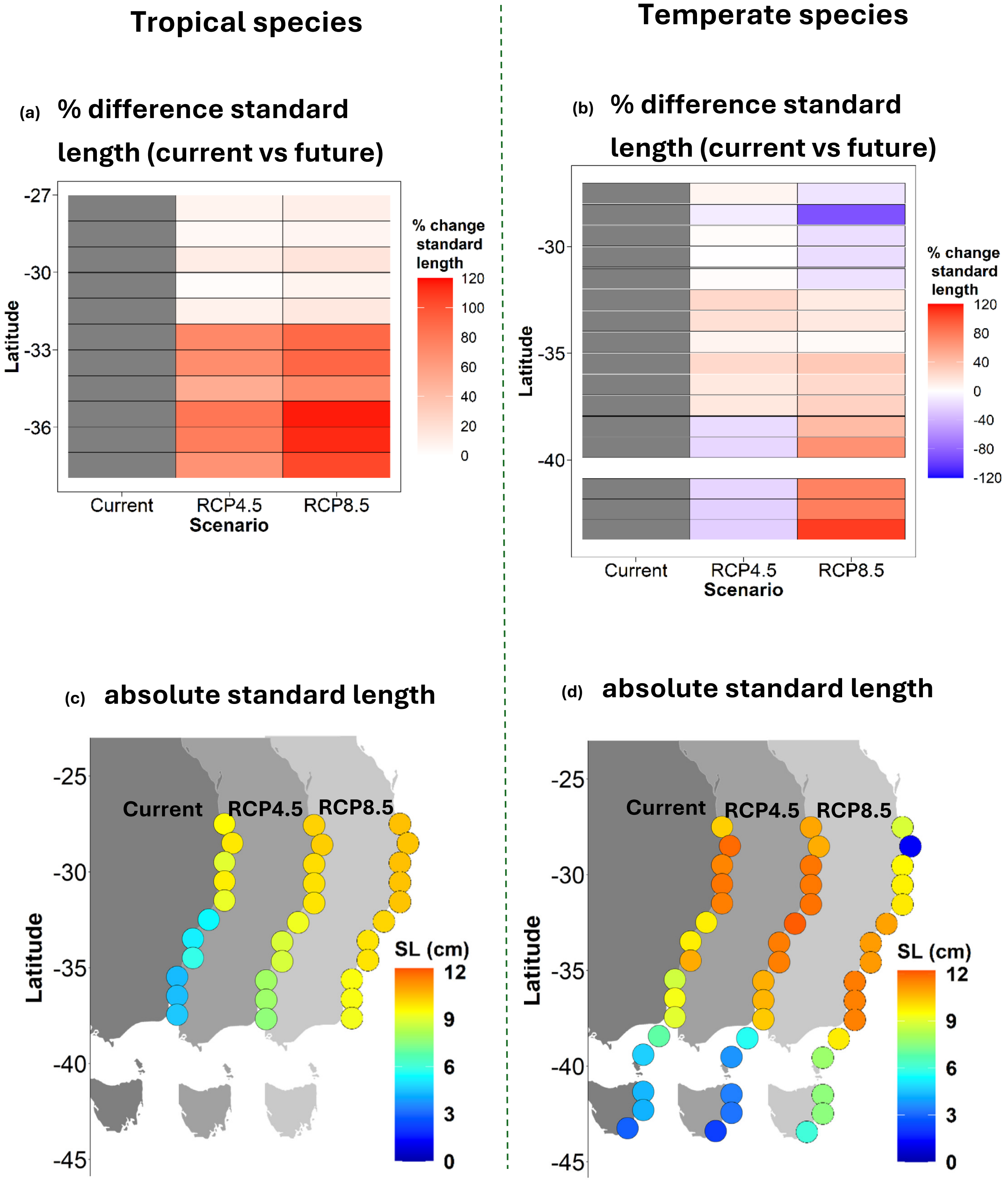


FIGURE 2 Simulated growth length using a model without interaction under a current ("Current") and two future ("RCP4.5" and "RCP8.5") climate change scenarios for the tropical species (a, c) and the temperate species (b, d). The results were expressed as percentage difference ("% difference standard length") in final standard length (SL) between a current and future scenario (calculated as 100 × (future SL − current SL)/current SL) (a, b), and as absolute standard length ("absolute standard length") (c, d). Latitudinal position is shown on the *y*-axis. The current simulation was performed at sites where the species are known to occur along the east coast of Australia (grey area = Australian continent).

tropical species is predicted to reach body lengths larger than that of the juvenile temperate species by 5.8%–15.8% at subtropical to warm-temperate latitudes (27.5–31.5°S) (Figure 2c,d) but not at colder latitudes (32.5–37.5°S). On average across all latitudes simulated, the length difference between the juvenile tropical and temperate species will be reduced from 40.0% under current conditions to 16.0% in the year 2100 under RCP 8.5, and to 21.0% under RCP 4.5.

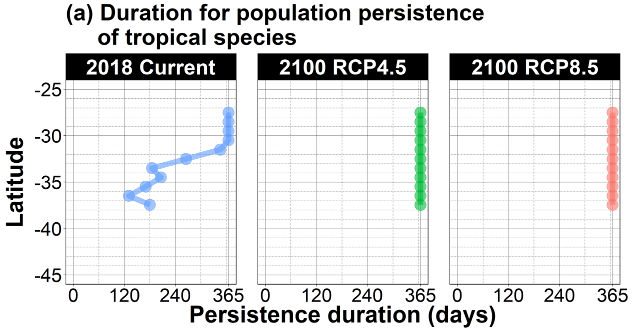
3.3 | The effect of climate change on population persistence (without novel species interactions)

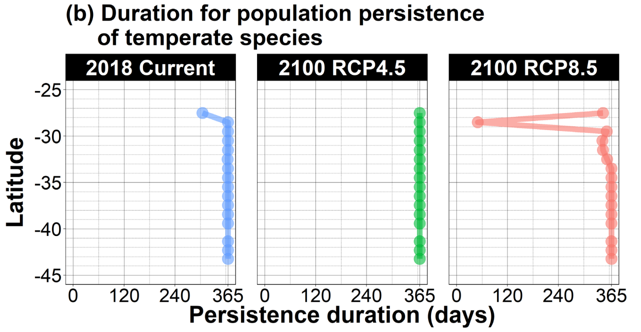
Our model forecasts that the local population persistence of the juvenile tropical species will increase at its cold range edge under RCP 4.5 and 8.5, compared to present-day conditions. Under present-day temperatures, full population persistence (i.e., 365 days) of the juvenile tropical species is only observed in subtropical waters (i.e., 27.5–30.5°S), whereas under RCP 4.5 and RCP 8.5 the juvenile tropical species is predicted to persist throughout the year in both warm- and mild-temperate latitudes (i.e., up to 37.5°S; Figure 3a). In contrast, the model for the juvenile temperate species predicts little to no changes in population persistence across its leading, core and trailing edges (27.5–43.3°S) under either RCP 4.5 or RCP 8.5, except for a reduction from 365 to 50 days at a single subtropical latitude (28.5°S) under RCP 8.5 (Figure 3b) where a highest summer temperature of 30.63°C is forecast.

Idiosyncratic changes in population persistence in response to ocean warming will alter the time window for the two species to interact. At the subtropical latitude of 28.5°S under RCP 8.5, the time window for novel interactions will drop from 365 to 50 days. However, at warm- to mild-temperate latitudes between 32.5 and 37.5°S, the time window for novel interactions between the two species will increase from an average of 189.5 days under current conditions (range between 130–240 days) to 365 days under both RCP 4.5 and RCP 8.5 scenarios (Figure 3c).

3.4 | The effect of novel ecological interactions on body length growth and population persistence

Including novel interactions in the model did not alter the population persistence of either species under either climate change scenario at any latitude studied (Figure S5a,b). In contrast, inclusion of species interactions altered the simulated body length increase of both species. Length of the juvenile tropical species increased when interacting with the juvenile temperate species by an average +25.8, +25.1 and +24.9% under present-day, RCP 4.5 and RCP 8.5 scenarios, respectively (Figure 4a). In contrast, that of the juvenile temperate species was reduced under novel interactions by an average −5.0, −5.9 and −5.3% under present-day, RCP 4.5 and RCP 8.5 scenarios, respectively (Figure 4b).


(a) Duration for population persistence of tropical species


(b) Duration for population persistence of temperate species

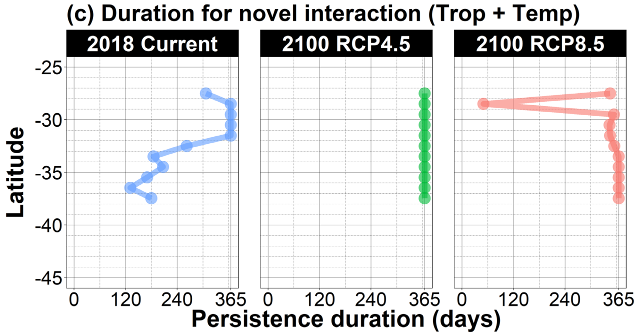

(c) Duration for novel interaction (Trop + Temp)

FIGURE 3 Population persistence for the tropical species (a) and the tempeate species (b) under the current ("2018 Current") and two future ("2100 RCP4.5" and "2100 RCP8.5") climate change scenarios based on a model without species interactions. Latitudinal position is shown on the y-axis and population persistence in days on the x-axis. (c) Duration of novel interactions indicates the total months for which the population persistence of both species overlapped. Colours used for different scenarios: Current (blue), RCP 4.5 (green) and RCP 8.5 (pink) scenarios, respectively.

The model further predicted that the effect of novel species interactions on the change in length growth in both species was greater at subtropical to warm-temperate latitudes (27.5–31.5°S) than warm- to mild-temperate latitudes (32.5–37.5°S) under present-day conditions (Figure 4a,b). This latitudinal pattern in novel interactions effect was observed in the body size of juvenile tropical species. Inclusion of novel interactions in the model simulated the body size of juvenile topical to be larger than that of juvenile temperate species by 7.8% to 26.3% at subtropical to warm-temperate latitudes (27.5–31.5°S) but smaller by 24.9% to 39.9% at warm-temperate to mild-temperate latitudes (32.5–37.5°S) (Figure 4c,d). Under RCP 4.5 scenario, this latitudinal decline effect is predicted to remain for the

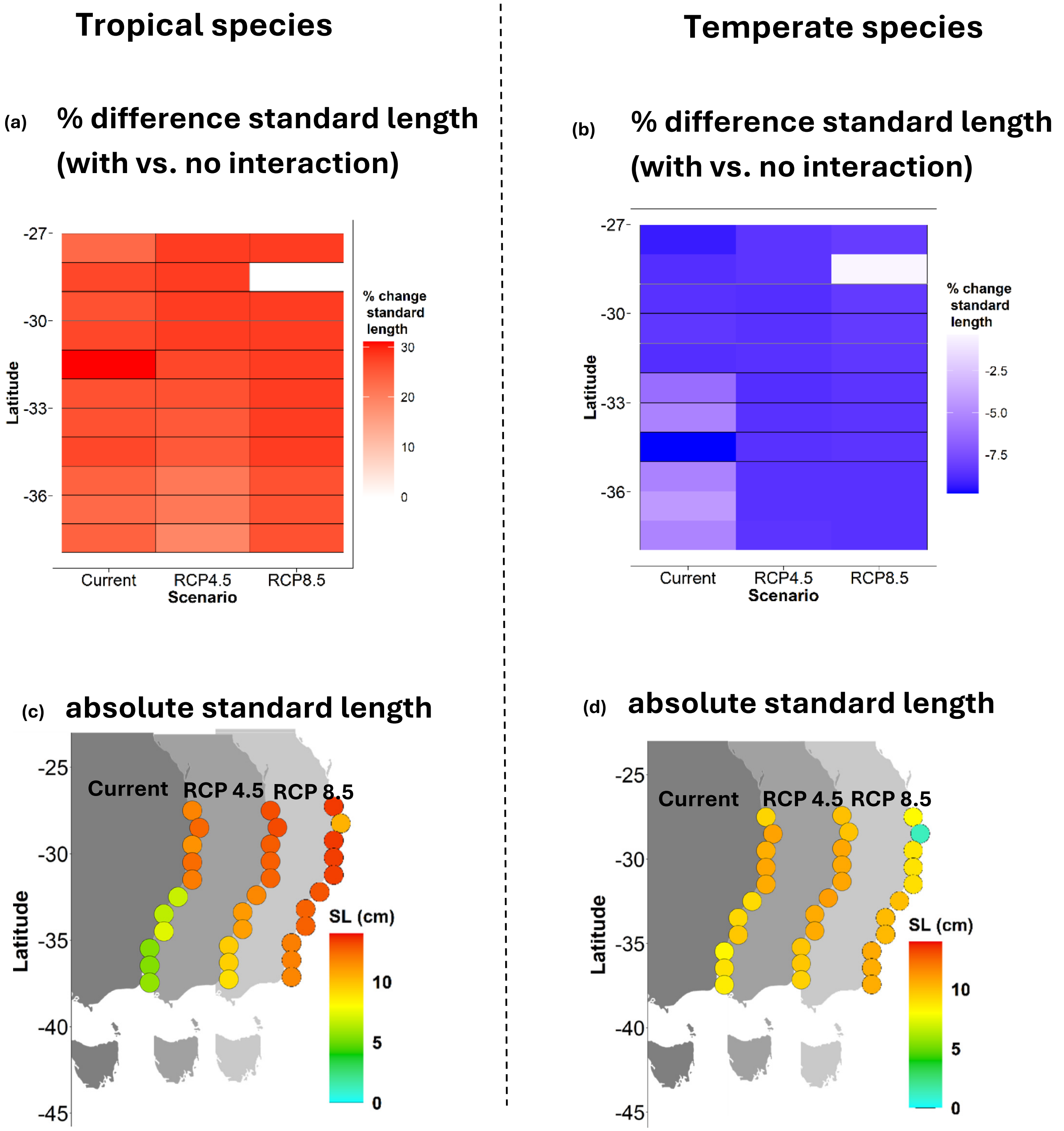


FIGURE 4 Changes in growth length between a model with interaction ("with") and without interaction ("no") under a current ("Current") and two future ("RCP4.5" and "RCP8.5") climate change scenarios for the tropical species (a) and the temperate species (b). The results were expressed as percentage difference ("% difference standard length") in final standard length (SL) between a model with interaction and without interaction (calculated as 100×(SL without interaction − SL with interaction)/SL with interaction) (a, b). The direction of body length change is indicated by different colours: Warm red colours = positive effects, cool blue colours = negative effects, and the magnitude of change in length is indicated by the colour gradients. Simulated absolute standard length using a model with interaction for the tropical species (c) and the temperate species (d). Latitudinal position is shown on the *y*-axis. The current simulation was performed at sites where the species are known to occur along the east coast of Australia (grey area = Australian continent).

juvenile tropical species, but increase at mild-temperate latitudes (27.5–37.5°S) for the juvenile temperate species. Under RCP 8.5, the change in length growth due to species interactions will become similar across latitudes for both species, except at latitude of 28.5°S for the juvenile temperate species (Figure 4b). The juvenile tropical species is predicted to reach body lengths larger than that of the juvenile temperate species by 3.8% to 5.6% at warm-temperate latitudes (32.5–34.5°S) (Figure 4c,d) under RCP 4.5 and by 10.7% to 12.3% at mild-temperate latitudes (35.5–37.5°S). The above patterns closely matched those for the duration for which the two species co-occur (i.e., novel interactions; Figure 3c).

4 | DISCUSSION

To predict the impacts of climate change on juvenile fish growth and their population persistence, we parameterised and used the Dynamic Energy Budget model addressing two factors: species-specific thermally-dependent physiological rates (mediated by abiotic factors) and the effect of novel species interactions (mediated by biotic factors). When simulating the impact of future warming without novel species interactions, our model showed that the juvenile tropical species, *Abudefduf vaigiensis* will likely benefit from future warming in terms of population persistence and magnitude of body length growth at its leading range edge in temperate ecosystems. In contrast, the juvenile temperate species, *Atypichthys strigatus*, is predicted to experience reduced growth at their trailing edge, and even suffer from inability to sustain positive growth during future summer temperatures (based on monthly average temperatures) under an RCP 8.5 scenario. When including the effects of novel species interactions, our model forecasts that these interactions will likely influence the length growth positively for the tropical species but negatively for the temperate species.

4.1 | Species responses to ocean warming

Temperature had significant effects on the population persistence and body length growth in both species within the simulated geographical range. However, due to differences in thermal sensitivity between the tropical and temperature species, future warming will act on them differently. More specifically, warmer winters will improve the yearly growth performance of the juvenile tropical species at its leading cool range edge, whereas warmer summers will reduce that of the juvenile temperate species at its trailing warm range edge.

Increased population persistence and somatic growth in the juvenile tropical species across simulated latitudinal range in the year 2100 agrees with the current understanding that: (1) growth potential of *Abudefduf vaigiensis* is not being fulfilled under current cool temperatures, but that: (2) under warming waters, physiological performance including overwintering (Figueira & Booth, 2010) and growth (Kingsbury et al., 2020) will improve. Under present-day conditions, the abundance of juvenile *A. vaigiensis* drops with decreasing ocean temperatures at increasing latitudes (Figueira & Booth, 2010) and only a fraction of the fish survive through winter in warm- and mild-temperate waters (Booth et al., 2018). Considering the predicted future winter warming, our results suggest that the potential for *A. vaigiensis* colonization along the temperate southeast coast of Australia could greatly increase if greenhouse gas emissions follow the trajectory predicted by RCP 4.5 or RCP 8.5. Although we did not simulate reproduction in the current study, the ability to overwinter and attain maximum (reproductive) body size suggests the potential for *A. vaigiensis* populations to increase with subsequent permanent establishment in most temperate SE Australian regions by the year 2100.

We found that summer ocean temperatures forecast for the year 2100 under an RCP 8.5 scenario will likely exceed the optimal temperature for the temperate species, *Atypichthys strigatus* at its trailing edge of distribution (i.e., at 28.5°S). This appears to result in reduced growth or even in losing thermally suitable habitat at subtropical latitudes. Our prediction is consistent with previous findings that populations of temperate species located at their warm range edge experience a reduction in growth (Neuheimer et al., 2011) or extirpation (Smale & Wernberg, 2013; Wernberg et al., 2013). As growth is aerobic, limited oxygen supply to match required oxygen demand (i.e., aerobic scope) due to thermal stress likely constraints growth (Pörtner & Knust, 2007). Considering that monthly averaged ocean temperature under RCP scenario 4.5 and 8.5 was sufficient to compromise growth performance of the juvenile temperate species at its trailing edges, further impairment of growth can be expected under extreme environmental conditions such as marine heat waves (Van der Walt et al., 2021). Losing thermally suitable habitat at their warm range edge is of great concern for this species as there is no landmass between Tasmania and Antarctica. This may lead to the temperate species having to contract its distributional range to a narrow band of latitudes, as also predicted for other species will eventually run out of suitable climate space (Freeman et al., 2018; Whitfield et al., 2016). However, the temperate species may be able to extend its ranges to deeper colder waters in response to climate stress as reportedly previously for other marine species (Nye et al., 2009; Perry et al., 2005; Pinsky et al., 2013), with *Atypichthys strigatus* shown to occur to depth of 30 m (Bray & Gomon, 2011). Nonetheless, the effect of future warming on the growth rate for this species will still likely be adverse at its trailing edge.

In the current study, we utilized average sea surface temperatures in our simulations; therefore, our results may differ under extreme weather conditions. Global climate change is projected to increase the frequency of extreme weather events (Seneviratne et al., 2021), and some studies have reported that such events can lead to population declines and local extirpations (Maxwell et al., 2019). While long-term exposure to warmer temperatures has been shown to increase ectotherms' critical thermal maximum (upper thermal tolerance of species) (Stewart et al., 2023) and improve aerobic performance at higher temperatures (Donelson et al., 2011), other research indicates that the capacity for maximum thermal tolerance remains relatively conserved even after acclimation to warmer water over multiple generations (Sandblom et al., 2016). If our temperate species are unable to enhance their maximum thermal tolerance in the future, their persistence duration is likely to be reduced during extreme weather events.

4.2 | Species responses to novel ecological interactions

The model predicted that the presence of novel interactions affected the growth rate positively in the juvenile tropical species but negatively in the juvenile temperate species because novel interaction increased functional response of the tropical species but decreased that of the temperate species.

The current modelled responses of novel interactions on juvenile body growth might differ from those in the wild because factors such as prey diversity, prey availability, mortality due to predation, and fish abundances were not accounted for in the laboratory experiment. For example, prey diversity is shown to positively correlate with the degree of food resource partitioning between species (Holbrook & Schmitt, 1989; Sánchez-Hernández et al., 2017). Indeed, in the field where multiple prey species are available, our studied species did not feed on the exact same prey species (Kingsbury et al., 2019). Unlike in nature, the two species were fed one prey species (*Artemia*) in the aquarium experiment, which could have forced two species to interact more often and induced a stronger magnitude of novel interactions (i.e., due to altered feeding conditions). Furthermore, currently available prey species might not be present in the future because of a mismatch in the rate of range shift between predatory fish and zooplankton under warming conditions. For example, copepod species exhibited poleward range shift with a rate of 99 km per decade (Chivers et al., 2017), compared to a rate of poleward extension of 277.5 km per decade for bony fish in general (Poloczanska et al., 2013). The abundance of species has also been reported to affect feeding interactions of our species. A field study revealed that numerically abundant temperate species interfered the tropical species from accessing prey by forming a barrier between the supplied food source and the tropical species (Coni et al., 2021). Likewise, Monaco et al. (2020) demonstrated that density feedback played important role in the growth of *A. vaigiensis* on earlier life stage (i.e., settler and juvenile). Although abundance of immigrants is usually lower than that of the resident fishes (de Souza & Dos Santos, 2023), these previous studies show the importance of fish abundance on the performance rate of the tropical species. As we used one individual of each species in our experiment, abundance-related modification of feeding behaviours was not included in our simulation. Although obtaining species feeding responses using a laboratory experiment was crucial for estimating parameters that are affected by the presence/absence of novel interactions, the ability of the aquarium experiment to replicate fish response in the nature is limited. Consequently, the results from our model should be interpreted according to our aquarium setting (limited resources and equal fish abundances).

4.3 | Overall implications

Our results suggest that some coastal fish species will face drastic changes in their juvenile length growth and population persistence under ocean warming expected to occur at the end of the century in temperate ecosystems if greenhouse gas emissions continue to increase. In a temperature mixing zone where tropical and temperate species co-occur, ocean warming will have opposing effects on species depending on their thermal affinities. This could subsequently alter present-day species interactions with ensuing effects on fish community compositions.

The contrasting growth responses shown by the two species in the subtropics to warm-temperate regions under RCP 8.5 will likely reverse the current body size advantage of the temperate species in the future. Our model forecasts that the juvenile tropical species could grow larger than the juvenile temperate species if the two species recruit at the same time at these latitudes under RCP 8.5 (but not RCP 4.5). The projected reversal in body size or reduction of inter-species body size differences might reshuffle the competitive interactions between tropical and co-schooling temperate fishes as body size has been shown to strongly mediate species interactions (e.g., Wissinger, 1988; Woodward & Hildrew, 2002). For example, in South America the number of attacks made by competitively superior invasive Nile tilapia (*Oreochromis niloticus*) towards native pearl cichlids (*Geophagus brasiliensis*) was greater when the size of tilapia was larger. However, tilapia attacked cichlids significantly less frequently when the size of cichlids was 30% or 50% larger than that of tilapia (Sanches et al., 2012). In our aquarium experiment, the temperate species was on average 21% larger than the tropical species across 16 of 20 mixed-species pairs. Thus, the magnitude of novel species interactions in the experiment was largely based on the case where the temperate species was larger than the tropical species. Alternatively, differences in body size between the tropical and temperate species might facilitate segregation in species interactions because the strength of species interactions can sometimes be higher between similar-sized individuals than different-sized individuals (Woodward & Hildrew, 2002; Kohda et al., 2008).

Warming winter will transform warm- to mild-temperate ecosystems to become more suitable for the juvenile tropical species, likely increasing the temporal duration of novel interactions between the temperate and the tropical species at higher latitudes under RCP 4.5 and 8.5. Relaxing winter environmental filtering with ongoing warming will likely facilitate other vagrant species that are known to occur along the east coast of Australia to overwinter as well and create novel interactions with a range of temperate fishes. For example, vagrant damselfish species from the genus *Abudefduf*, *Pomacentrus* and *Stegastes* displayed minimum temperature thresholds for winter survival of approximately 17°C, similar to our species *A. vaigiensis* (Figueira & Booth, 2010). The same applies to vagrant butterflyfish species from the genus *Chaetodon*, which displayed minimum temperature thresholds of a few degrees higher than *A. vaigiensis* (Figueira & Booth, 2010). Despite such predictions, we still have limited understanding as to how prolonged interactions of surviving tropical species during temperate winters will affect novel species interactions in more realistic communities (Sutton et al., 2021), in particular for competitive interactions (Hughes, 2012).

Although we limited our simulation to the juvenile stage, this does not imply that later stages can be neglected. Changing body size can have carry-over effects onto the next generation. For example, Wootton et al. (2022) showed that smaller-sized female zebrafish under warming displayed larger gonads than same-sized females at control temperatures, thus showing the potential for increased reproductive output under elevated temperatures. Conversely, smaller adult body sizes could also affect reproductive output negatively. For example, a smaller-sized mature female fish has been shown to reproduce disproportionally less than a larger female (Barneche et al., 2018). As such, it is important to assess the effect of changing body size on reproductive output and simulate the consequence of changing body size across generations.

We note that faster juvenile growth forecast in the current model may still lead to reduced maximum body size at later life stage (i.e., temperature-size rule, Atkinson, 1995). Higher but not stressful temperature has been found to shrink maximum body size in natural fish populations more strongly in active fish than sedentary fish (van Rijn et al., 2017). Furthermore, Ikpewe et al. (2021) found that increasing ocean temperatures enhanced length of juveniles of commercial species but decreased that of adults. As the adult stage was excluded from the current model, our findings of larger juvenile lengths for both tropical and temperate species should not directly be linked to adult size.

If the negative effects of novel interactions result in replacing native temperate species, this may lead to functional homogenisation where native species are replaced by non-native species (Olden et al., 2004). For example, our temperate species *Atypichthys strigatus*, is known as a generalist species as well as a facultative cleaner to other reef fish species (Glasby & Kingsford, 1994). Cleaner species provide important functions in the communities, such as enhancing the body condition of fish species (Grutter, 2010; Ros et al., 2020) and increasing fish abundance (Bshary, 2003). Replacement of ecological specialist species by widespread generalist can modify the functional diversity of a community (Olden et al., 2004), and a decrease in functional diversity might diminish overall community and ecosystem functioning (Tilman et al., 1997), stability (Sankaran & McNaughton, 1999) and resistance to environmental change by simply narrowing the available range of species-specific response (Stachowicz et al., 2002). Although the warming-facilitated arrival of range-shifting species can increase species richness in the receiving communities (Hiddink & Ter Hofstede, 2008; Steinbauer et al., 2018; Telwala et al., 2013), it is important to understand the nature of novel interactions and how this may shape functional diversity in the community.

4.4 | Model performance

We found that the accuracy of our model in predicting the effect of changing temperature on fish growth in the field depended on the model design (with or without species interactions). For example, the model without species interaction predicted maximum size of juvenile *A. vaigiensis* at subtropics and mild-temperate better than the model with the interaction, but the latter predicted fish size better at warm-temperate latitudes than at subtropics and mild-temperate (Figure S4). Given that our models already integrated the variation in thermal sensitivity (TA) and feeding rate (*f*), factors other than temperature and the interaction between these two species likely generated the difference between the predicted and the observed maximum body lengths. Indeed, earlier work using the DEB model emphasized that elucidating the factors that are responsible for generating variation in organismal physiological processes is critical for predictions (Alunno-Bruscia et al., 2011; Pecquerie et al., 2009; Stubbs et al., 2020; Thomas & Bacher, 2018). For example, Pecquerie et al. (2009) found that simulating the differences in hatching dates allowed them to obtain large observed variation in length at age 1 of anchovy. In our case, we selected the first of January for the recruitment to begin and initiated the simulation from the selected date consistently across all sampling site for both species. We used a single date instead of multiple dates because of limited understanding regarding the factors causing variation in the timing of recruitment in our species. Although it was possible for us to perform simulations with various recruitment start dates, uncertainty would likely propagate throughout the simulation and cause further difference between observed and predicted sizes, as previously suggested (Ren et al., 2020).

Secondly, our model used standard starvation mode where starved individual use energy for development to pay for somatic maintenance until reserve energy falls below threshold. This starvation mode may differ from realistic energy use because fish are known to have developed alternative strategies for energy allocation under stressful conditions. For example, during prolonged energy deprivation, fish can divert energy from fat storage (short-term starvation) and muscle protein (long-term starvation) (Bar, 2014; Furne & Sanz, 2017). These strategies mean that fish can survive even after losing muscle mass. Unfortunately, the starvation mode in our model did not allow diverting energy from the structural volume to sustain body function. Consequently, simulated individuals died soon after its alternative energy resource, maturity, was exhausted. Our model will greatly improve if we add new parameters accounting for the species-specific changes in energy requirement during starvation (e.g., Monaco et al., 2014). Implementing species-specific starvation mode may clarify the modulating effect of food intake, thus species interaction, on species response to temperature stress, as previously shown (Almeida et al., 2022; Biro et al., 2021; Hedström et al., 2017; Shoup & Wahl, 2011).

Although we could not provide a one-size-fits-all model for predicting in situ growth of the tropical and the temperate species, this does not prevent our models from becoming a useful tool for predicting species performance in the field, as one of our two models still predicted in situ body sizes with a relatively low error rate. We suggest that, rather than relying on a single model, using two models and obtaining a range of body sizes will enhance the ability of our models to predict species response to environmental change that is closely matched with field observations.

4.5 | Conclusions

While the presence of tropical vagrant species in cool temperate regions represent a precursor to poleward range-extension, vagrants are often excluded from predictive models as they are considered as noise. However, because these individuals interact and affect feeding rates of local species, excluding them from the models can neglect the important role of novel species interaction on species growth and population persistence under changing temperatures. We showed that using a dynamic energy budget approach, we can model the responses of tropical and interacting temperate species to future warming and novel interactions that are anticipated to occur in temperate coastal regions. Our study also highlighted the strong asset of the DEB model by showing its ability to simulate changes in fitness-related traits, as opposed to changes in habitat suitability as is the case for correlative species distribution models. Considering the strong link between body size and temperature, our study demonstrated a predictive model that provides a useful platform to simulate important fitness-related traits changes under changing environmental conditions.

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CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Parameters used for simulation is available in Table S2.

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BIOSKETCHES

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Author contributions: Minami Sasaki, David J Booth and Ivan Nagelkerken conceived the ideas for the manuscript. Minami Sasaki analysed the data and simulated the DEB model with help from Cristián J Monaco. Minami Sasaki wrote the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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