Received: 21 August 2021 | Accepted: 7 April 2022

DOI: 10.1111/1365-2656.13739

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Maximization of fitness by phenological and phenotypic plasticity in range expanding rabbitfishes (Siganidae)

Salvador Zarco-Perello[1,2] | **David Fairclough**[3] | **Chris Dowling**[3] | **Joey DiBattista**[4] | **Rachel Austin**[1] | **Thomas Wernberg**[1,5] | **Brett Taylor**[6]

[1]School of Biological Sciences and UWA Oceans Institute, The University of Western Australia, Perth, WA, Australia; [2]Harry Butler Institute, Murdoch University, Perth, WA, Australia; [3]Western Australian Fisheries and Marine Research Laboratories, Department of Primary Industries and Regional Development, Government of Western Australia, North Beach, WA, Australia; [4]Australian Museum Research Institute, Australian Museum, Sydney, NSW, Australia; [5]Institute of Marine Research, His, Norway and [6]University of Guam Marine Laboratory, UOG Station, Mangilao, GU, USA

Correspondence
Salvador Zarco-Perello
Email: salvador.zarco.perello@gmail.com

Funding information
Holsworth Wildlife Research Endowment, Grant/Award Number: RA/1/411/101

Handling Editor: Natalie Jones

Abstract

1. Global warming is modifying the phenology, life-history traits and biogeography of species around the world. Evidence of these effects have increased over recent decades; however, we still have a poor understanding of the possible outcomes of their interplay across global climatic gradients, hindering our ability to accurately predict the consequences of climate change in populations and ecosystems.
2. We examined the effect that changes in biogeography can have on the life-history traits of two of the most successful range-extending fish species in the world: the tropical rabbitfishes *Siganus fuscescens* and *Siganus rivulatus*. Both species have established abundant populations at higher latitudes in the northern and southern hemispheres and have been identified as important ecological engineers with the potential to alter the community structure of seaweed forests (Laminariales and Fucales) in temperate regions.
3. Life-history trait information from across their global distribution was compiled from the published literature and meta-analyses were conducted to assess changes in (i) the onset and duration of reproductive periods, (ii) size at maturity, (iii) fecundity, (iv) growth rates, (v) maximum body sizes and (vi) longevity in populations at the leading edge of range expansion in relation to sea surface temperature and primary productivity (a common proxy for nutritional resource levels).
4. Populations at highest latitudes had shortened their reproductive periods and reduced growth rates, taking longer to reach sexual maturity and maximum sizes, but compensated this with higher fecundity per length class and longer lifespans than populations in warmer environments. Low primary productivity and temperature in the Mediterranean Sea resulted in lower growth rates and

body sizes for *S. rivulatus*, but also lower length at maturity, increasing life-time reproductive output.

5. The results suggest that plasticity in the phenology and life-history traits of range-expanding species would be important to enhance their fitness in high latitude environments, facilitating their persistence and possible further poleward expansions. Quantifying the magnitude and direction of these responses can improve our understanding and ability to forecast species redistributions and its repercussions in the functioning of temperate ecosystems.

KEYWORDS
climate change, global warming, life-history traits, plasticity, rabbitfish, range-shifts, temperature-size-rule, tropicalization

1 | INTRODUCTION

Climate change is affecting the life-histories of terrestrial and marine species across the globe (Pecl et al., 2017). Global warming is forecasted to be irreversible and continue until the end of the century (IPCC, 2021). Temperature is one of the strongest environmental factors affecting the life-histories of living organisms, including physiology, morphology and behaviour (Brown et al., 2004; Sommer, 2020). Warming at the rear and core range distribution of species can reach upper critical thresholds for biological processes, leading to range contractions if populations lack the capacity to respond (Donelson et al., 2019; Hampe & Petit, 2005). Many species are responding to increases in temperatures earlier in the year by advancing their reproductive phenology, allowing their offspring to develop under the best thermal conditions during spring and summer (Burrows et al., 2011; Cohen et al., 2018). Recent evidence also suggests that species are decreasing their average body sizes as a consequence of warming (Baudron et al., 2014; Daufresne et al., 2009; Sheridan & Bickford, 2011). These changes align with the pervasive size-temperature patterns for endotherms (Bergmann's Rule) and ectotherms around the globe (Temperature-Size Rule), which describe a negative relationship between the body dimensions and temperature (Atkinson & Sibly, 1997; Meiri & Dayan, 2003). Biological explanations for these patterns are still debated today but it's generally hypothesized that smaller bodies could cope better with warming by experiencing less physiological stress related to heat-exchange and oxygen-supply for homeotherms and ectothermic aquatic organisms respectively (Verberk et al., 2021).

Global warming is also facilitating the poleward range expansion of many species. Gradual increments in temperature and extreme climatic events, such as heatwaves, are making previously uninhabitable regions more favourable for warm-affinity species at higher latitudes (i.e. poleward; Burrows et al., 2019). This has caused an increase in diversity at several temperate regions of the world, with predictions suggesting that this will accelerate in the future (Chaudhary et al., 2021). Changes in distribution can be beneficial for the conservation of species escaping thermal stress from lower latitudes (Urban, 2020); however, these can have important economic and ecological impacts. Range-shifting can modify natural resources between nations (e.g. fisheries) and create novel biotic interactions that destabilize the functioning and environmental services of receptive ecosystems (Blois et al., 2013; Pecl et al., 2017). Thus, identifying biological traits and ecological processes that allow changes in distribution is currently an important field of research (Sunday et al., 2015; Zettlemoyer & Peterson, 2021).

Populations at the leading edge of range-expansion could experience modifications of their life-history traits to maximize fitness in their novel environment (Atkinson & Sibly, 1997). While increases in mean temperature around the world are important, populations moving poleward would face thermal regimes with greater seasonal fluctuations of temperature (Amarasekare & Simon, 2020; Carbonell et al., 2021). Winters tend to be more severe and longer at higher latitudes, acting as a selective force that dictates developmental rates and survival of early ontogenetic stages (Osland et al., 2021). The establishment of new populations at higher latitudes thus could greatly rely on the successful reproduction and offspring survival through life-history adaptation. Experimental eco-evolutionary studies on microbes and insects have shown that range-expansions can lead to adaptations of behavioural and morphological traits that facilitate expansion by accelerating sexual maturation and increasing dispersal and reproductive output (Miller et al., 2020). For species with longer generational times, phenotypic plasticity could be key for range-expansion (Sommer, 2020; Zettlemoyer & Peterson, 2021). Life-history theory suggests that under longer winter seasons, populations may retard and shorten their reproductive activities to synchronize the rearing of their offspring with the warmest months in the year (Burrows et al., 2011; Cohen et al., 2018). While this would maximize offspring survival, development under lower temperatures would likely result in life-history modifications with trade-offs among different traits. For instance, colder environments can reduce growth rates and retard sexual maturity, but can promote longer life-spans and greater fecundity, leading to individuals that grow larger body sizes and reproduce for longer (Angilletta et al., 2004; Sheridan & Bickford, 2011; Vila-Gispert et al., 2002).

Knowledge of these responses is important because a better understanding of the drivers of species' persistence at higher latitudes could improve the accuracy of forecasts of range-shifts and its consequences for biological conservation and socio-economics (Valladares et al., 2014). However, despite the increase in range-shift studies in recent times, empirical evidence of life-history changes driven by range-expansion is scarce (Donelson et al., 2019). Field based studies are crucial because the magnitude and direction of change in traits will depend on the combined influence of several environmental factors. For instance, food availability is particularly important (the resource availability hypothesis), because poor nutrition results in limited somatic development even under optimal thermal conditions (Geist, 1987; Morales-Castilla et al., 2012). In a literature review of current empirical evidence of trait changes following climate-driven range-expansion, Chuang and Peterson (2016) reported only ten cases of invertebrate species, which mostly focused on one particular trait. To improve our understanding on the magnitude and direction of life-history variation for range-shifting species, we compiled information spanning 67° of latitude and conducted a meta-analysis of the phenological and phenotypic changes of two of the most successful range-expanding species of fish in the northern and southern hemispheres of the world: the rabbitfish (Siganidae) *Siganus fuscescens* and *Siganus rivulatus* (Akiyama et al., 2009; Bariche et al., 2003; Zarco-Perello et al., 2017). Specifically, we assessed how distributional shifts can affect (i) reproductive phenology: the start, peak and duration of their annual spawning period, (ii) batch fecundity (eggs per individual), (iii) minimum size at maturity, (iv) growth rates, (v) maximum body sizes and (vi) longevity. We hypothesized that range-expanding populations will experience (1) shorter spawning periods with onsets later in the year, (2) increases in fecundity factored by fish size, (3) increases in size at maturity and (4) decreases in growth rates that will lead to (5) increases in maximum sizes and longevity, in comparison with populations in warmer regions.

2 | MATERIALS AND METHODS

2.1 | Species of study

Species of the family Siganidae are considered important herbivores and ecological engineers which can influence the community structure of marine ecosystems through high consumption rates of macrophytes (Fox & Bellwood, 2008). Their range-expansion has been identified as a potential threat to the functioning of temperate ecosystems because they can contribute to overgraze the canopy-forming seaweed that constitute the foundation species (Sala et al., 2011; Zarco-Perello et al., 2021). This study focused on two successful range-expanding rabbitfish species. (1) *Siganus fuscescens* (Houttuyn 1782) has expanded its distribution to temperate western Australia following an unprecedented intensification of the Leeuwin Current during a marine heatwave in 2011 (Zarco-Perello et al., 2017, 2019) and to northern Japan following a gradual warming of the Kuroshio Current (Kumagai et al., 2018). (2) *Siganus rivulatus* (Forsskål & Niebuhr 1775) expanded its distribution from the Red Sea into the Mediterranean Sea following the opening of the Suez Canal, and continues to expand further as waters keep warming due to climate change (Azzurro et al., 2017).

2.2 | Data collection

Quantitative information was obtained from the literature using the following two independent search criteria in the Web of Science: {*Siganus OR rabbitfish* AND *reproduction OR fecundity OR spawning*} and {*Siganus OR rabbitfish* AND *size OR length OR growth OR Age OR abundance*}. Publications with useful information were then selected, and the references cited within, as well as the publications that had cited each of these works, were reviewed in turn to obtain more publications that were not detected by the initial online searches. *Siganus fuscescens* and *Siganus canaliculatus* were considered synonyms and data from studies of these were pooled (Hsu et al., 2011). In total, we obtained 46 studies related to reproduction, 14 studies related to growth and 91 studies related to body size (including studies that included both reproduction and growth). Data collected for *S. fuscescens* spanned tropical, subtropical and temperate environments across the Indian and Pacific Oceans, whereas data for *Siganus rivulatus* spanned subtropical and temperate environments across the Red Sea and Mediterranean Sea (Figure 1 and Table S1). Data were extracted from tables and scatterplot figures using the software DataThief (Flower et al., 2016). In all cases, length was standardized to fork length (FL) using the length-length equations reported in FishBase for *S. fuscesens* (Froese & Pauly, 2019), and by Shakman et al. (2008) for *S. rivulatus*.

2.3 | Reproduction

Information about the annual onset, period and peak of spawning (specific months and duration), its relationship with the moon cycle, minimum length at maturity (mm) and fecundity was extracted only from studies (n = 18) with consistent monthly sampling across the year, which determined reproductive stages by macroscopic examination of gonads, gonadosomatic index (GSI = [gonad weight/body weight] × 100) and batch fecundity (gravimetric total number of ripe eggs per individual = Eggs in gonad subsample × total gonad weight/gonad subsample weight) across multiple length classes of female fish (Table S1).

2.4 | Growth and longevity

Information on growth and longevity for both species of rabbitfish was only extracted from studies that reported growth curves based on length-at-age information produced from the analysis of sectioned sagittal otoliths of females and males. In addition, we estimated length-at-age information for populations of *S. fuscescens*

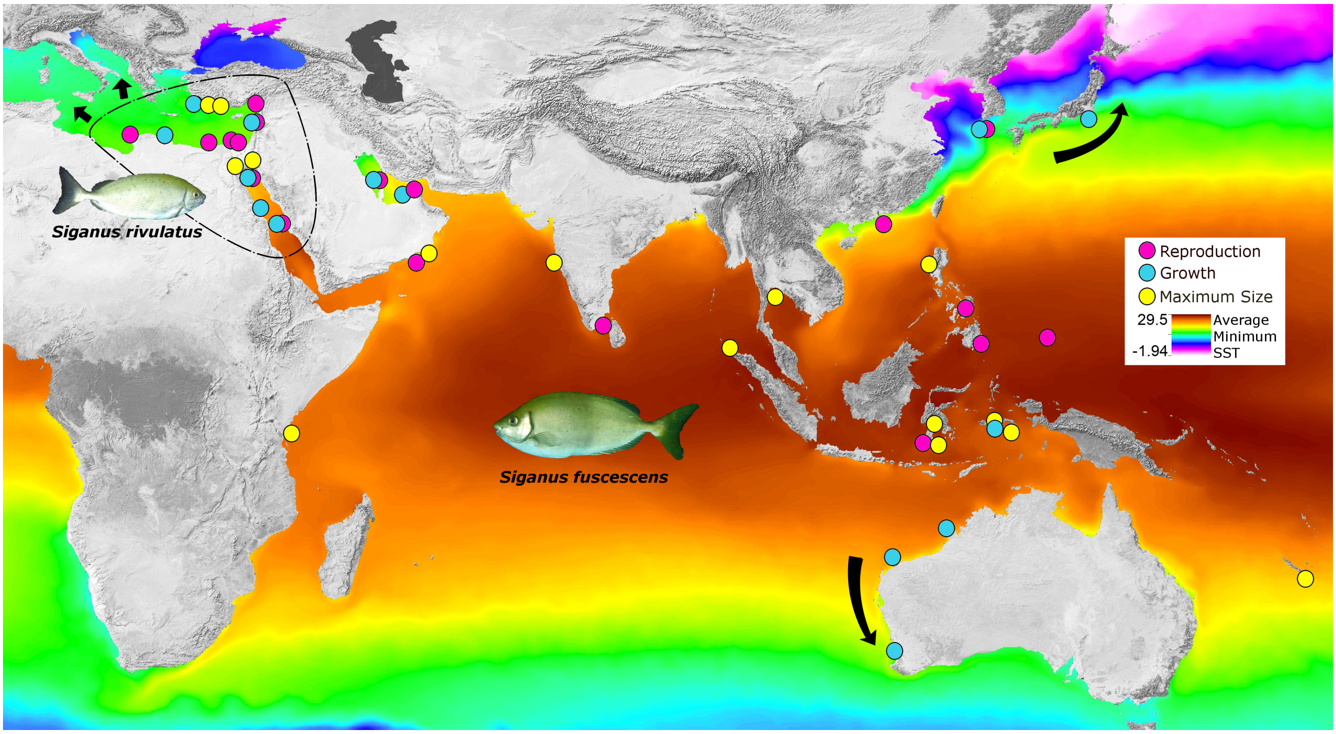

FIGURE 1 Sampling locations of information collected from the literature on reproduction (spawning and fecundity), growth rates, maximum length and longevity of *Siganus rivulatus* and *Siganus fuscescens*. Maximum body size information was also obtained from studies that included both reproduction and growth. Arrows indicate the direction of range expansion towards temperate environments

from temperate (Perth) and tropical environments (Pilbara and Kimberley) of Western Australia (WA). Temperate WA specimens (n = 387) were collected from 2012 to 2017 by hand seine net (Department of Primary Industries and Regional Development; DPIRD), purse-seine (donated by commercial fishermen) and spear-fishing (approval AEC201527 by the Animal Ethic Committee of Curtin University given to DiBattista J.), while tropical WA specimens from the Pilbara ($n = 62$) and Kimberley ($n = 109$) were caught between 2014 to 2017 with trawl nets by DPIRD vessels (Table S2). The total length and fork lengths of all specimens were measured (mm) and their sagittal otoliths extracted, dried, mounted on a microscope glass slide with thermoplastic resin (Crystal Bond) and grinded transversally with lapping film (30 µm) to the nucleus to expose its opaque and translucent bands (Taylor et al., 2017). The opaque bands in each otolith were counted under low-power magnification with reflected light against a black background (Figure S1). The final count was determined by a third independent reading of the otoliths and only values that matched any of the two previous readings were retained. The spawning period was determined based on the temperature-spawning patterns found in the global literature review about reproduction (see previous section). These were set as January–February for Perth, December–January for Pilbara and November for the Kimberley region; the estimated spawning dates in each year were assigned as 1 week after the new moon based on literature (Table S1). The spawning date, date of capture and count of opaque bands were used to determine decimal ages for all individuals.

von Bertalanffy growth curves (VBGF) were fitted to the length-at-age data (both sexes pooled) for (i) each climate (Tropical: 0–23°, Subtropical: 23–30°, Temperate: >30 °) and for (ii) each location independently for both species (Table S2), based on the original VBGF parameterization using the R package FSA (Ogle et al., 2020; R Core Team, 2019):

$$L \mid t] = L^{\infty} - (L^{\infty} - L0)^{-Kt,}$$

where $L|t]$ is the expected length at age t, $L\infty$ is the asymptotic length, K is the growth rate coefficient (year − 1) and $L0$ is the expected mean length at time zero (recruitment). Parameter values were estimated with non-parametric bootstrapping using the R package NLSTOOLS (Baty et al., 2015), except for L0 which was constrained to reported values of length at recruitment (age zero) for *S. fuscescens* (50 mm) and *S. rivulatus* (30 mm) to allow for a better comparison of the growth trajectories among locations (Bariche et al., 2004; Kanashiro et al., 1999). Average annual growth (mm/year) was extracted from the VBGF of each location for the years (age) shared by all climates for each species and used for statistical analyses. Longevity was estimated as the maximum age reported in each study of the literature review and the otolith analyzes of western Australia.

2.5 | Maximum size

Information about maximum size attained across different climate regimes for *S. fuscescens* was obtained from 45 studies reporting abundance and body length, which spanned 67 degrees of latitude (32°S–35°N) from Perth in Australia to Tateyama Bay in Japan; while 30 studies were obtained for *S. rivulatus*, spanning 10 degrees of latitude (28°N–39°N), from Jeddah in Saudi Arabia to Akbuk in Turkey (Figure 1 and Table S3). Only studies that reported extensive sampling of individuals per location were considered ($n > 30$), including the studies of reproduction and growth. The maximum length reported in each published work was extracted for statistical analyses.

2.6 | Environmental variables

Time-series of environmental data spanning the time frames of each study of reproduction and growth rates of *S. fuscescens* and *S. rivulatus* were obtained from the European Union's Copernicus Marine Service (EU's Earth Observation, 2021) for average (m), maximum (i.e. summer: max) and minimum (i.e. winter: min) monthly sea surface temperature (SST; C°) and primary productivity (mg m^{-2} day^{-1}) from the products GLORYS12V1 (1/12° horizontal resolution), GLOBAL_REANALYSIS_BIO_001_029 (1/4° horizontal resolution) and OCEANCOLOUR_GLO_CHL_L4 (1/27° horizontal resolution). For the analyses of maximum body size and longevity across temperature gradients, we obtained the long-term temperature variables for each location from the database BioOracle (Assis et al., 2018).

2.7 | Statistical analyses

The duration of spawning periods (number of months), onset of spawning (month of the year when spawning starts), minimum length at maturity and maximum body size were analysed with generalized linear models (GLM) using the R package STATS (R Core Team, 2019). Changes in traits were correlated with SSTm, SSTmin and SSTmax. However, collinearity among temperature covariates was detected with scatterplots and Spearman's rank correlation coefficients and only SSTmin was selected as predictor due to its stronger correlation with the dependent variables and its greater significance for physiological processes and life-history traits across latitude (Osland et al., 2021; Taylor et al., 2019). Changes in fecundity were analysed with GLMs considering an interaction between fork length and climate (temperate, subtropical and tropical). The change of longevity across temperature (SSTmin) was analysed with generalized linear mixed models (GLMM) including "study" as random factor with the R package *lme4* (Bates et al., 2015) and linear mixed quantile regression (QLMM) to the 80th and 90th percentile of the age distribution using the R package LQMM to evaluate differences specifically in the maximum ages attained by each population (Geraci, 2014).

Changes in growth rates were evaluated with GLMs considering primary productivity (proxy for food abundance and nutrition) and temperature as explanatory covariates interacting with age. For the analyses of *S. fuscescens*, most of the covariates had collinearity, except between SSTmin and mean primary productivity (PPm, mg m^{-2} day^{-1}); thus, only these variables were used. Whereas in the case of *S. rivulatus*, all covariates had collinearity, masking the effect of each other on growth rates; thus, we carried independent analyses considering SSTmin and PPm as explanatory variables across different ages.

In all cases, model fit was checked with AICc, graphical examination of predicted versus observed values and dispersion tests using the R package *DHARMa* (Hartig, 2020) and p-values were calculated with likelihood ratio tests with the R package LME4.

3 | RESULTS

3.1 | Reproductive life-history traits

The timing of the spawning periods of *S. fuscescens* differed between climates, with earlier reproductive onsets in warmer environments (GLM, $p < 0.01$, $t = 6.01$; Figure 2a,c). In tropical locations, there were usually two spawning periods per year, starting in December–January followed by June–July. However, spawning began at colder winters (i.e. higher latitudes, Figure S2) only when temperatures increased above 20°C, in March–April at subtropical locations and in July–August at temperate locations, representing a phenological shift of 6 months from tropical regions. Similar patterns were observed for *Siganus rivulatus*, where subtropical and temperate populations began to spawn in March–May in the Red Sea and June–July in the Mediterranean Sea, representing a shift of 2 months for the onset of reproduction (GLM, $p < 0.01$, $t = -7.7$; Figure 2b,d).

The duration of the spawning period for both species had a significant positive correlation with winter temperatures, where populations had shorter spawning periods as temperature decreased (GLM, $p < 0.01$, $t = 7.1$; Figure 2e). *Siganus fuscescens* in the tropics had spawning periods of up to 7 months, while in subtropical and temperate locations, they lasted between 3–4 months and only 2 months, respectively. Similarly, the spawning period of *S. rivulatus* in the Red Sea lasted 4–7 months, whereas at higher latitudes in the Mediterranean Sea, this was reduced to 1–2 months (GLM, $p < 0.01$, $t = 4.0$; Figure 2f).

Minimum length at maturity (MLM) for *S. fuscescens* had a significant negative correlation with SSTmin (GLM, $p = 0.01$, $t = -3.8$; Figure 3a). Reproductive *S. fuscescens* in the tropics (5°S–10°N) were as small as 120 ± 14 mm in length, whereas fish matured at lengths of 150 ± 10 mm in the subtropics (22–27°N) and 199 ± 31 mm in temperate locations (33–35°N). This relationship was not found across the latitudinal range of *S. rivulatus* (GLM, $p = 0.7$, $t = -0.03$; Figure 3b), where MLM did not differ significantly between populations in the Red Sea (21°N, 125 ± 13 mm) and the Mediterranean Sea (37°N, 133 ± 6 mm).

Fecundity varied according to the interaction between fish length and climate (GLMs, $p < 0.01$; Figure 3c,d). Populations of *S. fuscescens* in temperate locations had the highest number of eggs per individual on average across all fish length classes. The highest batch fecundity at maximum lengths (350 mm) in the tropics was

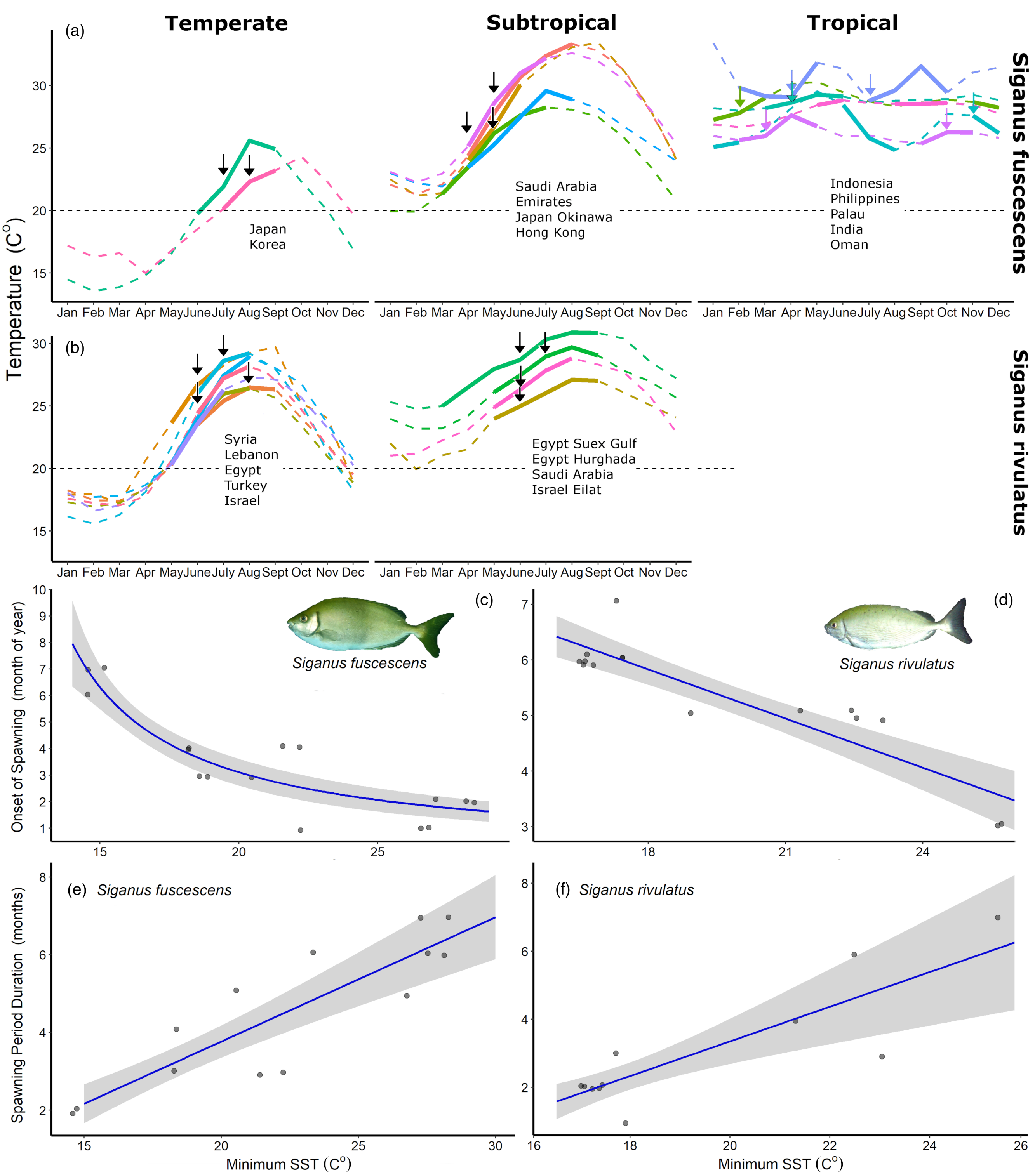

FIGURE 2 Period (continuous lines) and peak of spawning (arrows) with respect to sea surface temperature fluctuations (dashed lines; a, b), onset of annual spawning (c, d) and duration of spawning period (e, f) across minimum annual temperature in different climate regimes for the rabbitfish *Siganus fuscescens* and *Siganus rivulatus*. Error bands represent 95% confidence intervals of the regressions calculated with the function "predict" of the R package STATS

661,251 eggs ind-1, which was significantly lower than subtropical (1,164,209 eggs ind-1) and temperate individuals (1,063,377 eggs ind-1) of the same length (Figure 3c). Populations of *S. rivulatus* from temperate climates had higher average fecundity than populations of the Red Sea, but only at higher length classes (Figure 3d). The highest fecundity reported at subtropical locations was 488,408 eggs ind-1, while at temperate locations was 937,568 eggs ind-1 at comparable lengths (227 mm).

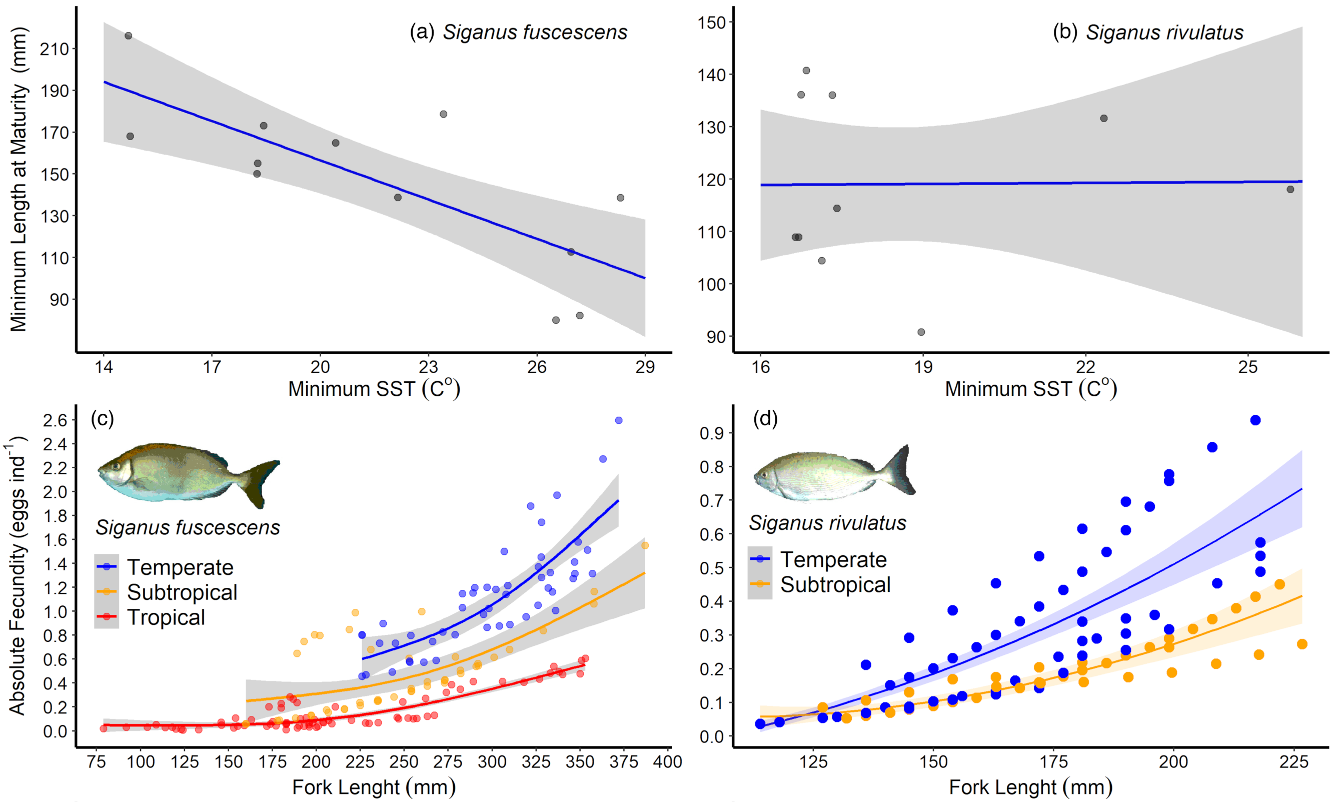

FIGURE 3 Relationships between minimum length at maturity across minimum annual temperature (a, b) and fecundity (millions of eggs) and fork length interacting with climate (c, d) for the range-extending rabbitfish *Siganus fuscescens* and *Siganus rivulatus*. Error bands represent 95% confidence intervals of the regressions derived from the function "predict" of the R package STATS

3.2 | Growth rates, maximum size and longevity

Temperate populations of *S. fuscescens* had lower von Bertalanffy growth coefficients (k, 0.4–0.6) but higher asymptotic lengths ($L\infty$, 300–326 mm) than subtropical (0.58–0.8, 300 mm) and tropical populations (1–1.16, 250–256 mm; Figure 4a, Table S2). Growth rates in the first year of life were higher in the tropics (153 ± 21 mm), followed by the subtropical (134 ± 7.9 mm) and temperate populations (103 ± 8.6 mm). However, by the second year, length increments of tropical fish fell below other regions, and by the third and subsequent years, temperate populations had the highest growth rates (Figure 4c). This resulted in a significant interaction between SSTmin and Age (GLM, $p = 0.018$), where individuals grew faster under the warmer winter conditions of the tropics but only during their first year of life (Figure 4e). Primary productivity (PPm) varied widely across the range of sampling locations but was not significantly related to growth rates (GLM, $p = 0.53$, Table S4, Figure 4g).

On the other hand, temperate populations of *S. rivulatus* had lower *k* coefficients (0.14–0.27) and $L\infty$ (252–310 mm) than subtropical populations (0.33–0.72; 273–336 mm; Table S2, Figure 4b). Growth rates in the first year of life were higher in the subtropical (100 ± 13.8 mm) versus the temperate locations (48.4 ± 7.9 mm), and this was maintained in the second (60.7 ± 3.4 vs. 38.4 ± 5.5 mm) and third years (37.8 ± 4.6 vs. 30.5 ± 3.8 mm), except for the fastest growing population in the Red Sea (Shalatein, Egypt), which also had the steepest decrease in growth rate with age, having lower length increments than temperate populations by the fourth year. The growth in other subtropical populations equaled those of temperate populations until the fifth year (20 ± 1 vs. 19.4 ± 1.7 mm; Figure 4d). SSTmin and PPm were higher in subtropical regions and both had a significant relationship with growth rates and significant interactions with age in independent statistical tests (GLM, $p < 0.05$, Table S4, Figure 4f,h).

The maximum sizes of *S. fuscescens* had a significant negative correlation with SSTmin, where biggest sizes were found in colder climates (GLM, $p < 0.01$, $t = -7.8$; Figure 5a). Similarly, longevity increased as winters got colder, from up to 3 years of age in the tropics to 8 years in the subtropics and 13 years in temperate locations at the highest latitude ($QLM_{0.9}$, $p < 0.01$; GLM, $p < 0.01$, $t = -5.7$; Figure 5c). The maximum sizes of *S. rivulatus* had a significant positive correlation with SSTmin, achieving bigger body sizes in warmer climates (GLM, $p < 0.01$, $t = 3.2$; Figure 5b), while longevity increased from 4–5 years in the subtropics to 10 years in the coldest temperate location ($QLM_{0.8}$, $p < 0.01$; GLM, $p < 0.01$, $t = 3.3$; Figure 5h).

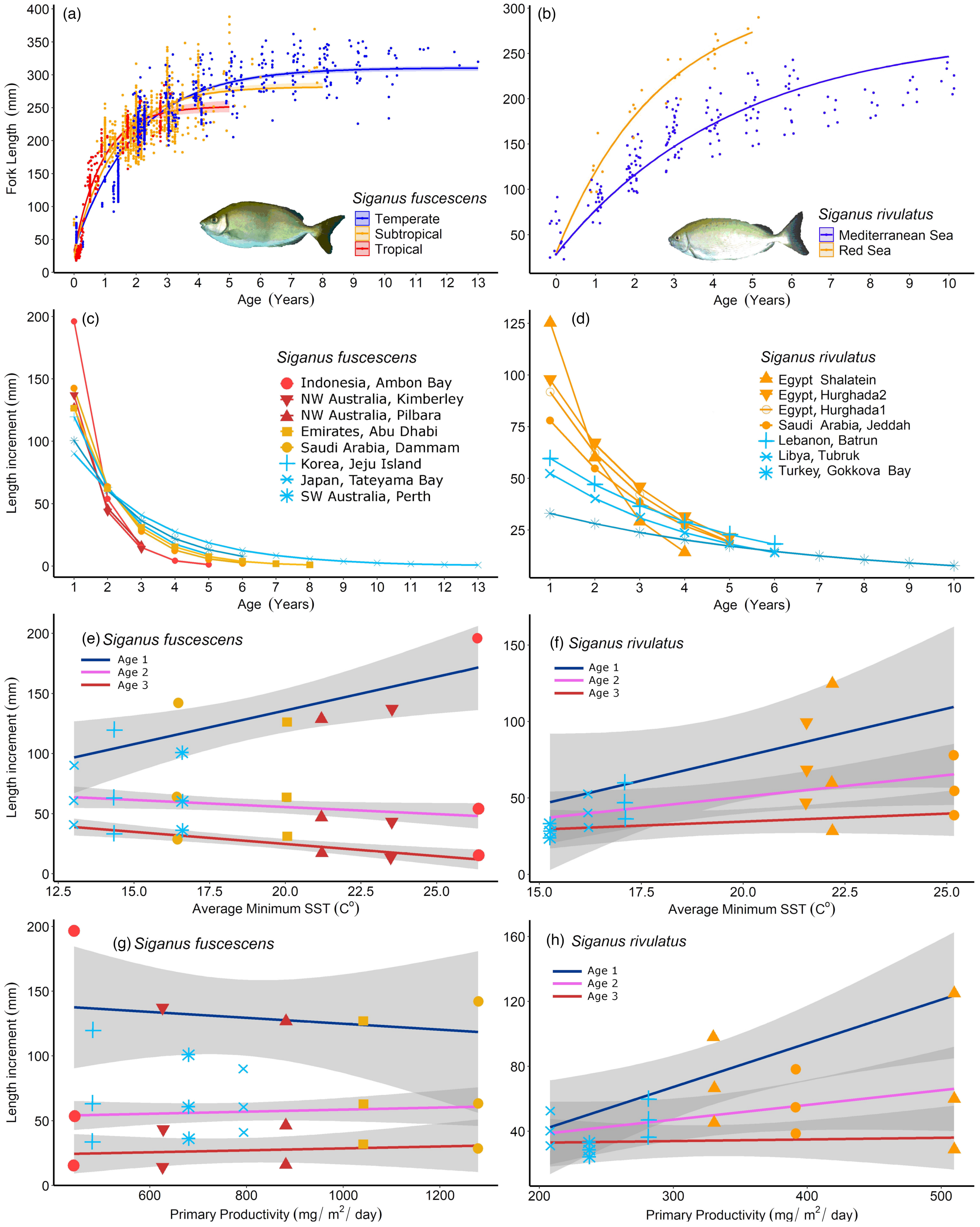

FIGURE 4 von Bertalanffy growth curves (a, b), corresponding average length increments by age (c, d) and the effect of winter temperatures (e, f) and primary productivity (g, h) on growth rates across latitude as reported in the literature for the rabbitfish *Siganus fuscescens* and *Siganus rivulatus* in temperate, subtropical and tropical locations. Maximum age reported in the tropics in panel A was 3 y/o, further years represent predicted length. Error bands represent 95% confidence intervals of the regressions derived from bootstrapping using the R package NLSTOOLS for von Bertalanffy growth curves and the function "predict" of the R package STATS for panels e–h

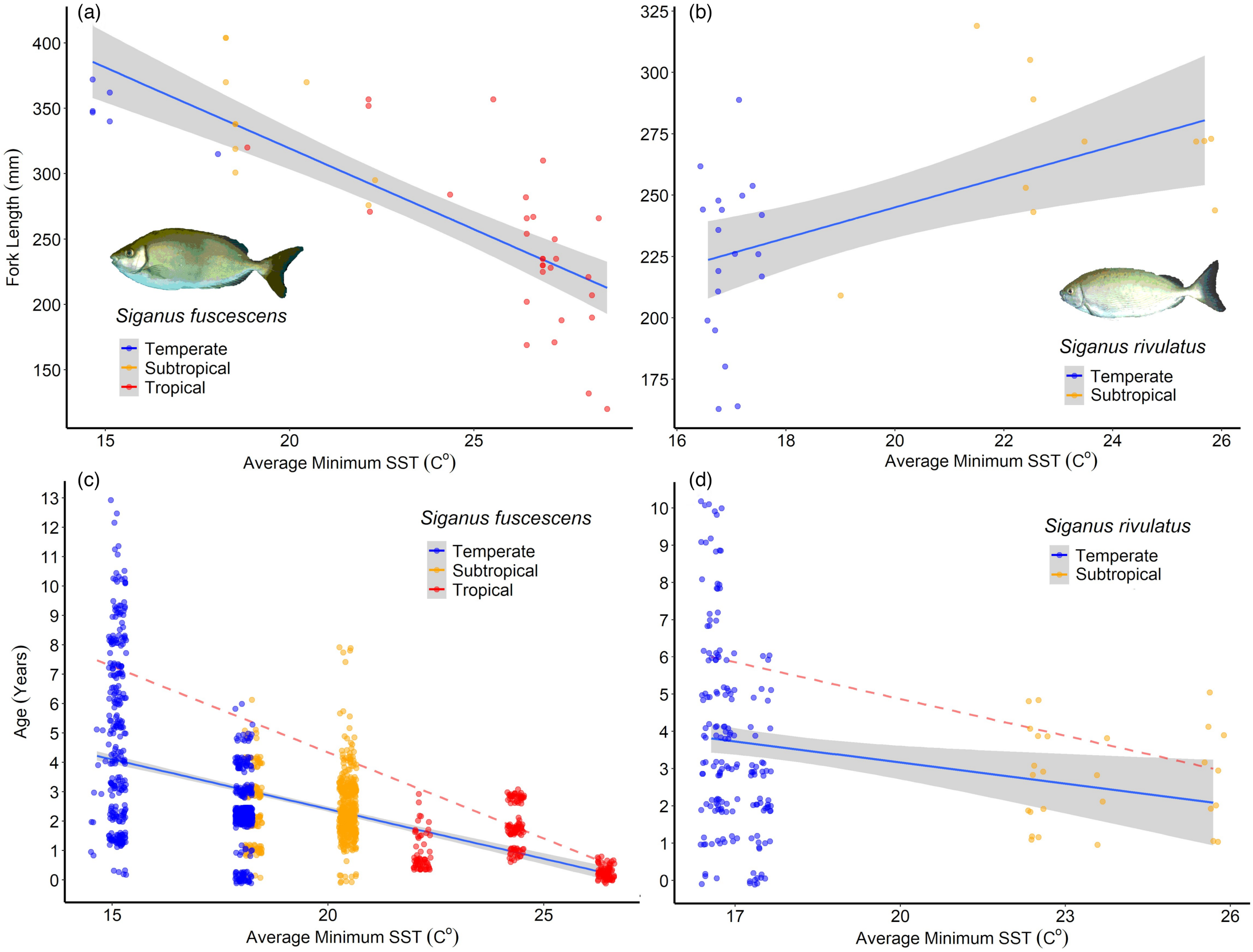

FIGURE 5 Relationships between maximum body size (a, b) and longevity (c, d) of the range-expanding rabbitfish *Siganus fuscescens* and *Siganus rivulatus* with winter sea surface temperature in temperate, subtropical and tropical locations across their global distributions. Dashed lines in c and d represent quantile regression at the 90th percentile. Error bands represent 95% confidence intervals of the regressions derived from the function "predict" of the R package STATS

4 | DISCUSSION

In this study, we sought to advance our understanding on how life-history traits can change in response to shifts in distribution to higher latitudes. For this, we analysed how the phenology and life-history traits of two of the most successful range-expanding species of fish differed between their original warmer ecosystems and their temperate habitats. We found that most of our hypotheses were supported, with a few exceptions, as temperature and primary productivity changed across time (age) and space.

Our results on phenological changes showed that populations at the leading edge of range expansion had shorter reproductive periods with later onsets, similar to previous findings (Slesinger et al., 2021). Shorter reproductive periods at higher latitudes are suggested to be an adaptation to the seasonality of physical and biological factors. Restricting spawning within the best conditions of temperature and food availability for larval development increases chances of survival, thereby maximizing recruitment success (Conover, 1992; Pankhurst & Porter, 2003). Many fish species at high latitudes spawn in spring and early summer, when temperatures are increasing, allowing longer growing seasons for their recruits and the ability to reach larger sizes. This increases their capacity to survive low temperatures and starvation and minimizes predation during the following winter (Sogard, 1997). Progeny spawned in late summer or autumn would be exposed to low and potentially lethal temperatures in the subsequent winter, leading to higher mortality rates (Hurst, 2007). We found that the spawning periods of rabbitfish populations started earlier and were reduced as winter temperatures decreased with increased latitude. Thermal seasonality in tropical regions was very low, within temperatures linked with peak spawning for *S. fuscescens* (~28°C). This results in long reproductive periods with bimodal peaks of spawning, similar to other species of rabbitfish in the tropics (Taylor et al., 2017). On the other hand, rabbitfish experienced wide seasonal fluctuations in subtropical and temperate regions and lower temperatures associated with peak spawning, restricting their reproductive periods to the months when temperatures increased, becoming strict spring-spawners (Pankhurst & Porter, 2003). Differences were lower between temperate and subtropical populations of *S. rivulatus* (1–3 vs. 4–7 months, respectively), likely because maximum temperatures in the temperate Mediterranean Sea can reach similar values to the subtropical Red Sea during summer. However, increases and decreases in temperature are steeper in the temperate locations, providing narrower thermal windows for reproduction and growth, influencing the onset and duration of the spawning period.

The shorter spawning periods of populations of rabbitfish at higher latitudes were potentially compensated with an increase in fecundity per fish length, supporting our second hypothesis stating that range-shifting populations would experience an acceleration in oogenesis. This trend has been found in other freshwater and marine species, where tropical populations have longer spawning seasons but lower fecundity (Vila-Gispert et al., 2002). The fecundity of both species of rabbitfish followed a similar pattern, where larger fish and colder winters resulted in higher egg production. Temperate populations of *S. fuscescens* had twice the fecundity in the smaller length class (FL, 220–250 mm) and three times greater fecundity at the biggest length class (300–350 mm) versus tropical populations; while differences between temperate and subtropical populations remained relatively stable across all length classes (1.5–1.8×). Similarly, the fecundity of temperate populations of *S. rivulatus* was higher by 1.4× in the lowest length class (110–150 mm) and by 2× in the biggest length class (>200 mm) vs subtropical populations. Fecundity has direct implications for recruitment success in natural environments; and greater egg production can compensate for narrower reproductive windows in colder climates (Conover, 1992). Faster egg production seems to start immediately after reaching maturity in both species of rabbitfish, thus, this can have important implications in the energy allocation for other biological processes, which are significantly modulated by temperature and nutrition (McBride et al., 2015).

Changes in the other life-history traits of *S. fuscescens* across the thermal gradient of its geographic distribution fit the expected patterns predicted by the temperature-size rule (TSR), corroborating the rest of our hypotheses. The biological processes explaining the TRS are still under debate; however, recent evidence supports the hypothesis that aquatic ectotherms with bigger bodies have limitations of oxygen supply under warmer environments (Verberk et al., 2021). This suggests that there might be selective pressures on individuals with genotypes prone to suffer oxygen supply limitations, favouring smaller body sizes and earlier maturity in warm environments (Pauly, 2021; Rubalcaba et al., 2020). Energetic cost of oogenesis is high and its oxygen requirements are added to those of somatic maintenance and routine activities, reducing the aerobic scope of organisms and prompting earlier sexual maturation in warmer environments before reaching untenable levels of respiratory distress (Forster et al., 2012; Pauly, 2021). The growth patterns of *S. fuscescens* across climates corroborated this, whereby tropical populations had faster initial growth but asymptoted to reach maturity sooner at smaller sizes compared with range-expanding populations experiencing colder winters. Higher latitude populations had lower growth rates, greater length/age at maturity, longer maximum sizes and lifespans.

Patterns of change in the life-history traits of *S. rivulatus* across climates did not meet the predicted outcomes by the TSR, except for changes in longevity. Range-extending populations had lower growth rates as expected; however, this did not translate into bigger body sizes and length at maturity than subtropical populations. A plausible explanation could be the differences found in primary productivity and temperatures between regions. The Mediterranean Sea is considered one of the seas with lower levels of nutrients in the world (Azov, 1991) and in combination with low temperatures could result in smaller bodies (Atkinson & Sibly, 1997; Munday et al., 2008), maturation earlier than expected and increased longevity (Berrigan & Charnov, 1994; Perrin, 1995). Reaching maturity sooner could be a life-history adaptation to maximize their life-time reproductive output (Berrigan & Charnov, 1994). Unlike populations living in warmer climates, temperate populations would not have limitations of aerobic scope, since metabolic rates would be low; however, given their very slow growth rates, reaching maturity at bigger sizes, as predicted by the TSR, would shorten their overall reproductive output considerably, carrying a high cost in fitness. For instance, maturing at the same size as temperate populations of *S. fuscescens* (200 mm) would take 5 years, risking complete reproductive failure for those individuals that perish before reaching maturation. This agrees with previous meta-analyses where a positive relationship was found between age at maturity and maximum age for all species of fish worldwide (Thorson et al., 2017).

The observed changes in longevity agreed with our hypothesis, where expanding populations of *S. rivulatus* and *S. fuscescens* experiencing the coldest winters had the oldest individuals (10–13 y/o respectively), in comparison with subtropical (5–8 y/o) and tropical populations (1–3 y/o). This pattern has been described for ectotherms and endotherms (Lee et al., 2013; Rollo, 2002; Taylor et al., 2019), and its possible causes have been linked to intrinsic (senescence) and extrinsic processes (mortality rates) which can be modulated by temperature, such as higher cellular oxidative damage (Burraco et al., 2020) and higher predation rates in warmer environments related to higher metabolic demands in carnivorous species (Lima & Dill, 1990; Werner & Anholt, 1993). Predation rates on rabbitfish at the leading edge of range expansion is uncertain, since populations will interact with new and heterogeneous communities of predators in each location. Nonetheless, predation may be low given that rabbitfish possess poisonous spines and because native predators may not recognize them as prey (HilleRisLambers et al., 2013).

Fishing, like predation, increases mortality rates and can affect the size and age structure of fish populations in synergy with environmental variables (Ahti et al., 2020; Hunter et al., 2015; Morrongiello et al., 2021). We could not perform quantitative analyses of its effect in our study because species-specific information on fisheries landings of rabbitfish is lacking around the world; the Food and Agriculture Organization of the United Nations reports total yearly catches at low taxonomic (family) and geographic resolution (country; FAO-FIGIS, 2019). However, available evidence indicates that this could have a minimal impact in the general patterns found. For instance, in Western Australia rabbitfish are not commonly targeted and only are caught as bycatch, yet the patterns between tropical and range-extending populations held. Fisheries effect on the traits of *S. rivulatus* may be low in the Red Sea, because individuals were larger (>250 mm) despite that trammel nets used in the region select for fishes >150 mm (Saber & Gewida, 2020); however, we cannot discard a potential fishery effect in the Mediterranean Sea since nets target fishes >200 mm, which could include the oldest and bigger individuals (Cerim et al., 2020; Soykan, 2020). Nonetheless, the global analyses of maximum sizes were robust. For instance, of the 45 studies examined about *S. fuscescens* across climates, maximum sizes below 250 mm were only reported in tropical locations from a total sample of 54,634 individuals. Likewise, of the 30 studies of *S. rivulatus*, maximum sizes below 200 mm were only reported in temperate locations from 32,563 fish individuals.

Climate change is influencing fish phenology, life-history traits and geographic distributions. Our results showed that these responses interplay in a predictable way by ecogeographical rules, as most of our hypotheses were supported. However, we also found that effects can vary among species, depending on the interaction between changes in temperature and other important factors such as primary productivity and its related influence on nutrition. Rising temperatures at low latitudes are affecting fish populations by reaching upper critical thresholds for core biological activities, reducing fitness, and leading to range contractions. In contrast, populations at the leading edge of range expansions, experiencing stronger seasonal fluctuations with colder winters, will need to adapt their life-history strategies to maximize fitness. We showed that this may be reflected in range-expanding rabbitfish through shorter reproductive periods occurring only when temperatures are rising in spring, which increases the survival of their progeny. In addition, higher fecundity and greater longevity could maximize their lifetime reproductive output, favouring their persistence at higher latitudes and further range expansions in the future, as temperatures rise and oceanographic variables favour the dispersal of higher numbers of eggs and larvae to nursery grounds at higher latitudes. The results of this study reflect the phenological and phenotypic adaptability that some range-expanding species could have in terms of the interacting characteristics of reproduction, growth, and longevity. These are important aspects to consider when predicting future species redistributions and their related impacts on the functioning and productivity of natural ecosystems.

AUTHORS' CONTRIBUTIONS

S.Z.-P. and B.T. conceived the ideas and designed methodology; S.Z.-P., D.F., C.D., J.D., R.A. and T.W. collected the data; S.Z.-P. analysed the data; S.Z.-P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We are grateful to Scott Bennett, Maarten De Brauwer, Samuel Payet, Sam Moyle and Mike Travers for helping in the field. We also thank Mike Travers and the staff of Aquatic Science and Assessment Division at the Western Australian Department of Primary Industries and Regional Development and the crew of the RV Naturaliste. This work was funded by The Holsworth Wildlife Research Endowment & The Ecological Society of Australia awarded to S.Z.-P. (RA/1/411/101). Open access publishing facilitated by The University of Western Australia, as part of the Wiley - The University of Western Australia agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.7pvmcvdw2 (Zarco-Perello, 2022).

ORCID

Salvador Zarco-Perello https://orcid.org/0000-0001-9435-8545
David Fairclough https://orcid.org/0000-0002-9620-5064
Joey DiBattista https://orcid.org/0000-0002-5696-7574
Thomas Wernberg https://orcid.org/0000-0003-1185-9745
Brett Taylor https://orcid.org/0000-0002-4746-7228

REFERENCES

Ahti, P. A., Kuparinen, A., & Uusi-Heikkilä, S. (2020). Size does matter – the eco-evolutionary effects of changing body size in fish. *Environmental Reviews*, *28*, 311–324.

Akiyama, S., Naganuma, M., & Katayama, S. (2009). Annual life cycle of rabbitfish Siganus fuscescens in Tateyama Bay, Chiba prefecture. *Fisheries Engineering*, *46*, 107–115.

Amarasekare, P., & Simon, M. W. (2020). Latitudinal directionality in ectotherm invasion success. *Proceedings. Biological Sciences/The Royal Society*, *287*, 20191411.

Angilletta, M. J., Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, *44*, 498–509.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, *27*, 277–284.

Atkinson, D., & Sibly, R. M. (1997). Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution*, *12*, 235–239.

Azov, Y. (1991). Eastern Mediterranean—a marine desert? *Marine Pollution Bulletin*, *23*, 225–232.

Azzurro, E., Franzitta, G., Milazzo, M., Bariche, M., & Fanelli, E. (2017). Abundance patterns at the invasion front: The case of Siganus luridus in Linosa (Strait of Sicily, Central Mediterranean Sea). *Marine and Freshwater Research*, *68*, 697.

Bariche, M., Harmelin-Vivien, M., & Quignard, J. P. (2003). Reproductive cycles and spawning periods of two Lessepsian siganid fishes on the Lebanese coast. *Journal of Fish Biology*, *62*, 129–142.

Bariche, M., Letourneur, Y., & Harmelin-Vivien, M. (2004). Temporal fluctuations and settlement patterns of native and lessepsian herbivorous fishes on the lebanese coast (eastern mediterranean). *Environmental Biology of Fishes*, *70*, 81–90.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Baty, F., Ritz, C., Charles, S., Brutsche, M., Flandrois, J.-P., & Delignette-Muller, M.-L. (2015). A toolbox for nonlinear regression in R: The package nlstools. *Journal of Statistical Software*, *66*, 1–21.

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Marshall, C. T. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, *20*, 1023–1031.

Berrigan, D., & Charnov, E. L. (1994). Reaction norms for age and size at maturity in response to temperature: A puzzle for life historians. *Oikos*, *70*, 474.

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change and the past, present, and future of biotic interactions. *Science*, *341*, 499–504.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789.

Burraco, P., Orizaola, G., Monaghan, P., & Metcalfe, N. B. (2020). Climate change and ageing in ectotherms. *Global Change Biology*, *26*, 5371–5381.

Burrows, M. T., Bates, A. E., Costello, M. J., Edwards, M., Edgar, G. J., Fox, C. J., Halpern, B. S., Hiddink, J. G., Pinsky, M. L., Batt, R. D., García Molinos, J., Payne, B. L., Schoeman, D. S., Stuart-Smith, R. D., & Poloczanska, E. S. (2019). Ocean community warming responses explained by thermal affinities and temperature gradients. *Nature Climate Change*, *9*, 959–963.

Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., Brown, C., Bruno, J. F., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., Kiessling, W., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F. B., Sydeman, W. J., & Richardson, A. J. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, *334*, 652–655.

Carbonell, J. A., Wang, Y.-J., & Stoks, R. (2021). Evolution of cold tolerance and thermal plasticity in life history, behaviour and physiology during a poleward range expansion. *The Journal of Animal Ecology*, *90*, 1666–1677.

Cerim, H., Soykan, O., & Gülşahin, A. (2020). Mortality and exploitation of marbled spinefoot, Siganus rivulatus (Actinopterygii: Perciformes: Siganidae), from southern Aegean Sea small-scale fishery. *Acta Ichthyologica et Piscatoria*, *50*, 183–190.

Chaudhary, C., Richardson, A. J., Schoeman, D. S., & Costello, M. J. (2021). Global warming is causing a more pronounced dip in marine species richness around the equator. *Proceedings of the National Academy of Sciences*, *118*(15), e2015094118. https://doi.org/10.1073/pnas.2015094118

Chuang, A., & Peterson, C. R. (2016). Expanding population edges: Theories, traits, and trade-offs. *Global Change Biology*, *22*, 494–512.

Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, *8*, 224–228.

Conover, D. O. (1992). Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology*, *41*, 161–178.

Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 12788–12793.

Donelson, J. M., Sunday, J. M., Figueira, W. F., Gaitán-Espitia, J. D., Hobday, A. J., Johnson, C. R., Leis, J. M., Ling, S. D., Marshall, D., Pandolfi, J. M., Pecl, G., Rodgers, G. G., Booth, D. J., & Munday, P. L. (2019). Understanding interactions between plasticity, adaptation and range shifts in response to marine environmental change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *374*, 20180186.

EU's Earth Observation (2021). Copernicus Marine Service. https://marine.copernicus.eu/

FAO-FIGIS (2019). FAO Fisheries and Aquaculture Department. https://www.fao.org/fishery/en/collection/capture

Flower, A., McKenna, J. W., & Upreti, G. (2016). Validity and reliability of graphclick and datathief III for data extraction. *Behavior Modification*, *40*, 396–413.

Forster, J., Hirst, A. G., & Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 19310–19314.

Fox, R. J., & Bellwood, D. R. (2008). Remote video bioassays reveal the potential feeding impact of the rabbitfish Siganus canaliculatus (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs*, *27*, 605–615.

Froese, R. & Pauly, D. (2019). FishBase. http://www.fishbase.org

Geist, V. (1987). Bergmann's rule is invalid. *Canadian Journal of Zoology*, *65*, 1035–1038.

Geraci, M. (2014). Linear quantile mixed models: The lqmm package for laplace quantile regression. *Journal of Statistical Software*, *57*, 1–29.

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, *8*, 461–467.

Hartig, F. (2020) *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. Computer Software. R package.

HilleRisLambers, J., Harsch, M. A., Ettinger, A. K., Ford, K. R., & Theobald, E. J. (2013). How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences*, *1297*, 112–125.

Hsu, T. H., Adiputra, Y. T., Burridge, C. P., & Gwo, J. C. (2011). Two spinefoot colour morphs: Mottled spinefoot Siganus fuscescens and white-spotted spinefoot Siganus canaliculatus are synonyms. *Journal of Fish Biology*, *79*, 1350–1355.

Hunter, A., Speirs, D. C., & Heath, M. R. (2015). Fishery-induced changes to age and length dependent maturation schedules of three demersal fish species in the Firth of Clyde. *Fisheries Research*, *170*, 14–23.

Hurst, T. P. (2007). Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, *71*, 315–345.

IPCC (2021). In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Climate change 2021: The physical science basis. contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge University Press.

Kanashiro, K., Motonaga, F., & Kimura, M. (1999). Settlement of White-spotted Spinefoot, Siganus canaliculatus (Pisces: Siganidae), in the Coastal Waters off Okinawa Island, Japan. *Nippon Suisan Gakkaishi*, *65*, 19–25.

Kumagai, N. H., García Molinos, J., Yamano, H., Takao, S., Fujii, M., & Yamanaka, Y. (2018). Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 8990–8995.

Lee, W.-S., Monaghan, P., & Metcalfe, N. B. (2013). Experimental demonstration of the growth rate--lifespan trade-off. *Proceedings Biological Sciences/The Royal Society*, *280*, 20122370.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640.

McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J., Alonso-Fernández, A., & Basilone, G. (2015). Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, *16*, 23–57.

Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, *30*, 331–351.

Miller, T. E. X., Angert, A. L., Brown, C. D., Lee-Yaw, J. A., Lewis, M., Lutscher, F., Marculis, N. G., Melbourne, B. A., Shaw, A. K., Szűcs, M., Tabares, O., Usui, T., Weiss-Lehman, C., & Williams, J. L. (2020). Eco-evolutionary dynamics of range expansion. *Ecology*, *101*, e03139.

Morales-Castilla, I., Rodríguez, M. Á., & Hawkins, B. A. (2012). Deep phylogeny, net primary productivity, and global body size gradient in birds. *Biological Journal of the Linnean Society. Linnean Society of London*, *106*, 880–892.

Morrongiello, J. R., Horn, P. L., Maolagáin, C. Ó., & Sutton, P. J. H. (2021). Synergistic effects of harvest and climate drive synchronous somatic growth within key New Zealand fisheries. *Global Change Biology*, *27*, 1470–1484.

Munday, P. L., Kingsford, M. J., O'Callaghan, M., & Donelson, J. M. (2008). Elevated temperature restricts growth potential of the coral reef fish *Acanthochromis polyacanthus*. *Coral reefs (Online)*, *27*, 927–931.

Ogle, D.H., Wheeler, P. & Dinno, A. (2020) *FSA: Fisheries Stock Analysis*. Computer Software, R.

Osland, M. J., Stevens, P. W., Lamont, M. M., Brusca, R. C., Hart, K. M., Waddle, J. H., Langtimm, C. A., Williams, C. M., Keim, B. D., Terando, A. J., Reyier, E. A., Marshall, K. E., Loik, M. E., Boucek, R. E., Lewis, A. B., & Seminoff, J. A. (2021). Tropicalization of temperate ecosystems in North America: The northward range expansion of tropical organisms in response to warming winter temperatures. *Global Change Biology*, *27*, 3009–3034.

Pankhurst, N. W., & Porter, M. J. R. (2003). Cold and dark or warm and light: Variations on the theme of environmental control of reproduction. *Fish Physiology and Biochemistry*, *28*, 385–389.

Pauly, D. (2021). The gill-oxygen limitation theory (GOLT) and its critics. *Science Advances*, *7*(2), eabc6050. https://doi.org/10.1126/sciadv.abc6050

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Perrin, N. (1995). About Berrigan and Charnov's life-history puzzle. *Oikos*, *73*, 137.

R Core Team. (2019). *R: A language and environment for statistical computing*. Computer Software, R Foundation for Statistical Computing.

Rollo, C. D. (2002). Growth negatively impacts the life span of mammals. *Evolution & Development*, *4*, 55–61.

Rubalcaba, J. G., Verberk, W. C. E. P., Hendriks, A. J., Saris, B., & Woods, H. A. (2020). Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 31963–31968.

Saber, M. A., & Gewida, A. G. A. (2020). The influence of trammel net fishing on the Rabbit fish (*Siganus rivulatus*) stocks in Suez Gulf, Red Sea, Egypt. *Egyptian Journal of Aquatic Biology and Fisheries*, *24*, 135–145.

Sala, E., Kizilkaya, Z., Yildirim, D., & Ballesteros, E. (2011). Alien marine fishes deplete algal biomass in the Eastern Mediterranean. *PLoS ONE*, *6*, e17356.

Shakman, E., Winkler, H., Oeberst, R., & Kinzelbach, R. (2008). Morphometry, age and growth of Siganus luridus Rüppell, 1828 and Siganus rivulatus Forsskål, 1775 (Siganidae) in the central Mediterranean (Libyan coast). *Revista de Biología Marina y Oceanografía*, *43*, 521–529.

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*, 401–406.

Slesinger, E., Jensen, O. P., & Saba, G. (2021). Spawning phenology of a rapidly shifting marine fish species throughout its range. *ICES Journal of Marine Science*, *78*, 1010–1022.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of Marine Science*, *60*, 1129–1157.

Sommer, R. J. (2020). Phenotypic plasticity: From theory and genetics to current and future challenges. *Genetics*, *215*, 1–13.

Soykan, O. (2020). Maximum size of Marbled spinefoot (Siganus rivulatus Forsskal & Niebuhr, 1775) for Aegean Sea. *Aquatic Sciences and Engineering*, *36*, 42–45.

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, *18*, 944–953.

Taylor, B. M., Choat, J. H., DeMartini, E. E., Hoey, A. S., Marshall, A., Priest, M. A., Rhodes, K. L., & Meekan, M. G. (2019). Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. *The Journal of Animal Ecology*, *88*, 1888–1900.

Taylor, B. M., Gourley, J., & Trianni, M. S. (2017). Age, growth, reproductive biology and spawning periodicity of the forktail rabbitfish (*Siganus argenteus*) from the Mariana Islands. *Marine and Freshwater Research*, *68*, 1088.

Thorson, J. T., Munch, S. B., Cope, J. M., & Gao, J. (2017). Predicting life history parameters for all fishes worldwide. *Ecological Applications*, *27*, 2262–2276.

Urban, M. C. (2020). Climate-tracking species are not invasive. *Nature Climate Change*, *10*, 382–384.

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H., & Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, *17*, 1351–1364.

Verberk, W. C. E. P., Atkinson, D., Hoefnagel, K. N., Hirst, A. G., Horne, C. R., & Siepel, H. (2021). Shrinking body sizes in response to warming: Explanations for the temperature-size rule with special emphasis on the role of oxygen. *Biological Reviews of the Cambridge Philosophical Society*, *96*, 247–268.

Vila-Gispert, A., Moreno-Amich, R., & García-Berthou, E. (2002). Gradients of life-history variation: An intercontinental comparison of fishes. *Reviews in Fish Biology and Fisheries*, *12*, 417–427.

Werner, E. E., & Anholt, B. R. (1993). Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *The American Naturalist*, *142*, 242–272.

Zarco-Perello, S. (2022). Data from: Maximization of fitness by phenological and phenotypic plasticity in range expanding rabbitfish (Siganidae). *Dryad Digital Repository*. https://doi.org/10.5061/dryad.7pvmcvdw2

Zarco-Perello, S., Bosch, N. E., Bennett, S., Vanderklift, M. A., & Wernberg, T. (2021). Persistence of tropical herbivores in temperate reefs constrains kelp resilience to cryptic habitats. *Journal of Ecology*, *109*(5), 2081–2094. https://doi.org/10.1111/1365-2745.13621

Zarco-Perello, S., Langlois, T. J., Holmes, T., Vanderklift, M. A., & Wernberg, T. (2019). Overwintering tropical herbivores accelerate detritus production on temperate reefs. *Proceedings. Biological Sciences/The Royal Society*, *286*, 20192046.

Zarco-Perello, S., Wernberg, T., Langlois, T. J., & Vanderklift, M. A. (2017). Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports*, *7*, 820.

Zettlemoyer, M. A., & Peterson, M. L. (2021). Does phenological plasticity help or hinder range shifts under climate change? *Frontiers in Ecology and Evolution*, *9*, 689192.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Zarco-Perello, S., Fairclough, D., Dowling, C., DiBattista, J., Austin, R., Wernberg, T., & Taylor, B. (2022). Maximization of fitness by phenological and phenotypic plasticity in range expanding rabbitfishes (Siganidae). *Journal of Animal Ecology*, *91*, 1666–1678. https://doi.org/10.1111/1365-2656.13739