Coral Reefs (2026) 45:81–91
https://doi.org/10.1007/s00338-025-02683-0

RESEARCH

Predicting demography from species traits: larval development time and its sensitivity to warming depend on egg size in corals

Joana Figueiredo[1] · **Andrew H. Baird**[2] · **Saki Harii**[3] · **Sean R. Connolly**[4]

Received: 20 October 2024 / Accepted: 2 June 2025 / Published online: 19 June 2025

Abstract In the absence of demographic data, readily measurable life history traits, like egg size, can be used to predict how demographic rates vary across species, facilitating modeling and analysis of high-diversity assemblages. We assessed the larval survival and competency acquisition dynamics, both determinants of larval dispersal, of four previously unstudied coral species at current and warmed temperatures. This dataset was combined with comparable data for three other coral species to assess how well egg size predicts larval mortality, the minimum time to competency and their sensitivity to warming. Minimum time to competency increased with egg size; moreover, warming-induced reductions in time to competency were greater for species with larger eggs. In contrast, mortality rate and its response to warming were both independent of egg size. These findings show how assemblage-level responses to environmental change can be inferred for diverse communities and indicate how warming-induced changes in larval biology may reshape reef coral metacommunities.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-025-02683-0.

✉ Joana Figueiredo
jfigueiredo@nova.edu

[1] National Coral Reef Institute, Nova Southeastern University, 8000 N Ocean Drive, Dania Beach, FL 33004, U.S.A.

[2] James Cook University, Townsville, QLD, Australia

[3] Sesoko Marine Research Station, Tropical Biosphere Research Center, University of the Ryukyus, Sesoko, Okinawa, Japan

[4] Smithsonian Tropical Research Institute, Panama City, Panama

Resumo Na ausência de dados demográficos, podem ser utilizadas características facilmente mensuráveis do historial de vida, como o tamanho do ovo, para prever como as taxas demográficas variam entre espécies, facilitando a modelação e a análise de communidades de alta diversidade. Avaliámos a sobrevivência larvar e a dinâmica de aquisição de competência, ambas determinantes da dispersão larvar, de quatro espécies de corais não estudadas anteriormente a temperaturas atuais e aquecidas. Este conjunto de dados foi combinado com dados comparáveis para três outras espécies de corais para avaliar o quão bem o tamanho do ovo prevê a mortalidade das larvas, o tempo mínimo para a competência e a sua sensibilidade ao aquecimento. O tempo mínimo para a competência aumentou com o tamanho do ovo; além disso, as reduções induzidas pelo aquecimento no tempo para a competência foram maiores para as espécies com ovos maiores. Em contraste, a taxa de mortalidade e a sua resposta ao aquecimento foram ambas independentes do tamanho do ovo. Estas descobertas mostram como as respostas ao nível da comunidade às alterações ambientais podem ser inferidas para comunidades diversas e indicam como as alterações induzidas pelo aquecimento na biologia larvar podem remodelar as metacomunidades de recifes de coral.

Keywords *Acropora tenuis* · *Acropora digitifera* · Broadcast spawners · Climate change · *Ctenactis echinata* · Larval competency · *Lobophyllia corymbosa* · Meta-analysis · Trait-based ecology

Introduction

Predicting how species and metacommunities will respond to environmental change is a key challenge for ecology (Orr et al. 2020; Thompson et al. 2021). For relatively species-poor communities, this can be accomplished using models of metacommunity dynamics calibrated by direct measurements of growth, intra- and interspecific competition and/or facilitation, reproduction, recruitment and dispersal (e.g., Pacala et al. 1996). Such models not only help us answer ecological and evolutionary questions, such as about the relative importance of different coexistence mechanisms (Adler et al. 2010), they can also be used to inform management decisions, such as the design of networks of protected areas (Born et al. 2008; Edwards et al. 2010). For species-rich communities, however, such demographic data are rarely available, nor easily collectable, for the vast majority of species (Urban et al. 2016). One solution to this is to characterize how the demographic characteristics of species vary with more readily measurable species traits (Adler et al. 2014; Madin et al. 2016; Wieczynski et al. 2021), and to infer species-level demography based on species' portfolios of traits.

Egg size is an easy-to-measure, highly conserved life history trait (Robertson and Collin 2015) which, in many organisms with a dispersal life stage, can serve as proxy for larval development time, and consequently dispersal potential. Larger eggs tend to have greater energy content (McEdward and Morgan 2001; Robertson and Collin 2015) and produce larger feeding larvae or newly metamorphosed recruits (Strathmann 1977; Sinervo 1990; Bernardo 1996; Fox and Czesak 2000; García-Barros 2000; Marshall and Keough 2008; Allen and Marshall 2014). Egg size is inversely related to larval development time (Berrill 1935; Steele 1977; Emlet et al. 1987; García-Barros 2000), both within (Marshall and Bolton 2007) and among species (Staver and Strathmann 2002) with the same feeding modes and at similar temperature. Increased metabolic demands for oxygen, coupled with a decrease in the capacity to acquire oxygen by diffusion, have been hypothesized to explain this pattern (Einum et al. 2002). Because planktonic period affects dispersal potential, egg size can also be a good proxy for larval dispersal potential in some groups, particularly those whose larvae are weak swimmers (see Shanks 2009 for a study on the influence of larval swimming on homing behaviors that can limit dispersal). Dispersal is a particularly important demographic process because, alongside post-settlement processes that influence survival, growth and fecundity (Keesing and Halford 1992; Fraschetti et al. 2003; Ritson-Williams et al. 2009; Penin et al. 2010; Riegl and Purkis 2015), it influences species distribution, persistence, gene flow and local adaptation, as well as the capacity for degraded areas to recover via the arrival of larvae from connected undisturbed locations.

For stony corals, the main structure-formers of coral reef ecosystems, dispersal is limited to the egg, embryo and larval stages. How long larvae remain alive and when they become able to settle are important determinants of coral larval dispersal patterns. However, corals are a highly diverse group, and the parameterization of competency dynamics for all coral species in the metacommunity would be time-consuming and costly. In broadcast spawning corals, egg size explains *ca.* 80% of the variation in time to motility (i.e., the time it takes from egg fertilization to the acquisition of cilia and start of movement; Figueiredo et al. 2013); however, the potential relationship between egg size and the minimum time to competency (when larvae have developed the necessary structures to settle and metamorphose when exposed to suitable settlement cues) has not yet been assessed, nor has the relationship between egg size and mortality rate. Such relationships could facilitate inferences about assemblage-level changes in dispersal potential in reef corals, particularly if egg size explains a substantial proportion of the interspecific variation in these parameters.

Larval dispersal patterns of corals are expected to be affected by climate change, mostly driven by changes in larval development dynamics (Figueiredo et al. 2022). Warming accelerates embryogenesis and larval development of most marine ectothermic species (Hoegh-Guldberg and Pearse 1995; O'Connor et al. 2007), including multiple broadcast spawning corals (Nozawa and Harrison 2007; Heyward and Negri 2010), altering their larval dispersal potential. Specifically, local retention of coral larvae increases (Figueiredo et al. 2014) and reef connectivity decreases (Figueiredo et al. 2022) when larval development time is shorter. However, the magnitude of interspecific variability in such responses, and the role of modulators such as egg size, have not been assessed. In this study, we experimentally assessed the larval survival and competency acquisition dynamics of four previously unstudied coral species at current and warmed temperatures. We then combined these new data with previously collected data from three other coral species in metaregressions. Specifically, we estimate the magnitude of interspecific variation in these demographic quantities, assess the extent to which key parameters driving larval dispersal potential are predicted by egg size and determine whether egg size predicts the magnitude of warming-induced changes in those parameters. Our findings highlight how changes to the larval survival and competency acquisition dynamics (hereafter, "larval development dynamics") might influence dispersal and consequently the metacommunity structure and dynamics of reef coral assemblages in the coming decades, and illustrate how readily measurable trait values can inform projected changes to high-diversity communities more broadly.

Material and methods

Larval survival and competency experiments

Six colonies of *Ctenactis cf. echinata, Acropora aff. digitifera*, *Acropora aff. tenuis* and *Lobophyllia cf. corymbosa* were collected nearshore at Sesoko Island (Okinawa, Japan) and transferred to a flow-through raceway before spawning in June or July 2013. The colonies were identified in the field following Nishihira and Veron (1995). After spawning in the laboratory at Sesoko Marine Research Station of University of the Ryukyus, the gametes of all colonies of the same species were collected and mixed. Except for *A. tenuis*, fifty eggs of each species were measured under a stereomicroscope with a calibrated micrometer; the eggs size of *A. tenuis* was taken from Tan et al. (2020) which performed measurements in colonies from the same site. Embryos/larvae of each species were reared at three temperatures: current temperature after spawning in the reef of Sesoko, + 2 and + 4 °C (respectively, 27, 29 and 31 °C), except for *A. digitifera* whose embryos/larvae were only reared at current and + 4 °C, due to an insufficient number of larvae for an intermediate temperature treatment. Temperature was maintained using water baths with thermostats (± 0.5 °C) and monitored at least twice a day with a digital thermometer (± 0.1 °C). Larvae were not stirred nor provided artificial light, following the natural diel cycle with PAR reaching a maximum of 10 µmol photons m^{-2} s^{-1}.

For all species, larval survival was assessed using four replicates of 50 embryos/larvae per temperature. Each 200 mL glass jar (replicate) was filled with filtered (0.2 µm) seawater and stocked with 50 embryos (2 h post-spawning). The total number of larvae alive from the initial stock was counted daily; water was changed daily during this process.

For *A. digitifera* and *L. corymbosa*, the larval competency at each temperature was assessed using four replicates of 100 embryos (2 h post-spawning). In each replicate, embryos were stocked to a 200 mL glass jar filled with filtered (0.2 µm) seawater with a 2 × 2 × 0.5 cm pre-conditioned ceramic tile to induce settlement and metamorphosis. The tiles were pre-conditioned for at least one month on the reef flat in front of Sesoko Station from where the adult colonies had been collected. Every day, the tile was removed from the jar, censused under a scope for metamorphosed corals, and replaced by another tile; censuses were performed until the day no larvae were observed settling in any temperature treatment. The number of larvae that remained alive but had not settled until the end of the experiment was also counted.

For *C. echinata* and *A. tenuis*, embryos were reared in three or more 2L bowls per temperature (starting 2 h post-spawning). To assess competency at each temperature, every day until day 6, and then on days 9, 16, 20 and 30 post-fertilization, four replicates of twenty larvae were haphazardly collected from all bowls and placed in 200 mL glass jars filled with filtered seawater at the same temperature and provided a 2 × 2 × 0.5 cm pre-conditioned ceramic tile to induce settlement and metamorphosis. A day later the larvae that had settled and metamorphosed at each temperature were recorded.

Larval dynamics modeling

The larval survival and competency acquisition dynamics from seven species [four from this study (above) and three previously published (Figueiredo et al. 2014, 2022) identified in the field using Nishihira and Veron (1995) in Sesoko, and Veron (2000) in the Great Barrier Reef] representing a wide range of egg diameter (mean ± SE) [*Ctenactis cf. echinata* (256 ± 2.1 µm), *Cyphastrea japonica* (297 ± 2.6 µm), *Favites stylifera* (454 ± 4.8 µm), *Acropora aff. digitifera* (521 ± 3.4 µm), *Acropora aff. millepora* (540 ± 4.7 µm), *Lobophyllia cf. corymbosa* (593 ± 2.7 µm) and *Acropora aff. tenuis* (602 ± 3.3 µm, Tan et al. 2020); the "cf." and "aff." abbreviations reflect the ongoing taxonomic revision but will not be used hereafter] were modeled using standard likelihood formulations, and parameters were estimated using maximum likelihood (Figueiredo et al. 2014, 2022, detailed in Supplement). These species are broadcast spawners and produce aposymbiotic gametes. For each species, we used model selection to assess whether there was support for temperature-dependent mortality and competency rates by comparing a model where all parameters were independent of temperature with models where different combinations of parameters were dependent on temperature, using Akaike's information criterion corrected for small samples (AIC_c) and likelihood ratio tests. The time to 25% mortality (M25) was estimated as the time when the probability of having already died, calculated as $1 - e^{(-\lambda t)^{\nu}}$ (where t is time, and λ and ν are mortality parameters that allow a monotonic decrease in mortality rate over time, Figueiredo et al. 2022), was equal to 0.25. The variances of the minimum time to competency (t_c, i.e., the time it takes an embryo of broadcast spawning coral species to develop, settle and metamorphose when exposed to suitable settlement cues) and M25 were calculated by randomly generating 1000 (multivariate normal) estimates of survival and competency model parameters [including temperature-(in)dependent $\log(t_c)$ and survival parameters $\log(\mu)$ and $\log(\nu)$] using the variance–covariance matrix (i.e., inverse of the hessian matrix, evaluated at the maximum likelihood), then using each parameter set to generate 1000 estimates of the time to 25% mortality and t_c, and from these calculate their respective variance (Table 1).

Effect of egg diameter on coral larval development and its sensitivity to warming

To describe the relationship between egg diameter and the minimum time to competency (t_c) at current temperature conditions in corals (Table 1), a mixed-effects metaregression was conducted using the maximum likelihood estimate of t_c and its estimated sampling variance for the same seven species, with species identity as a random factor and egg diameter (µm) as a moderator. To determine the effect of

Table 1 Mean (and SD) egg diameter (µm) and minimum time to competency (t_c) and time to 25% mortality (M25) and its estimated standard deviation (SD) for each temperature for the seven species used in the metaregressions, with *n* being the sample size. * indicates species which egg size and larval dynamics were previously published in Figueiredo et al. (2014). ** indicates species which egg size (but not larval dynamics) was published in Tan et al. (2020). Note that in some cases the standard deviations (SD) for M25 are considerably large because mortality never reached 25% during the experimental period

Species	Egg diameter (µm)	Minimum time to competency, t_c (h) (SD)				Time to 25% mortality, M25 (h) (SD)			
		27 °C (current)	**29 °C (+2 °C)**	**31 °C (+4 °C)**	**n**	**27 °C (current)**	**29 °C (+2 °C)**	**31 °C (+4 °C)**	**n**
Ctenactis echinata	256	28.35 (3.61)	28.35 (3.61)	28.35 (3.61)	54	4 (1.21)	2 (0.55)	1 (0.14)	132
*Cyphastrea japonica**	297	50.00 (1.45)	42.63 (2.11)	41.86 (2.34)	72	44 (6.48)	39 (6.10)	12 (3.47)	198
*Favites stylifera**	454	60.04 (0.45)	51.57 (1.30)	44.12 (1.85)	81	194 (23.21)	194 (23.21)	194 (23.21)	198
Acropora digitifera	521	97.00 (1.31)		81.88 (0.30)	72	305 (85.74)		30 (9.48)	152
*Acropora millepora**	540	103.81 (1.04)	86.34 (0.47)	62.67 (0.44)	120	18 (3.73)	5 (1.27)	3 (0.65)	360
Lobophyllia corymbosa	593	83.26 (1.14)	79.02 (1.75)	55.14 (1.70)	96	57 (6.44)	57 (6.44)	57 (6.44)	120
*Acropora tenuis***	602	85.32 (2.07)	60.27 (1.04)	41.66 (0.33)	120	1659 (531)	647 (151)	361 (74)	360

egg diameter on the minimum time to competency (t_c) at current temperature, this metaregression was compared with one where the egg diameter was not included as moderator using $\mathrm{AIC_c}$ and the likelihood ratio test (LRT); both metaregressions were run using the maximum likelihood method (as opposed to restricted maximum likelihood) to allow for the comparison of models with different fixed-effects structures (Zuur et al. 2009). The variance explained by the egg size was quantified using a pseudo-R^2 statistic which estimates the proportional reduction in the variance of the model with the moderator (egg size), relative to the model without it (using ML). Once the best model was identified, this was refit using restricted maximum likelihood to obtain less biased parameter estimates. The same methodology was used to test the effect of egg diameter on the time to 25% mortality (M25) at current temperature conditions.

To assess the effect of egg diameter on the warming-induced reduction of the minimum time to competency, we used a two-step metaregression analysis. First, for each species, a fixed-effects metaregression of the minimum time to competency was conducted using the estimated minimum time to competency at each temperature and its variance (Table 1), and temperature as moderator. Then, a mixed-effects metaregression of the estimated slopes of each species' metaregression ($\Delta t_c/\Delta T$, in h/°C) and their variance (calculated by squaring the product of the estimated slope by number of temperatures tested minus 1) was conducted using species identity as a random effect and egg diameter as the moderator. To assess the effect of egg diameter on the warming-induced changes to the minimum time to competency, this metaregression was compared, using the $\mathrm{AIC_c}$ and LRT, with one where egg diameter was not included as moderator. The best model was refit using restricted maximum likelihood (REML). The total interspecific variance explained by the moderator was estimated as the proportional reduction in the variance component of the model with the moderator, relative to the model without it (using ML). The same methodology was used to test the effect of egg diameter on the warming-induced changes to the time to 25% mortality (M25).

Results

Larval survival and competency dynamics

For the species examined experimentally in this study, warming accelerated the acquisition of competency (i.e., reduced minimum time to competency by third to half) in *A. tenuis*, *A. digitifera* and *L. corymbosa* and increased larval mortality (ca. 25–33%) of *C. echinata, A. digitifera* and *A. tenuis*, particularly during the early stages of larval development (embryogenesis). In contrast, the larval competency dynamics of *C. echinata* and the larval survival of *L. corymbosa* were not affected by warming (Fig. 1, and Tables S1-4 and Figures S1-4 in Supplement).

Effect of egg diameter on coral larval development and its sensitivity to warming

Combining our estimates from the data above with those obtained from previous work in a meta-analysis revealed that the minimum time to competency (t_c) at current temperature (Table 1) significantly increased with egg diameter, taking 17.2 ± 3.6 h (mean ± SE) longer to develop per each 100 µm increase in egg diameter (LRT: $p = 1.4 \times 10^{-3}$, Fig. 2):

$$tc = -7.53 + 0.17 \times Eggdiameter(\mu m)$$

with 77% of the total interspecific variance being explained by egg diameter. Minimum time to competency decreased by about 5.6 ± 1.5 h (mean ± SE) per each increased degree in temperature (°C); $\Delta t_c/\Delta T$ is normally distributed (one-sample Kolmogorov–Smirnov test, D = 0.24, p = 0.75), and it varies considerably among species (SD = 3.6). The decrease in the minimum time to competency of coral larvae, Δt_c (h), with temperature increase, ΔT (°C), increases with the mean egg diameter of the species (µm) (LRT, p = 0.0085) and can be described by the following (Fig. 3):

$$\Delta tc/\Delta T(h/^{\circ}C) = 5.83 - 2.41 \times 10^{-2} \times EggDiameter(\mu m)$$

with 62% of the interspecific variance in $\Delta t_c/\Delta T$ explained by egg diameter. This suggests that as temperature increased,

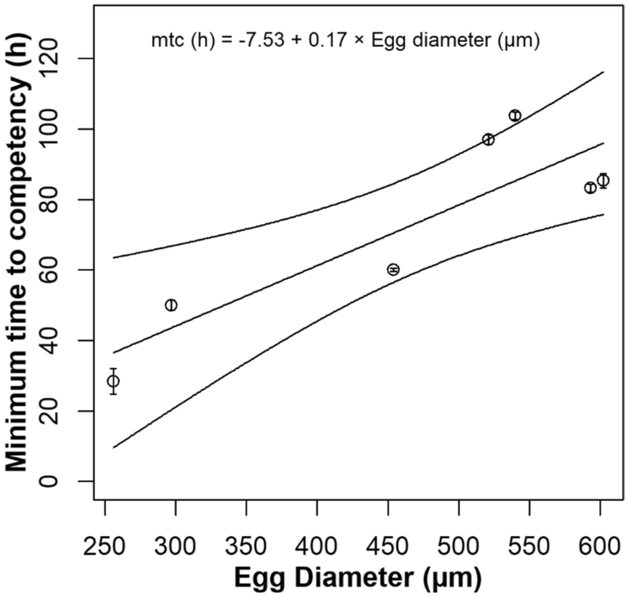

Fig. 2 Relationship between egg diameter (µm) and minimum time to competency (h) at current-day conditions. The middle/straight line represents the line of best fit and the upper, and lower lines represent the 95% confidence interval of the regression. The circles and error bars represent the mean ± SD for each coral species

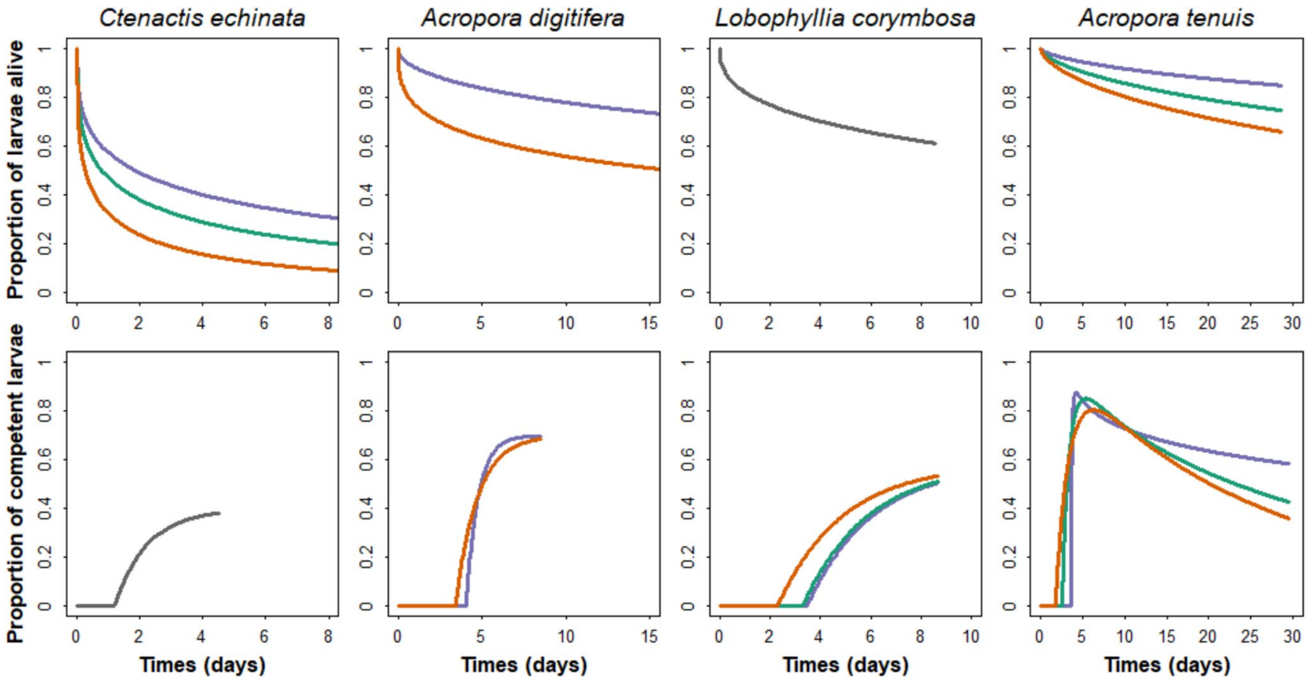

Fig. 1 The larval survival and competency models of *Ctenactis echinata*, *Acropora digitifera*, *Lobophyllia corymbosa* and *Acropora tenuis*, at current-day temperature during spawning time in Okinawa, Japan (27 °C, purple) and 2 °C warmer (29 °C, green) and 4 °C warmer (31 °C, orange). The gray line indicates cases where the model is equal for the three temperatures

species with larger egg diameter experienced a greater reduction in the minimum time to competency.

At current temperature, larvae took on average 96.3 ± 41.6 h (± SE) to reach 25% mortality (M25), and this time decreased by about -2.4 ± 1.5 h on average (± SE) for every degree increase in temperature (°C) (Table 1). Both M25 and its sensitivity to warming ($\Delta M25/\Delta T$) varied substantially among species (SD = 3.6 and SD = 101.9, respectively). Model selection did not favor including egg diameter as a predictor of the time until 25% mortality at current temperature (log likelihood ratio test, $p = 0.30$), nor did egg size predict the sensitivity of increased mortality to temperature (LRT, $p = 0.22$), suggesting that it explains, at most, a small proportion of the total interspecific heterogeneity in mortality.

Discussion

In this study, we identified strong relationships between egg size and minimum time to competency in a number of broadcast spawning corals. These relationships suggest that a substantial proportion of the interspecific variation in larval competency acquisition dynamics, and how this is affected by warming, is predictable from readily measurable characteristics of the eggs. Specifically, the minimum time to competency increases with egg diameter, making the larvae of species with larger eggs to develop slower. Additionally, species with larger eggs also experienced more substantial reductions of the minimum time to competency with increasing temperatures. As a result, as the climate continues to warm, broadcasting spawning coral species with larger eggs are expected to experience greater changes to their dispersal patterns than species with smaller eggs. The estimated trait-based relationships provided by this study, including the distribution of the warming-induced increase in mortality, the relationship between egg diameter and minimum time to competency and the relationship between egg diameter and warming-induced changes to the minimum time to competency, can therefore facilitate projections of metacommunity scale responses to environmental change.

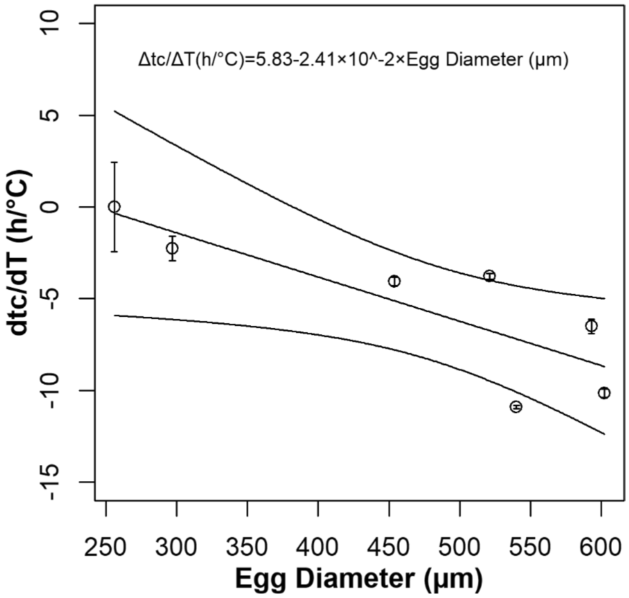

Fig. 3 Relationship between egg diameter (μm) and change in minimum time to competency with increased temperature ($\Delta t_c/\Delta T$, h/°C). The middle/straight line represents the line of best fit, and the upper and lower lines represent the 95% confidence interval of the regression. The circles and error bars represent the mean ± SD for each coral species

The diameter of the eggs of broadcast spawning corals was a good predictor of their minimum time to competency at current temperature conditions (Fig. 2) likely because, as in other animals, larger eggs have lower respiratory exchange and thus longer larval development times. The relationship between egg size and larval development time has been previously documented using data for other coral species (Figueiredo et al. 2013; Randall et al. 2024); however, both existing studies used different metrics. Figueiredo et al. (2013) found a relationship between egg diameter and time to motility [i.e., time until larvae start rotating, t_m (h) = 0.0596 × egg size (μm) + 0.067, $R^2 = 0.80$] using the data from 20 broadcasting coral species, while Randall et al. (2024) found a relationship between egg diameter and the time until 50% of the larvae were competent [t_c50 (days) = 0.0037 × egg diameter + 2.32, $R^2 = 0.26$] for 21 broadcasting coral species. While these are not directly comparable to this study, the trend is similar. For coral species with smaller eggs, the predictions of time to motility are very similar to the minimum time to acquire competency, as one would expect from species with a very fast larval development; the time to 50% competency occurs later as larvae within the same cohort typically acquire competency at different rates (Fig. S5 in Supplement). As egg size increases, the time to motility becomes increasingly shorter than the minimum time to competency (Fig. S5 in Supplement) as expected for species with longer development times. For species with larger eggs, mostly *Acropora*, the minimum time to motility is relatively similar to the time to 50% competency (Fig. S5 in Supplement) which suggests *Acropora* species tend to be have a relatively higher intra-cohort synchrony in the acquisition of competency and/or the optimal settlement cues for this genus are better identified. With respect to dispersal, the most important trait is the minimum time to competency because this is the point at which larvae can swim directionally and thus can leave the plankton and start exploring the benthos. The relationship between egg size and larval development time is not unique to corals. From marine to aquatic environments, within closely related animals which inhabit the same temperature regime, species with larger eggs typically take longer to complete larval development (Staver and Strathmann 2002). Egg size has been found to be a good proxy for larval development time in multiple animal groups, including amphipods (Steele and Steele 1973), ascidians (Berrill 1935; Staver and Strathmann 2002), bivalves (Staver and Strathmann 2002), butterflies (García-Barros 2000), copepods (McLaren 1966), decapods (Wear 1974), fish (Duarte and Alcaraz 1989), frogs (McLaren and Cooley 1972), gastropods (Staver and Strathmann 2002), hydromedusas (Staver and Strathmann 2002), nudibranchs (Wray and Hadfield 1987) and seastars (Strathmann and Staver 2002). The relationship between egg size and larval development time is mostly explained by the ratio of the surface area to the volume of the egg, as this determines the rate of respiratory exchange and thus control development rate (Rubalcaba et al. 2020; Pettersen et al. 2022; White et al 2022). However, it is not oxygen diffusion that limits larval development as during early stages development does not require much oxygen, and oxygen consumption increases relatively slowly with increasing egg mass (Berrill 1935; Einum et al. 2002). Interestingly, it appears to be driven by carbon dioxide, which can be very toxic and thus needs to be removed from the egg. As egg size (and ratio of the surface area to the volume) increases, the elimination of CO_2 from the egg and embryo surfaces is progressively harder, requiring a reduction in the pace of larval development so that CO_2 generation does not outpace its elimination (Berrill 1935).

The minimum time to competency of the larvae of broadcast spawning coral species decreases as temperatures warm (Table 1, Fig. 1) because the latter accelerates metabolic rates and consequently larval development. Temperature is of greatest influence upon the duration of larval development for all species (Thorson 1950), not just corals. Within a species' tolerance range, low temperatures lengthen the pelagic life, while high temperatures shorten it (provided food availability or maternal reserves are high enough to support the increased metabolic rate at these high temperatures) (Berrill 1935; O'Connor et al. 2007). This trend has been reported in multiple marine and freshwater animals, such as amphipods (Steele and Steele 1973), ascidians (Berrill 1935), brine shrimp (Figueiredo et al. 2009), copepods (McLaren 1966), decapods (Wear 1974; Kumlu et al. 2000; Figueiredo and Narciso 2006), fish (Duarte and Alcaraz 1989), frogs (McLaren and Cooley 1972), sea cucumber (Asha and Muthiah 2005) and other corals (Nozawa and Harrison 2007; Randall and Szmant 2009a,bHeyward and Negri 2010), and is commonly exploited by aquaculture facilities to accelerate production (Rothlisberg 1998; Morais et al. 2016). Warmer temperature increases the activity of enzymes, accelerating fundamental biochemical processes and consequently metabolic rates (Clarke and Fraser 2004) and larval development.

Together with previous observations, the additional warm-induced larval dynamics provided in this study confirm that the hastening of larval development under warmer conditions likely extends to all broadcasting spawning coral species. Our findings suggest that estimates of the change in minimum time to competency with increased temperature can be randomly generated from a normal distribution (mean = -5.6 and SD = 3.6). The ability to produce estimates of the minimum time to competency, i.e., the minimum time larvae are obligatorily planktonic and dispersing, without information on the reproductive ecology of the species in a community, can improve estimates of demographic connectivity of coral populations. However, these estimates can be even further improved if the egg size of the coral species present in a community is known.

The extent of the reduction of minimum time to competency under warmer temperatures is directly related to egg size, with coral species with larger eggs experiencing greater reductions (Fig. 3). For each degree (°C), temperature increases, and coral species with larger eggs (> 450 µm) will become ready to settle ca. 5-10 h earlier, while species with smaller eggs (< 300 µm) will only develop ca. 1-2 h faster. This is likely a result from having a longer larval development, and thus, any acceleration in development shortens considerably more the time required for their larvae to become competent. The greater the increase in temperature, the more striking these differences become. For example, a 4 °C increase leads to a hastening of development of ca. 0-8 h for species with small eggs vs. 20-40 h for species with large eggs. This magnitude of shortening of larval development (1 day or more) can cause a substantial change in coral larval dispersal patterns and connectivity, namely an increase in local retention and self-recruitment and a weakening of connectivity (Figueiredo et al. 2022), with important consequences for the persistence and recovery of populations following disturbances (Figueiredo et al. 2022), as well as genetic diversity and adaptation processes. Since the experiments used to estimate this relationship did not expose the adult coral colonies to warmer conditions, the proposed equation presumes that their egg diameter will not be altered by warming. Existing studies suggest that egg size may vary with some environmental conditions, but temperature stress seems to have a minor effect on egg size. Corals associated with the more thermally tolerant algal *Durusdinium* symbionts produced eggs with a lower lipid content and smaller size than the ones associated with the thermally sensitive *Cladocopium*; however, while exposure of adult corals to warming also reduced the number and lipid content of the eggs produced, it did not affect the size of their eggs (Jones and Berkelmans 2011). Temperature differences between seasons have also been found not alter the egg size nor fecundity of four biannually spawning coral species (Foster and Gilmour 2020). This evidence is still insufficient to determine if and to which extent the egg size of coral species will be altered by warming. However, if the egg size of corals does shrink under warmer temperatures, since egg size is directly related to the minimum time to competency, the reduction of time to competency under warm conditions described above would be even more pronounced than predicted here.

For most coral species studied, larval mortality increased with temperature (Nozawa and Harrison 2007; Randall and Szmant 2009a,b; Heyward and Negri 2010; Figueiredo et al. 2014; Putnam and Gates 2015; Graham et al. 2017; Matsuda et al. 2021; Figueiredo et al. 2022, this study) and independently of egg size. The observed increased mortality of corals during embryogenesis and larval development at higher (than optimal/current-day) temperatures is common among ectotherms (e.g., echinoderms [Byrne et al. 2013], fish [Madeira et al. 2016] and crustaceans [Quinn 2017]) and explained by an acceleration of enzyme activity under warmer temperatures that accelerates cell division and in the process potentially increases the chances of malformation due to lack of synchronicity among tissues. However, the magnitude of increase in coral larval mortality with temperature was independent of egg size, suggesting that even if egg size partially explains the differential mortality among coral species, its effect will be much smaller than the effects of parental genotype, history of stress exposure, food quantity and quality and/or symbiont community (Jones and Berkelmans 2011; Baums et al. 2013; Padilla-Gamiño et al. 2013; Kirk et al. 2018).

Coral species with larger eggs are expected to disperse further but as oceans warm, they will experience greater reductions in dispersal distance and connectivity. Since coral larvae are mostly passive dispersers (Hata et al. 2017), the direct relationship between egg size and time to competency, and of the latter with dispersal potential (Figueiredo et al. 2013, 2014, 2022), means species with larger eggs have a greater potential to disperse away from their parental habitat. Furthermore, as the reduction of the minimum time to competency with warming is greater in species with larger eggs, we project that as oceans warm, these species will experience greater reductions in dispersal distance and connectivity. Reducing the time larvae spend in the plankton (pre-competency time) will also increase the probability larvae will settle before being flushed from their natal reef, thus experiencing a greater relative increase in local retention and self-recruitment. The broadcast spawning corals with the largest eggs are from the genera *Lobophyllia* and *Acropora*. *Acropora* is the most diverse and abundant genus of reef-building corals (Veron 2000); their branching morphology provides habitat to a multitude of reef fish species. An increase in local retention and self-recruitment and reduction in connectivity of these species are expected to reduce the inter-reef genetic exchange, increasing isolation and reducing gene flow and recruitment subsidies following disturbance. Considering that *Acropora* are also some of the most susceptible species to bleaching (Marshall and Baird 2000), these changes are likely to considerably reshape metacommunities worldwide, particularly in the Indo-Pacific, which is still dominated by this genus.

Measuring demographic parameters to predict assemblage-level responses to environmental change in highly diverse communities is extremely challenging, but readily measurable life history traits, like egg size, may at least in some cases be used to characterize interspecific differences and thus facilitate modeling analysis and predictions. Existent projections of how demographic parameters, and consequently species abundance and distribution, will be affected by environmental change use empirically calibrated models or the ecological niche of the species based on time-series distributions over large spatial scales (e.g., Bozec et al. 2022 and Cresswell et al. 2024 [corals]; O'Connor et al. 2007 [marine fish and invertebrates]; Buckley et al. 2011 [butterflies]; Bowler et al. 2017 [many groups]; Sanchez-Salguero et al. 2017 [trees]; Simon-Nutbrown et al. 2020 [coralline algae]; and Benedetti et al. 2021 [plankton]). For corals, projections of warm-induced changes to larval dispersal patterns and connectivity have been based on "generic" larval dynamics (Wood et al. 2016), thus not reflecting the interspecific variability, or focused on a single species (Figueiredo et al. 2022; Holstein et al. 2022); projections of dispersal for entire coral communities are inexistent. Experimentally assessing how demographic parameters of a species will change with warming often requires access to a temperature-controlled laboratory and is time-consuming, labor-intensive and expensive; for larval development dynamics, data collection is often restricted to one annual reproductive event. Early coral post-settlement interactions are another aspect of the life cycle that is a critical demographic bottleneck but where getting data is extremely difficult, and thus, it is another great candidate for using approaches like this one as more information accumulates. Doing experimental calibrations for all species of a diverse taxonomic group, such as corals, is virtually impossible. The relationships between readily measurable life history traits and effects of environmental change on demographic parameters, such as the one described here for corals, allow us to bypass that, facilitating estimations of future abundance and ability to recover from disturbances for unstudied species and, more importantly, entire metacommunities. For corals, projections of future dispersal using the relationship between egg size and warm-driven changes in larval development time would greatly benefit the design of networks of marine protected areas and siting of reef restoration efforts that aim to counteract the negative effects of climate change. The relationship between egg size and warming effects on larval development has not been studied in other taxonomic groups, and thus, it is not clear if the species with larger eggs within other taxonomic groups are also expected to experience greater declines in dispersal. However, considering (within taxonomic group and habitat) relationships between egg size and larval development time, and the known relationship between temperature and larval developmental rates, it is quite possible that that is the case. Further studies have the potential to greatly expand our ability to predict the dispersal, and consequently the persistence, of large multi-taxon communities.

Conflict of Interests

J.F. serves as a Topic Editor for Coral Reefs.

Author Contribution J.F., A.B. and S.C. designed the study. J.F., A.B. and S.H. collected data. J.F. and S.C. performed modeling work, the meta-analysis and analyzed results. J.F. wrote the first draft of the manuscript. All authors contributed substantially to revisions.

Funding Australian Research Council,DP110101168,DP110101168,DP0880544,Japan Society for the Promotion of Science,Queensland Government,Smart Futures Fellowship

Data Availability Data is provided within the manuscript or supplementary information and/or from the authors.

References

Adler PB, Ellner SP, Levine JM (2010) Coexistence of perennial plants: an embarrassment of niches. Ecol Lett 13:1019–1029

Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C et al (2014) Functional traits explain variation in plant life history strategies. Proc Nat Acad Sci Bio 111:740–745

Baums IB, Devlin-Durante MK, Polato NR, Xu D, Giri S, Altman NS, Ruiz D et al (2013) Genotypic variation influences reproductive success and thermal stress tolerance in the reef building coral, *Acropora palmata*. Coral Reefs 32:703–717

Benedetti F, Vogt M, Elizondo UH, Righetti D, Zimmermann NE, Gruber N (2021) Major restructuring of marine plankton assemblages under global warming. Nat Commun 12:5226

Bernardo J (1996) The particular maternal effect of propagule size, especially egg size: Patterns, models, quality of evidence and interpretations. Am Zool 36:216–236

Berrill NJ (1935) Studies in tunicate development III. Differential retardation and acceleration. Philos Trans R Soc Lond B 225:255–326

Born C, Hardy OJ, Chevallier M-H, Ossari S, Attéké C, Wickings EJ et al (2008) Small-scale spatial genetic structure in the Central African rainforest tree species *Aucoumea klaineana*: a stepwise approach to infer the impact of limited gene dispersal, population history and habitat fragmentation. Mol Ecol 17:2041–2050

Bowler DE, Hof C, Haase P, Kröncke I, Schweiger O, Adrian R et al (2017) Cross-realm assessment of climate change impacts on species' abundance trends. Nat Ecol Evol 1:0067

Bozec YM, Hock K, Mason RA, Baird ME, Castro-Sanguino C, Condie SA et al (2022) Cumulative impacts across Australia's Great Barrier Reef: a mechanistic evaluation. Ecol Monogr 92(1):e01494

Buckley LB, Waaser SA, MacLean HJ, Fox R (2011) Does including physiology improve species distribution model predictions of responses to recent climate change? Ecology 92:2214–2221

Byrne M, Gonzalez-Bernat M, Doo S, Foo S, Soars N, Lamare M (2013) Effects of ocean warming and acidification on embryos and non-calcifying larvae of the invasive sea star *Patiriella regularis*. Mar Ecol Prog Ser 473:235–246

Clarke A, Fraser KPP (2004) Why does metabolism scale with temperature? Funct Ecol 18:243–251

Cresswell AK, Haller-Bull V, Gonzalez-Rivero M, Gilmour JP, Bozec YM, Barneche DR et al (2024) Capturing fine-scale coral dynamics with a metacommunity modelling framework. Sci Rep 14(1):24733

Duarte CM, Alcaraz M (1989) To produce many small or few large eggs: a size independent reproductive tactic of fish. Oecologia 80:401–404

Edwards HJ, Elliott IA, Pressey RL, Mumby PJ (2010) Incorporating ontogenetic dispersal, ecological processes and conservation zoning into reserve design. Biol Conserv 143:457–470

Einum S, Hendry AP, Fleming IA (2002) Egg-size evolution in aquatic environments: does oxygen availability constrain size? P Roy Soc Lond B Bio 269:2325–2330

Emlet R, McEdward L, Strathmann R (1987) Echinoderm larval ecology viewed from the egg. In: Langoux M, Lawrence J (eds) Echinoderm Studies. A. A. Balkema, Rotterdam, pp 55–136.

Figueiredo J, Narciso L (2006) Productivity improvement of *Lysmata seticaudata* (Risso, 1816) larval rearing protocol through modelling. Aquaculture 261:1249–1258. https://doi.org/10.1016/j.aquaculture.2006.09.003

Figueiredo J, van Woesik R, Lin J, Narciso L (2009) *Artemia franciscana* enrichment model – How to keep them small, rich and alive? Aquaculture 294:212–220. https://doi.org/10.1016/j.aquaculture.2009.05.007

Figueiredo J, Baird AH, Connolly SR (2013) Synthesizing larval competence dynamics and reef-scale retention reveals a high potential for self-recruitment in corals. Ecology 94(3):650–659. https://doi.org/10.1890/12-0767.1

Figueiredo J, Baird AH, Harii S, Connolly SR (2014) Increased local retention of reef coral larvae as a result of ocean warming. Nat Clim Change 4:498–502. https://doi.org/10.1038/nclimate2210

Figueiredo J, Thomas CJ, Deleersnijder E, Lambrechts J, Baird AH, Connolly SR, Hanert E (2022) Global warming decreases connectivity among coral populations. Nat Clim Change 12:83–87. https://doi.org/10.1038/s41558-021-01248-7

Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. Annu Rev Entomol 45:341–369

Fraschetti S, Giangrande A, Terlizzi A, Boero F (2003) Pre- and post-settlement events in benthic community dynamics. Oceanol Acta 25 (2003) 285–295.

García-Barros E (2000) Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). Biol J Linn Soc 70:251–284

Graham EM, Baird AH, Connolly SR, Sewell MA, Willis BL (2017) Uncoupling temperature-dependent mortality from lipid depletion for scleractinian coral larvae. Coral Reefs 36:97–104

Hata T, Madin JS, Cumbo VR, Denny M, Figueiredo J, Harii S, Thomas CJ, Baird AH (2017) Coral larvae are poor swimmers and require fine-scale reef structure to settle. Sci Rep 7(1):2249. https://doi.org/10.1038/s41598-017-02402-y

Hoegh-Guldberg O, Pearse JS (1995) Temperature, food availability and the development of marine invertebrate larvae. Am Zool 35:415–425

Holstein DM, Smith TB, van Hooidonk R, Paris CB (2022) Predicting coral metapopulation decline in a changing environment. Coral Reefs 41:961–972

Jones AM, Berkelmans R (2011) Tradeoffs to thermal acclimation: energetics and reproduction of a reef coral with heat tolerant *Symbiodinium* Type-D. J Mar Biol 185890.

Keesing JK, Halford AR (1992) Importance of postsettlement processes for the population dynamics of *Acanthaster planci* (L.). Aust J Mar Freshwater Res. 43:635–651

Kirk NL, Howells EJ, Abrego D, Burt JA, Meyer E (2018) Genomic and transcriptomic signals of thermal tolerance in heat-tolerant corals (*Platygyra daedalea*) of the Arabian/Persian Gulf. Mol Eco 27:5180–5194

Kumlu M, Eroldogan OT, Aktas M (2000) Effects of temperature and salinity on larval growth, survival and development of *Penaeus semisulcatus*. Aquaculture 188(1–2):167–173

Madeira D, Costa PM, Vinagre C, Diniz MS (2016) When warming hits harder: survival, cellular stress and thermal limits of *Sparus aurata* larvae under global change. Mar Biol 163:91

Madin JS, Hoogenboom MO, Connolly SR, Darling ES, Falster DS, Huang D et al (2016) A trait-based approach to advance coral reef science. Trends Ecol Evol 31:419–428

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163

Marshall DJ, Keough MJ (2008) The evolutionary ecology of offspring size in marine invertebrates. Adv Mar Biol 53:1–60

Matsuda SB, Chakravarti LJ, Cunning R, Huffmyer AS, Nelson CE, Gates RD et al (2021) Temperature-mediated acquisition of rare heterologous symbionts promotes survival of coral larvae under ocean warming. Global Change Biol 28:2006–2025

McLaren IA (1966) Predicting development rate of copepod eggs. Biol Bull 131:457–459

McLaren IA, Cooley JM (1972) Temperature adaptation of embryonic development rate among frogs. Physiol Zool 45:223–228

Morais S, Aragão C, Cabrita E, Estevez A, Yúfera M, Valente LMP, Conceição LEC, Dias J, Engrola S, Gisbert E, Costas B, Constenla M, Mañanós E, Duncan N, Dinis MT (2016) New developments and biological insights into the farming of Solea senegalensis reinforcing its aquaculture potential. Rev Aquac 6:1–37. https://doi.org/10.1111/raq.12091

Nishihira M, Veron JEN (1995) Hermatypic corals of Japan. Kaiyusya, Tokyo. 439 pp.

Nozawa Y, Harrison PL (2007) Effects of elevated temperature on larval settlement and post-settlement survival in scleractinian corals, *Acropora solitaryensis* and *Favites chinensis*. Mar Biol 152:1181–1185

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP et al (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Nat Acad Sci USA 104:1266–1271

Orr JA, Vinebrooke RD, Jackson MC, Kroeker KJ, Kordas RL, Mantyka-Pringle C et al (2020) Towards a unified study of multiple stressors: divisions and common goals across research disciplines. P Roy Soc B Bio 287:20200421

Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest modles defined by field measurements : estimation, error analysis and dynamics. Ecol Monogr 66:1–43

Padilla-Gamiño JL, Bidigare RR, Barshis DJ, Alamaru A, Hédouin L, Hernández-Pech X et al (2013) Are all eggs created equal? A case study from the Hawaiian reef-building coral *Montipora capitata*. Coral Reefs 32:137–152

Penin L, Michonneau F, Baird AH, Connolly SR, Pratchett MS, Kayal M, Adjeroud M (2010) Early post-settlement mortality and the structure of coral assemblages. Mar Ecol Prog Ser 408:55–64

Pettersen AK, Schuster L, Metcalfe NB (2022) The evolution of offspring size: a metabolic scaling perspective. Integr Comp Biol 62(5):1492–1502

Putnam HM, Gates RD (2015) Preconditioning in the reef-building coral *Pocillopora damicornis* and the potential for trans-generational acclimatization in coral larvae under future climate change conditions. J Exp Biol 218:2365–2372

Quinn BK (2017) Threshold temperatures for performance and survival of American lobster larvae: A review of current knowledge and implications to modeling impacts of climate change. Fish Res 186:383–396

Randall CJ, Szmant AM (2009a) Elevated temperature affects development, survivorship and settlement of the elkhorn coral, *Acropora palmata* (Lamarck 1816). Biol Bull 217:269–282

Randall CJ, Szmant AM (2009b) Elevated temperature reduces survivorship and settlement of the larvae of the Caribbean scleractinian coral, *Favia fragum* (Esper). Coral Reefs 28:537–545

Randall CJ, Giuliano C, Stephenson B, Whitman TN, Page CA, Treml EA et al (2024) Larval precompetency and settlement behaviour in 25 Indo-Pacific coral species. Comm Biol 7(1):142

Riegl B, Purkis S (2015) Coral population dynamics across consecutive mass mortality events. Glob Change Biol 21:3995–4005

Ritson-Williams R, Arnold SN, Fogarty ND, Steneck RS, Vermeij MJA, Paul VJ (2009) New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithsonian Contributions to the Marine Sciences:437–457.

Robertson DR, Collin R (2015) Inter- and Intra-specific variation in egg size among reef fishes across the Isthmus of Panama. Front Ecol Evol 2:84

Rubalcaba JG, Verbeck WCEP, Hendriks AJ, Saris B, Woods HA (2020) Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. Proc Nat Acad Sci 117(50):31963–31968

Sanchez-Salguero R, Camarero JJ, Gutiérrez E, Rouco FG, Gazol A, Sangüesa-Barreda G et al (2017) Assessing forest vulnerability to climate warming using a process-based model of tree growth: bad prospects for rear-edges. Global Change Biol 23:2705–2719

Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. Biol Bullet 216:373–385

Simon-Nutbrown C, Hollingsworth PM, Fernandes TF, Kamphausen L, Baxter JM, Burdett HL (2020) Species distribution modeling predicts significant declines in coralline algae populations under projected climate change with implications for conservation policy. Frontiers Mar Sci 7:575825

Sinervo B (1990) The evolution of maternal investment in lizards - an experimental and comparative analysis of egg size and its effects on offspring performance. Evolution 44:279–294

Staver JM, Strathmann RR (2002) Evolution of fast development of planktonic embryos to early swimming. Biol Bull 203:58–69

Steele DH (1977) Correlation between egg size and developmental period. Am Nat 111:371–372

Steele DH, Steele VJ (1973) The biology of *Gammarus* (Crustacea, Amphipoda) in the- northwestern Atlantic. VII. The duration of embryonic development in five species at various temperatures. Can J Zool 51:995–999

Tan ES, Izumi R, Takeuchi Y, Isomura N, Takemura A (2020) Molecular approaches underlying the oogenic cycle of the scleractinian coral. Acropora Tenuis Sci Rep 10:9914

Thompson P, Hürlemann S, Altermatt F (2021) Species Interactions Limit the Predictability of Community Responses to Environmental Change. Am Nat 198:694–705

Urban MC, Bocedi G, Hendry AP, Mihoub J-B, Pe'er G, Singer A et al. (2016) Improving the forecast for biodiversity under climate change. Science 353(6304): aad8466.

Veron JEN (2000) Corals of the World, vol. 1–3. Australian Institute of Marine Science and CRR Ald Pty Ltd, Queensland, Australia.

White CR, Alton LA, Bywater CL, Lombardi EJ, Marshall DJ (2022) Metabolic scaling is the product of life-history optimization. Science 377:834–839

Wieczynski DJ, Singlaa P, Doana A, Singletona A, Han Z-Y, Votzkea S et al (2021) Linking species traits and demography to explain complex temperature responses across levels of organization. P Natl Acad Sci-Biol 118(42):e2104863118

Wood S, Baums IB, Paris CB, Ridgwell A, Kessler WS, Hendy EJ (2016) El Niño and coral larval dispersal across the eastern Pacific marine barrier. Nat Commun 7:12571

Zuur A, Ieno E, Walker N, Saveliev A, Smith, G (2009) Mixed effects models and extensions in ecology with r. New York: Springer