Ocean warming and the demography of declines in coral body size

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ABSTRACT: Reductions in body size are hypothesized to be a universal response to climate warming, yet the proximate causes of change remain unresolved. In this study, we combined field evidence and demographic models to explore mechanisms relevant to temperature-related declines in the body size of an ectotherm exhibiting indeterminate growth. Our field data demonstrate that the body size of cup corals *Balanophyllia elegans* has decreased by ~35% over nearly 4 decades (1969–2007), during which seawater temperatures have increased by 0.6°C in the San Juan Islands, Washington State, USA. We developed a modeling framework, based on the Arrhenius equation and temperature–size theory, to explore the thermal dependence of maximum body size. Our models identified the growth rate of corals as a key demographic leverage point for changes in maximum body size, but temperature alone was likely insufficient to cause the observed magnitude of change. Our case study provides a simple template for integrating detailed demographic data with predictions derived from the temperature–size theory, in order to evaluate empirically the magnitude of body size decline in the context of climate warming.

KEY WORDS: *Balanophyllia elegans* · Climate change · Temperature–size rule

INTRODUCTION

Reductions in animal body size have been documented for numerous taxa in a variety of ecosystems over the past 2 centuries (Gardner et al. 2011). These reductions have been attributed to several mechanisms, including predation (Salo et al. 1989), human harvesting (Roy et al. 2003, Erlandson et al. 2011), and climate change (Yom-Tov 2001, Caruso et al. 2014). The latter has received considerable attention in recent years, and reductions in body size are now hypothesized to be a universal response to warming temperatures (Daufresne et al. 2009, Gardner et al. 2011, Sheridan & Bickford 2011).

Manipulative experiments and spatial comparisons of animals across thermal gradients also frequently reveal an inverse correlation between body size and temperature; this pattern is referred to as the temperature–size rule (Ray 1960, James 1970, Atkinson 1994). Many conceptual and mathematical explana-

tions have been proposed for the temperature–size rule, but few have garnered empirical support (Angilletta & Dunham 2003, Angilletta et al. 2004). Recently, theoretical (Zuo et al. 2012) and empirical (Forster et al. 2011) studies support the hypothesis that the temperature–size rule can be explained by differential temperature dependence of developmental rate and growth rate (van der Have & de Jong 1996). Although temperature accelerates growth, it also hastens development, resulting in smaller size at maturity and lower maximum sizes. However, the available empirical data were limited in their taxonomic scope and thus the generality of this hypothesis remains to be validated. Specifically, much of the data were from a single phylum, Arthropoda, and within only 2 lineages, viz. insects and copepods (Forster et al. 2011, Zuo et al. 2012).

A major life history feature of insects and copepods is that they exhibit determinate growth. That is, once a determinate grower reaches sexual maturity, the

individual stops growing and surplus energy is diverted towards reproduction (Kozłowski et al. 2004). One key implication of this strategy is that the overall duration of development and growth is exactly the same. However, many ectotherms exhibit indeterminate growth, especially fish and aquatic invertebrates (reviewed by Sebens 1987). If high temperatures constrain growth later in adulthood, or at larger sizes, organisms would follow the temperature–size rule (Angilletta & Dunham 2003). Thermal constraints on growth can arise when the scaling of energy intake and cost are differentially sensitive to temperature (e.g. Strong & Daborn 1980), and the limited available data support the hypothesis that the thermal optimum for growth decreases with increasing body size (Angilletta & Dunham 2003).

Given the historical nature of the data necessary for temporal comparisons of body size change, assigning causal mechanisms to observed change is challenging. However, size-structured demographic models offer a promising approach to evaluating the contribution of individual-level vital rates (e.g. reproduction, mortality, growth) to population-level characteristics (e.g. body size, population growth rate) (e.g. Hughes 1984, Sebens 2002). Such models have been used to identify likely mechanisms underlying observed demographic shifts in response to climate change (Ozgul et al. 2010, Vindenes et al. 2014), and for predicting the long-term demographic consequences of climate change from organism-level responses (Madin et al. 2012, Radchuk et al. 2013).

In this study, we combine field evidence and a demographic model to test the hypothesis that warming temperatures are related to declines in body size in the temperate cup coral *Balanophyllia elegans*. This solitary, azooxanthellate coral is a conspicuous and common member of temperate intertidal and subtidal communities in the northeast Pacific Ocean (Gerrodette 1979). Unlike many other corals, the gonochoric *B. elegans* broods relatively few and large larvae that tend to disperse over short (<1 m) distances (Gerrodette 1981, Fadlallah 1983). This feature, together with its indeterminate growth and longevity (6–11 yr; Fadlallah 1983), permits an instructive contrast to the relative wealth of information on short-lived and highly fecund taxa (e.g. arthropods) in the context of the temperature–size rule.

Here we present the sequence of queries, which alternate between empirical and modeling approaches, used to address climate-related declines in body size. First, we tested whether body size of *B. elegans* in Washington State, USA, has declined over

nearly 4 decades, during which seawater temperature has increased (Elahi et al. 2013). We then used empirical demographic data to parameterize an integral projection model (Easterling et al. 2000) for the modern population and implemented a perturbation analysis to assess which parameters had the strongest effect on population growth rate and body size change. Finally, we used explicit predictions based on the Arrhenius equation in the context of the perturbation analysis and temperature–size theory (Angilletta et al. 2004, Kingsolver & Huey 2008), to simulate the effects of temperature on maximum body size.

MATERIALS AND METHODS

We compared historic (1969–1972) and modern (2007–2010) populations of the temperate cup coral *Balanophyllia elegans* using photographs of quadrats on subtidal rock walls in the San Juan Islands, Washington, USA. Quadrats were located at the same site (Shady Cove, 48° 33′ 08″ N, 123° 00′ 20″ W), but modern samples did not overlap identically with historic samples. Two additional sites were sampled for coral size–frequency distributions in 2007 but not in 1969 (Point George, 48° 33′ 33″ N, 122° 59′ 18″ W; O'Neal Island, 48° 36′ 17″ N, 123° 05′ 34″ W). Details of the sampling designs for historic and modern data are provided in the Supplement at www.int-res.com/articles/suppl/m560p147_supp.pdf.

We used historic and modern images for 2 related, but distinct, purposes. First, the 2 sets of images permitted a historical comparison of population size structure, density, and growth rates. Details of coral measurements are provided in the Supplement. Second, we used the modern set of images to estimate the demographic parameters necessary to parameterize an integral projection model (IPM). Additional modern images from intervening time points (December 2008, December 2009) were used to track the survival of recruits and calculate recruitment probabilities. New recruits were defined as individuals clearly present in a quadrat that were not identifiable in the quadrat during the previous year.

Historical comparison

We tested the null hypotheses that (1) the population size structure and density of corals, and (2) growth rates of corals, did not differ between eras (historic vs. modern). To test our hypotheses, we used

linear mixed effects models (Bates et al. 2014), implemented in R 3.0.2 (R Development Core Team 2013), to reflect the unbalanced and hierarchical nature of the dataset. For 2 sets of models (coral size, growth) that treated individual corals as replicates, we included a random intercept for quadrat, because we hypothesized that corals in different quadrats exhibit variation in vital rates due to local environmental conditions. The inclusion of a random intercept for transect did not explain any additional variance, and thus we removed it for simplicity in the latter models. However, to test for differences in population density, quadrats were treated as replicates, and thus we included a random intercept of transect to reflect the spatial arrangement of quadrats.

With respect to population size structure, we focused only on corals that were suitable for estimating size (described below) in the first census (either 1969 or 2007). These initial census data were used to compare average size and size–frequency distributions among historic and modern populations at Shady Cove, along with 2 additional sites (Point George and O'Neal Island) within 5 km of Shady Cove in 2007. Due to the positive skew in the size–frequency distribution of historical coral sizes, the residuals displayed increasing variance with the fitted values. Therefore, to provide a more conservative test of the hypothesis that average size was different during the historic era, we removed 13 corals larger than 1.0 cm^2 from the historic population. The residuals for this model did not display a pattern of increasing variance. We used Kolmogorov-Smirnov tests to determine whether size–frequency distributions differed between historic and modern populations.

Unlike population size structure, population density and growth rates were estimated for the Shady Cove population only (not for Point George or O'Neal Island), because this was the spatial comparison most relevant for testing an effect of era. Specifically, we tested for differences in population density between 1969 and 2007 by comparing a model that included an effect of era with a null model. To determine whether growth rates have changed over 4 decades, we ensured that corals were suitable for size measurements in the first census, and determined whether they had unequivocally survived or died after 3 yr. Surviving corals were measured (if suitable) in the second census 3 yr after the first (at time $t + 3$). We used a census interval of 3 yr to obtain reliable estimates of growth because *B. elegans* is small (<2 cm diameter) and grows slowly (<1 mm yr^{-1} in diameter; Fadlallah 1983). Finally, to test for differences in

growth rate among eras, we compared models with a size × era interaction against the complete set of simpler, nested models. For the latter analyses, we restricted the range of sizes to be comparable for both eras by removing 6 corals larger than 0.95 cm^2 from the historic population (the largest coral suitable for growth measurements from the modern population was 0.92 cm^2). We note, however, that inclusion of the 6 large corals from the historic population does not change the interpretation of our analysis.

We used model selection to infer the importance of predictors in our models (Burnham & Anderson 2002). Model fit based on maximum likelihood scores was compared using the small-sample Akaike information criterion (AIC$_c$), a metric that considers both model fit and complexity (i.e. number of parameters, K). The difference in AIC$_c$ (Δi) between each model and the best model (i.e. lowest AIC$_c$) was calculated to emphasize the most plausible models given the data. Finally, Akaike weight (w_i), or the relative likelihood of each model, was obtained by normalizing the likelihood across the entire set of candidate models. Model fit was assessed using plots of residuals and observed values against fitted values.

Demographic model

IPMs are data-driven models that require estimation of the statistical relationships between a quantitative phenotypic trait (typically size) and individual-level survival, growth, and fecundity (Easterling et al. 2000). Size-dependent survival and growth relationships were estimated from photographs. Size-dependent fecundity was estimated using data from a coral population in central California (Fadlallah 1983) together with data on coral density and recruitment in the 24 modern quadrats. Equations and estimated parameters for the integral projection models are provided in Table 1. We adapted R code for the IPM from previous studies (Easterling et al. 2000, Merow et al. 2014, Rees et al. 2014). Details of the modeling framework and parameterization are provided in the Supplement.

Perturbation analysis of the IPM

We used a perturbation analysis of the base IPM to examine the elasticity of population-level traits to a small change in the demographic parameters. Specifically, we increased independently each of the empirical parameters derived from the modern popu-

Table 1. Life-history parameters for the cup coral *Balanophyllia elegans*. Survival, growth, recruit size, and recruitment probability was estimated for the modern (2007–2010) population at Shady Cove, Washington. Survival was fit using a generalized linear mixed effects model, and growth was fit using a linear mixed effects model. Size at maturity and embryo number were calculated using data from a coral population in central California (Fadlallah 1983) and corrected for delayed maturation in cooler temperatures in Washington. Growth was also estimated for the historic (1969–1972) population at Shady Cove. See 'Materials and methods' for more details

Model component	Statistical description
Survival, $s(z)$	$\mathrm{logit}(s) = 1.71 + 0.45z$
Growth, $g(z', z)$	
1969–1972	$z' = 0.20 + 0.87z$; $\sigma^2 = 0.10$
2007–2010	$z' = 0.21 + 0.78z$; $\sigma^2 = 0.11$
Recruit size, $z_{recruit}$	$z_{recruit} = 0.16$; $\sigma^2 = 0.09$
Size at maturity, z_{mat}	$z_{mat} = 0.49$
Embryo number, $e(z)$	$e = -20.23 + 41.61z$; $\sigma^2 = 0.3$
Recruitment probability, $p_{recruit}$	$p_{recruit} = 0.14$; $\sigma^2 = 0.22$

lation by 10%, and calculated the percent change in growth rate (λ), mean size, and maximum size (99th percentile size of the stable size distribution). The results of this perturbation analysis prompted the comparison of growth among eras described above, and informed the temperature simulations described below.

Temperature measurements

To permit temperature simulations of our base IPM, and to place the historical comparison of coral populations into a thermal context, we calculated mean annual temperatures for the historic and modern Washington populations. We chose to calculate the mean temperature over a 10 yr period preceding the final sampling date (1962–1971 and 2001–2010), because the average lifespan of *B. elegans* in the warmer California population is approximately a decade (Fadlallah 1983).

The available temperature data for Shady Cove was limited to 2007 to 2011. Therefore, we used daily surface seawater temperatures from a long-term dataset (1921 to present) collected at the Race Rocks lighthouse, Vancouver Island, British Columbia, Canada, in the Salish Sea (www.racerocks.com/racerock/abiotic/temperature/seatemperature.htm). The Race Rocks lighthouse (48° 17′ 52″ N, 123° 31′ 53″ W) is ~60 km from Shady Cove. We calculated a regression of daily temperature taken at Race Rocks against daily mean temperature (48 measurements d^{-1}) at

Shady Cove between December 2007 and September 2011 ($t_{1,1354} = 116.25$, p < 0.001, $r^2 = 0.91$). This regression was then used to calculate the predicted daily temperatures at Shady Cove for the historic and modern decadal periods.

Temperature simulation of the IPM

We tested the effects of warming on coral size by simulating temperature-mediated changes to individual growth rates. The Arrhenius equation can be used to understand the effects of temperature on physiological rates underpinned by metabolism. Physiological rates are an exponential function of temperature in the Arrhenius equation:

$$R = ae^{-E_a/(kT)} \tag{1}$$

where R is a rate, a is a species- and rate-specific constant, E_a is the activation energy, k is Boltzmann's constant, and T is temperature (in Kelvin). Importantly, the sensitivity to temperature depends on the rate in question. In the Arrhenius equation, this sensitivity is represented by E_a, which varies from 0.2 to 1.2 eV for a range of physiological and ecological traits (mean = 0.65 eV from Dell et al. 2011). This range of E_a corresponds to a 1.3 to 6.0 range of Q10 (mean = 2.7).

This approach assumed that the temperature range (8–9.5°C) over which the simulations were conducted does not exceed the coral's thermal optimum. Beyond the thermal optimum, cellular processes are disrupted and proteins are denatured, leading to a sharp decline in physiological processes (Hochachka & Somero 1984). We accepted this assumption because at our study site, *B. elegans* experiences annual fluctuations between 7 and 12°C (Elahi et al. 2013).

First, we describe the initial temperature adjustment of the fecundity function. The original piecewise linear function $e(z)$, relating coral size and number of embryos, was based on data from central California (Fadlallah 1983). However, the resulting stable size distribution from a preliminary IPM did not match the observed size distribution (see 'Results'). We hypothesized that the mismatch was related to the single vital rate that was not measured for our study population: the fecundity function. It is well known that size at maturity declines with increasing temperature (Berrigan & Charnov 1994, Angilletta et al. 2004), and thus we expected delayed sexual maturity in the cooler waters of Washington (~4°C lower than central California; see below). This

effect was achieved through a negative effect of temperature on the *x*-intercept of $e(z)$ using the Arrhenius equation. We used Eq. (1) to adjust the intercept of $e(z)$ to match the modern temperature at Shady Cove, and used this baseline IPM for our temperature simulations on growth rate. We estimated the value of the activation energy (E_a) for the temperature-adjustment of the fecundity function by using a maximum likelihood (ML) approach to fit the observed size distribution (2007 and 2010, combined; see Madin et al. 2012 for another example of this approach). The ML estimate of E_a was 0.655, a value very similar to our *a priori* expectation of 0.65 (Dell et al. 2011).

Next, we calculated growth rates over a range of temperatures (8.0–9.5°C) and the plausible range of activation energies (E_a = 0.2, 0.4, 0.6, 0.8, 1.0, 1.2). These new rates were calculated assuming baseline estimates of the parameters using E_a = 0.65 and a 9.2°C temperature (the mean annual temperature at the Shady Cove site between 2001 and 2010) for the baseline condition. Our decision to simulate the effects of temperature on growth rate was motivated by congruence between our empirical results (e.g. perturbation analysis, historical comparison of vital rates) and previous work on other scleractinian corals.

Namely, we expected larger individuals to grow disproportionately slower than small individuals with increasing temperature (Edmunds 2006, 2008). The putative mechanism for reduced growth in large corals relates to their disproportionately high tissue biomass and mass transfer limitation at high temperatures in corals with thick tissues (Nakamura & van Woesik 2001). This effect was achieved through a negative effect of temperature on the slope of $g(z', z)$, and is supported by the results of the perturbation analysis. Despite empirical and theoretical support for increased mortality rates at higher temperatures (Pauly 1980, McCoy & Gillooly 2008), our empirical comparison suggested increases in survival during the warmer modern period (see 'Results'). Therefore, we chose not to model the effects of temperature on survival directly. We compared the simulated maximum sizes with observed maximum sizes from the populations at Shady Cove (1969–1972, 2007–2010).

To place the observed changes in coral size into a broader context of temperature–size experiments, we compared our results to a meta-analysis of temperature–size responses (Forster et al. 2012). In the latter study, marine metazoans exhibited reductions of up to ~9% change in mass per 1°C. We used an empirical relationship between coral surface area and biomass to estimate biomass for the largest observed corals in historic and modern quadrats (Fig. S1 in the Supplement). We then calculated the percent reduction in biomass, normalized to a 1°C change, for comparison with Fig. 2 in Forster et al. (2012). We also used the biomass and surface area data to test the assumption that large corals possess disproportionately higher tissue biomass than small corals. We expected log tissue biomass to scale allometrically with log surface area, and tested the null hypothesis of isometry (β = 1) using reduced major axis regression.

RESULTS

Mean annual temperatures displayed an increasing trend at Shady Cove between 1962 and 2010 (Fig. 1A), and daily temperatures (Fig. 1B) were lower during the historic (1962–1971) vs. modern period (2001–2010; 8.6 ± 1.0 and 9.2 ± 1.2°C, respectively; mean ± SD). The temperate cup coral *Balanophyllia elegans* was smaller in 2007 than in 1969 at our study sites (Fig. 2A). Mean calyx area was 0.2 cm² smaller in 2007, representing a 35% decrease from 1969. In comparison to a hierarchical mixed model with a fixed effect of era on coral size, a null model with only an intercept term was not plausible (Δi = 19.0). Even when corals larger than 1.0 cm² were excluded from the analysis, the null model remained implausible (Δi = 8.7; Table 2). Further, Kolmogorov-Smirnov tests between corals at Shady Cove in 1969 and corals at each of 3 sites in 2007 revealed significant differences in the size–frequency distributions (D = 0.29–0.4, p < 0.001). These differences appear to be driven by 2 characteristics of the boxplots and size probability density functions (the violin plots in Fig. 2A). First, the median and mode of coral size is smaller in modern quadrats. Second, modern corals exhibit truncated size distributions. The observed maximum size in the modern era (2007–2010; 1.0 cm²) was 40% smaller than the observed maximum in the historic era (1969–1972; 1.7 cm²). We detected no difference in the population density of corals (Fig. 2B, Table 2).

The integral projection model was parameterized initially with empirical data from 2007–2010 (Table 1) and published data on coral fecundity (Fadlallah 1983). Coral size influenced both survival and growth (Tables 1 & 2). Embryonic production increased with coral size (Fadlallah 1983), with size at maturity estimated as the *x*-intercept of the regression line for the original California population
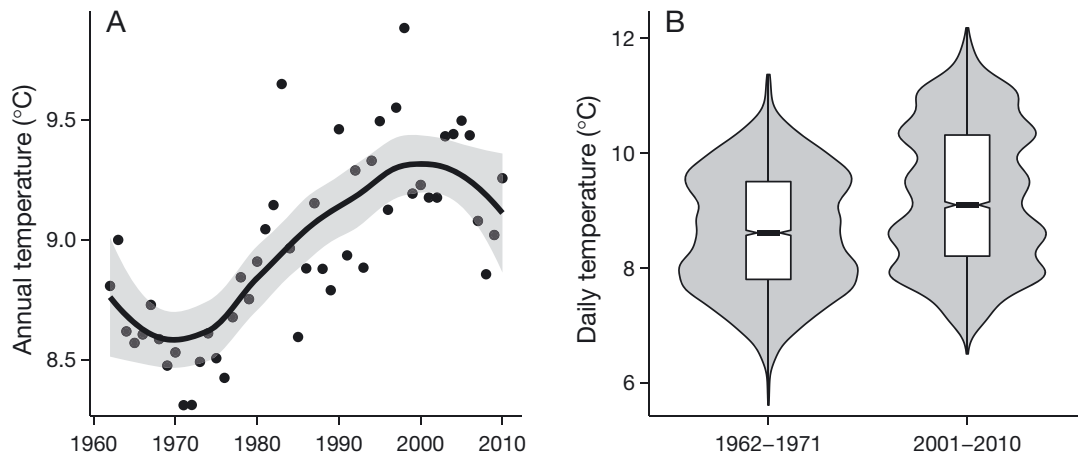
Fig. 1. (A) Mean annual temperatures between 1962 and 2010 and (B) daily temperatures for the historic and modern study periods at Shady Cove, Washington (USA). In (A), the line represents a locally weighted polynomical regression (LOESS) with 95 % confidence intervals (shaded area). In (B), the boxplots indicate the median and quartiles with whiskers reaching up to 1.5 times the interquartile range. Notches can be used to interpret significant differences between medians; if notches do not overlap, the medians are different. The violin plot outlines the kernel probability density; the width of the shaded area represents the proportion of data at that temperature
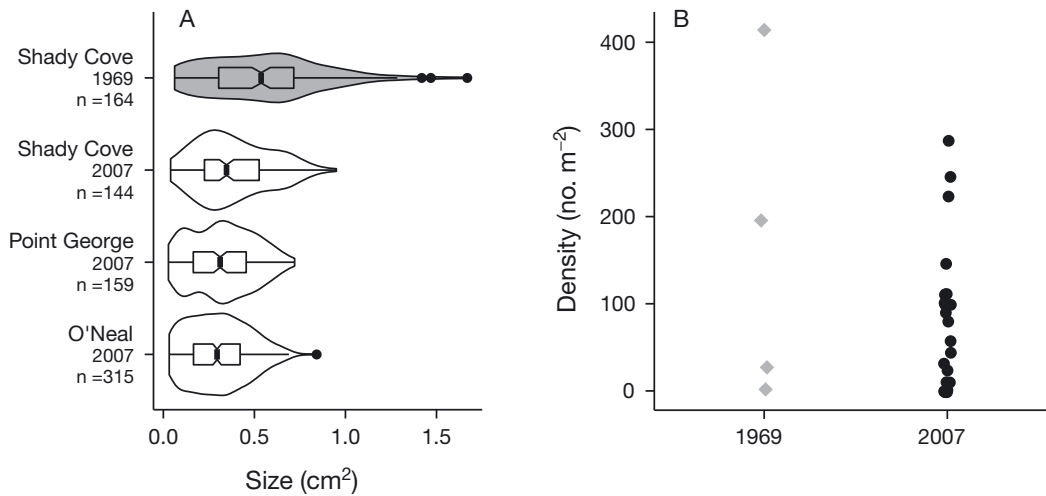

Fig. 2. (A) Size–frequency distributions of the cup coral *Balanophyllia elegans* at 1 site in 1969 and 3 sites in 2007, and (B) coral population densities at 1 site at both time points (Shady Cove). Parameters of boxplots and violin plots in panel (A) are as described in Fig. 1. Circles beyond boxplot whiskers represent outliers whose values are >1.5 times the third quartile. In (B), each point represents the population density for a single quadrat. The total area surveyed for coral population density was 1.0 and 2.2 m^2 for the historic population (Shady Cove) and each modern population (Shady Cove, Point George, O'Neal Island), respectively

(0.27 cm^2), and for the Washington population (0.49 cm^2) after adjusting for temperature (Fig. 3A). A preliminary IPM parameterized with the original fecundity function was not deemed appropriate because the resulting stable size distribution was not consistent with the observed size distribution. However, by modifying the size at maturity in accordance with theoretical expectations rooted in temperature–size theory, the resulting stable size distribution

and predicted maximum size better fit the observed data (Fig. 3B).

The discordance between the stable size distributions fit with the original and modified fecundity functions (Fig. 3B) is related not only to the obvious change in the vital rate itself (i.e. the translated regression line in Fig. 3A), but the indirect consequences of this shift on recruitment probability ($p_{recruit}$). This is because recruitment probability was

Table 2. Summary of model selection statistics from the mixed effects models testing the effect of era (historic vs. modern) on cup coral *Balanophyllia elegans* size and population density, as well as the effects of era and size on coral growth. The datasets for coral size and growth were truncated (coral size <1.0 cm^2) so that the range of coral sizes was comparable between historic and modern populations. Listed is the number of parameters (K), Akaike's information criterion adjusted for small sample size (AIC$_c$), delta AIC$_c$ (Δi), model likelihood, weighted model likelihood (w_i), log likelihood, and cumulative weights of the models. For each response variable, candidate models are arranged by ascending AIC$_c$

Model	K	AIC$_c$	Δi	Model likelihood	w_i	Log likelihood	Cumulative weight
Size							
Era	5	−330.62	0	1	0.987	170.35	0.99
Null model	4	−321.91	8.71	0.013	0.013	164.98	1
Density							
Null model	3	344.21	0	1	0.578	−168.6	0.58
Era	4	344.84	0.63	0.729	0.422	−167.55	1
Growth							
Era + Size	5	−226.61	0	1	0.4	118.51	0.4
Size	4	−226.29	0.31	0.855	0.342	117.29	0.74
Era × Size	6	−225.72	0.88	0.643	0.257	119.16	1
Era	4	−19	207.6	0	0	13.64	1
Null model	3	−13.33	213.28	0	0	9.75	1

calculated as the number of observed recruits per quadrat in 2010 (necessarily constant) divided by the total number of embryos per quadrat (predicted by the fecundity function). Therefore, the calculated 3 yr recruitment probability was considerably lower for

the original fecundity function (2.2 ± 2.7%; mean ± SD) than the modified fecundity function (13.8 ± 21.7%). Due to the poor fit of the original fecundity function, the remainder of the results and discussion will pertain to the temperature-adjusted fecundity function.

We compared the 3 yr recruitment probability ($p_{recruit}$) to annual recruitment probabilities (p_{annual}), which were 4.3 ± 9.4, 8.9 ± 21.7, and 2.1 ± 5.0% (mean ± SD) for 2008, 2009, and 2010, respectively. Averaged across years, the mean annual recruitment probability (5.1 ± 8.7%; mean ± SD) was lower than the 3 yr recruitment probability (13.8 ± 21.7%), although variability in both estimates was high. Most (90%) of the recruits alive in 2010 were between 0.05 and 0.3 cm^2.

The base IPM parameterized with the modern empirical data (Table 1) not only fit the observed size–frequency distribution well (Fig. 3B), but also matched the observed increases in population density of corals between 2007 and 2010. Population growth rate (λ), calculated as the dominant eigenvalue of the IPM matrix representing changes in population size over
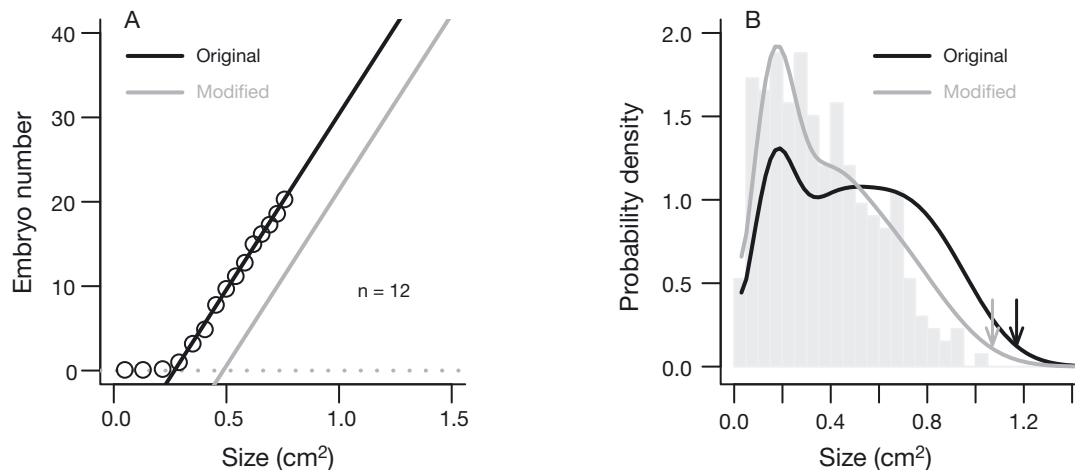

Fig. 3. (A) Estimated fecundity relationship used to parameterize an integral projection model predicting (B) the observed size–frequency distribution of *Balanophyllia elegans* in Washington between 2007 and 2010. In (A), the number of embryos increased linearly with size beyond the onset of sexual maturity. The black line represents the linear model for the original fecundity data (points; Fadlallah 1983), while the gray line represents the adjusted linear model to account for delayed sexual maturity due to colder temperatures experienced by the Washington population. In (B), the observed size distribution (light gray bars) is overlaid with stable size distributions derived from integral projection models parameterized with the original and modified linear models for embryonic production. The arrows denote the 99th percentile maximum size for the predicted stable size distributions. See Table 1 for other model parameters
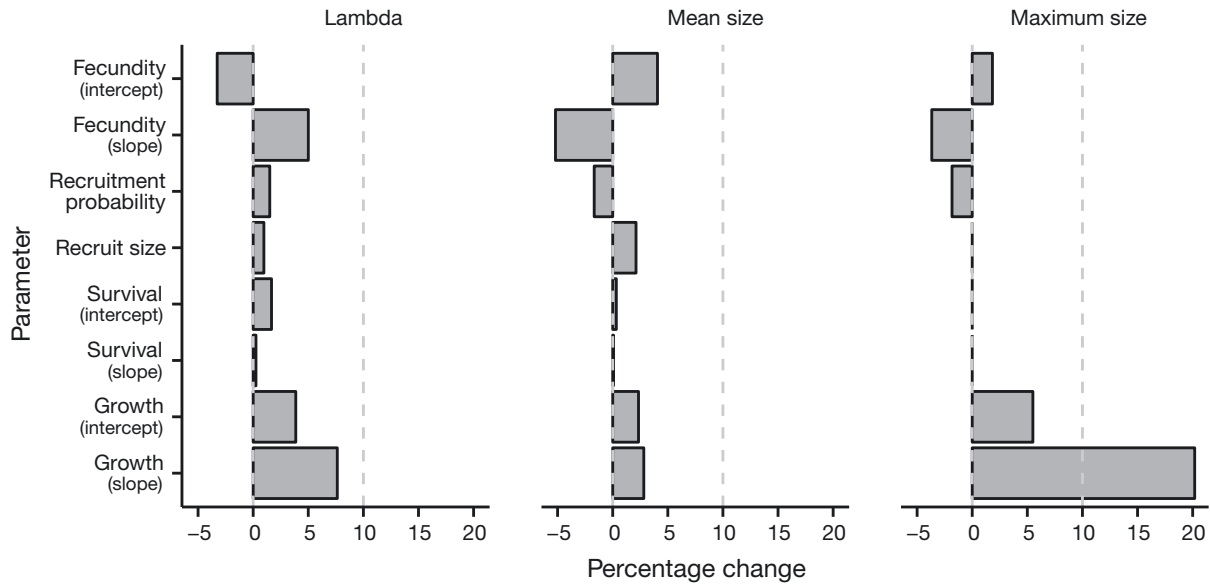
Fig. 4. Results of a perturbation analysis to the integral projection model parameterized with empirical data from the modern (2007–2010) population of the cup coral *Balanophyllia elegans* at Shady Cove. For each model simulation, we increased 1 of the parameters (*y*-axis) by 10% (represented by the gray dashed line), and measured the percentage change in population growth rate (λ), mean size, and maximum size (99th percentile of stable size distribution)
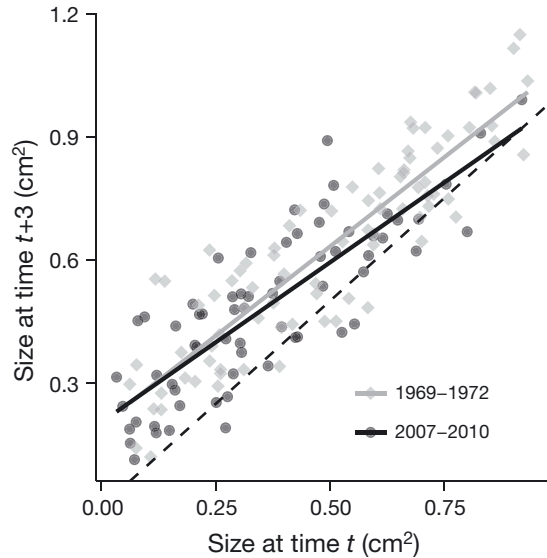

Fig. 5. Comparison of growth rates of the cup coral *Balanophyllia elegans* by historic (1969–1972) and modern (2007–2010) eras. Size at the second census (time *t* + 3) is plotted as a function of size at the first census (time *t*; 1969 or 2007). The dashed line represents unity. Solid lines represent the results of linear mixed effects models; the interaction between era and size was supported by model selection (Table 2)

a 3 yr period, was 1.29. This value was consistent with an empirical measure of population growth rate, estimated independently as the ratio of final (2010) to initial (2007) population density in quadrats with at

least 1 coral (1.2 ± 0.3; mean ± SD; n = 19). Both measures indicate a growing population at Shady Cove between 2007 and 2010.

The perturbation analysis of the base IPM parameterized in reference to the modern population revealed population growth rate (λ) and mean body size to be relatively insensitive to small (10%) adjustments in model parameters. However, maximum size was disproportionately sensitive to changes in growth rate (Fig. 4). Increases in the slope of somatic growth caused increases in maximum size (Fig. 4) and prompted the comparison of this trait among eras. Based on the perturbation analysis, we expected the slope of the growth function to be higher for the historic population because corals were larger during the historic period.

Indeed, the empirical comparison of growth was consistent with the perturbation analysis. The slope of the growth function was marginally higher for corals in 1969–1972 (0.87 ± 0.05; slope ± SE) than in 2007–2010 (0.78 ± 0.07; Fig. 5). This empirical difference was supported by model selection (Table 2); the Era × Size model for growth was not the best model, but received considerable support (Δ*i* = 0.88).

To determine how small differences in the observed growth functions between eras (Fig. 5) corresponded to changes in coral size, we refit the base IPM using the empirical data for growth from the historic population (Fig. 6). The simulated maximum
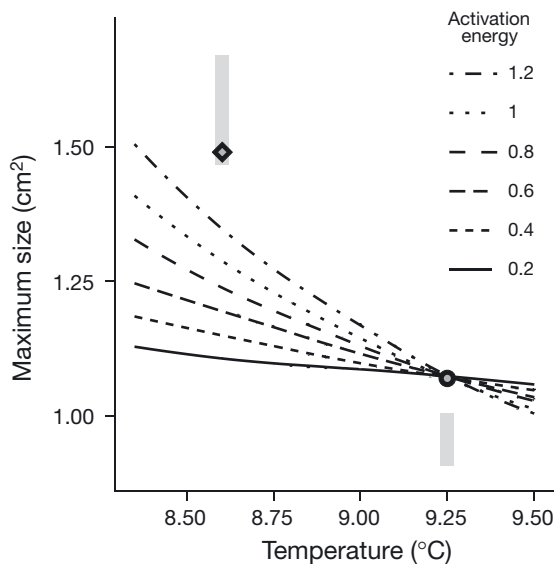
Fig. 6. Predicting the effects of temperature and activation energy on the maximum size (99th percentile) of the cup coral *Balanophyllia elegans*. Temperature is assumed to influence the slope of the growth function in the integral projection model (IPM), and the lines represent predictions based on a range of activation energies (i.e. thermal sensitivities). The open circle represents the predicted maximum size for Shady Cove in 2007–2010, based on the IPM parameterized with data from the modern population. The open diamond represents the predicted maximum size for Shady Cove in 1969–1972, based on the original IPM but substituting the empirically obtained growth function for the historic population. The gray rectangles represent field estimates of maximum size for Shady Cove in 1969–1972 and 2007–2010. The upper and lower boundaries of the rectangles represent the observed and 99th percentile maximum size, respectively

size (99th percentile) increased from 1.1 to 1.5 cm^2 with the modified growth parameter (Fig. 6), and was smaller than the largest coral in the historical population, but within the largest 1% of historical corals (Fig. 6). We compared the latter observed and predicted maximum sizes with a temperature-simulation of growth rates using a series of IPMs. These simulations under-predicted the empirical estimate of historical maximum size, as well as the IPM prediction of maximum size using the historical growth function (Fig. 6), even at the highest temperature sensitivity ($E_a = 1.2$).

The observed reduction in coral size was an order of magnitude larger than that observed in a meta-analysis of temperature–size responses (Forster et al. 2012). We estimated a 44% reduction in maximum coral biomass (99th percentile) over the study period (Fig. S1), during which temperatures increased by 0.6°C. When normalized to a 1°C change, our data suggest that corals experienced a 2.0-fold decrease

in mass °C^{-1}. In contrast, marine metazoans exhibited up to −9% change in mass °C^{-1} in laboratory experiments manipulating temperature (Forster et al. 2012). Our estimate of percent change should be interpreted with caution because the prediction of historical biomass required extrapolation beyond the available size range of the modern coral population (Fig. S1). As expected, log tissue biomass scaled allometrically with log surface area ($\beta = 2.4$, 95% limits = 1.9, 3.0; p < 0.0001).

DISCUSSION

We have presented field evidence that cup corals *Balanophyllia elegans* in the San Juan Islands (Washington, USA) have exhibited a marked decline in body size in less than 4 decades. Concurrently, seawater temperatures have warmed. As body size decline has been proposed recently to be a general response to climate warming (Gardner et al. 2011, Sheridan & Bickford 2011), we developed a simple size-structured IPM to describe coral population dynamics, and used it to explore whether temperature-driven changes in demographic rates were able to explain the observed reduction in maximum body size. We found that a reduction in somatic growth of the largest corals, caused by a 0.6°C increase in temperature according to the Arrhenius equation, may indeed lead to a decline in coral maximum size, even though our theoretical predictions were unable to fully explain the observed reduction in maximum body size.

The effect of somatic growth on maximum body size was revealed through a perturbation analysis of the IPM. This analysis showed that while several model parameters might affect the population growth rate of *B. elegans*, the IPM predicted larger maximum sizes (as observed in the cooler historical period) only through increases in the somatic growth of larger corals (i.e. steeper slope of the growth function). We verified this possibility empirically, and found that larger corals displayed higher growth during the cooler historic period. Although the difference in growth was small (a 13% increase in the slope term), its inclusion in a modified IPM resulted in a ~39% increase in maximum body size.

Was the empirical difference in growth rate consistent with predictions based on temperature effects? Below the thermal optimum, temperature is generally thought to increase growth (Berrigan & Charnov 1994, Angilletta et al. 2004). However, growth was slightly lower in large corals during the warmer,

modern era. In general, the effects of temperature on growth throughout ontogeny, or size, are poorly understood. We are unaware of pertinent data for solitary corals, but several studies on colonial reef corals have demonstrated size-dependent thermal effects on survival and growth. During periods of excessive seawater warming, large coral colonies suffer disproportionately high bleaching and mortality (Loya et al. 2001, Brandt 2009). All else being equal, large colonies sustain thicker boundary layers (Mann & Lazier 2006) and experience lower rates of mass transfer (e.g. per-area diffusion of oxygen) than small colonies (Nakamura & van Woesik 2001), which, under thermally stressful conditions, may cause physiological harm (van Woesik et al. 2012). Furthermore, field observations and laboratory experiments demonstrate that warmer temperatures depress the scaling of somatic growth rate in juvenile corals (Edmunds 2006, 2008). A related mass-transfer explanation for these observations is that the thicker tissue and biomass of larger colonies limits the stimulated physiological rates at high temperatures, ultimately causing reductions in growth (Edmunds 2008). Nearly all organisms display an allometric relationship between surface area and tissue biomass (Schmidt-Nielsen 1984), including *B. elegans* (Fig. S1). Therefore, we hypothesize that rate-limitation at warmer temperatures reduced the growth rates of large corals (>0.5 cm^2) during the warmer period, similar to observations made for tropical reef corals (Edmunds 2006, 2008). Interestingly, this mechanism is consistent with the idea that oxygen limitation is a major driver of the temperature–size rule in aquatic ectotherms (Forster et al. 2012).

When we incorporated the hypothesized temperature effect on the growth function of the demographic model, we observed a reduction in maximum size. Yet, even at the highest temperature sensitivity ($E_a = 1.2$), the model under-predicted the size of the largest corals at Shady Cove in 1969–1972. Therefore, we infer that the hypothesized temperature effect on the growth function was consistent with the direction, but not the magnitude, of coral body size change. It is possible that our use of the Arrhenius equation did not fully capture the severity of the effects of increasing temperature on somatic growth. The range of temperature simulated by the model (8–9.5°C) was well within the observed range of annual variation experienced by *B. elegans* during the study period (7–12°C; Elahi et al. 2013), and thus we assumed that *B. elegans* has not reached its thermal limit. However, physiological effects of temperature can be strongly non-linear, leading to a sharp

decline in organismal processes (Hochachka & Somero 1984). In fact, for intertidal anemones *Anthopleura elegantissima* collected ~12 km from our Shady Cove study site, somatic growth peaks at 10°C (Sebens 1980), suggesting that the growth of *B. elegans* may be compromised during the warmest months of the year.

We also cannot exclude the role of differential thermal dependence of growth and development (Forster et al. 2011, Zuo et al. 2012) because we lacked size-at-age data. The latter could be obtained through the use of growth rings in solitary corals. For example, across a spatial gradient of 2°C in the Mediterranean Sea, length-at-age varied predictably in a zooxanthellate solitary congener, *B. europaea* (Goffredo et al. 2008). A comparison of growth rings in modern and museum specimens of *B. elegans* is the next step in identifying the mechanisms underlying historical shifts in coral body size.

It is interesting to note that the observed reduction in coral size (i.e. biomass) in the modern era was an order of magnitude larger than that observed in a meta-analysis of temperature–size laboratory experiments (Forster et al. 2012). This suggests 2 non-exclusive hypotheses. It is plausible that (1) laboratory manipulations of temperature under-predict responses in the field, and (2) other mechanisms contributed to the decline in coral body size. One mechanism is anthropogenic acidification of the ocean, which has contributed to a pH decline in Puget Sound, including the San Juan Islands (Feely et al. 2010). The threat of acidification has prompted many manipulative and natural experiments of pCO$_2$ on marine calcifying organisms. For example, net calcification rates of temperate corals (including *B. europaea*) decline along natural pH gradients (Rodolfo-Metalpa et al. 2011, Fantazzini et al. 2015), and elevated pCO$_2$ reduces the survival of *B. elegans* (Crook et al. 2013). Therefore, acidification-related reductions in the growth and/or survival of *B. elegans* may have contributed to our observations of coral body size decline.

Top-down processes can also shift prey populations to smaller size distributions (Salo et al. 1989, Roy et al. 2003, Erlandson et al. 2011). We observed a higher percentage cover of available space (i.e. bare rock and algal crusts) associated with higher densities of omnivorous grazers (urchins, chitons) in historic communities (Elahi et al. 2013). Urchins in particular can reduce the densities of coral recruits through the physical disturbance associated with feeding (Sammarco 1982). However, when sufficiently large, anthozoans deter urchin grazing with their nemato-

cysts (Levenbach 2008). Therefore, higher grazing rates in historic communities would most likely remove small corals directly through disturbance, but indirectly benefit the larger, established corals by consuming their sessile competitors (e.g. ascidians). Both of these mechanisms would serve to shift the size-frequency distribution to the right, towards larger corals in the historic communities. Indeed, the peak of the coral size distribution is below the median size for modern quadrats, but is greater than the median size of the historic quadrats (Fig. 2A), suggesting that smaller corals suffered greater mortality in the past at Shady Cove.

In summary, our empirical data provide evidence that *B. elegans* declined in size at our study site while temperatures increased during the study period. The hypothesis that temperature may explain part of the observed reduction in body size cannot be discounted on the basis of our model explicitly incorporating temperature effects on somatic growth according to the Arrhenius equation. Our case study provides a simple template for integrating detailed demographic data with predictions derived from temperature–size theory, in order to evaluate empirically the magnitude of body size decline in the context of climate warming.

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