



Historical comparisons of body size are sensitive to data availability and ecological context

ROBIN ELAHI,^{1,4} LUKE P. MILLER,² AND STEVEN Y. LITVIN^{1,3}

¹Hopkins Marine Station, Stanford University, 120 Ocean View Boulevard, Pacific Grove, California 93940 USA

²Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, California 92182 USA

³Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, California 95039 USA

Citation: Elahi, R., L. P. Miller, and S. Y. Litvin. 2020. Historical comparisons of body size are sensitive to data availability and ecological context. *Ecology* 00(00):e03101. 10.1002/ecy.3101

Abstract. Historical comparisons of body size often lack pertinent details, including information on the sampling protocol and relevant ecological covariates that influence body size. Moreover, historical estimates of body size that rely on museum specimens may be biased towards larger size classes because of collector preferences, and thus size thresholds have been used to focus attention on maximum body size. We tested the consequences of sampling design, ecological covariates, and size thresholds on inferences of body-size change using field-contextualized historical records, rather than museum specimens. In 2014–2015, we revisited historical (1947–1963) size-frequency distributions of three gastropods (*Tegula funebris*, *Lottia digitalis*/*L. austrodigitalis*, *Littorina keenae*) in the context of population density and tidal height. In general, gastropods declined in size. However, our inferences regarding body-size decline were tempered when the variation between sampling units was taken into consideration, resulting in greater uncertainty around the estimate of proportional change in body size. Gastropod size was correlated with population density and tidal height, and these relationships varied over time. Finally, the magnitude and direction of body-size change varied with the amount of data available for analysis, demonstrating that the use of size thresholds can lead to incomplete conclusions.

Key words: climate change; ectothermic; gastropods; population; rocky intertidal; size structure; temperature.

INTRODUCTION

Body size is a fundamental trait that influences the biology of individuals (Schmidt-Nielsen 1984). Temperature is a master environmental factor that controls the tempo of life (Hochachka and Somero 1984). The body size of an individual is dictated, in part, by temperature: metabolic costs increase with temperature and may negatively impact growth, particularly if feeding rates are unable to compensate. For ectotherms, developmental rate increases with temperature, resulting in a smaller individual size at sexual maturity (Ray 1960, Atkinson 1994). This phenomenon is known as the temperature–size rule and has garnered recent attention as a universal response of climate warming (Daufresne et al. 2009, Sheridan and Bickford 2011). Given that the temperature–size rule operates on individuals, the appropriate data to test whether historical changes in body size are due to the temperature–size rule and climate warming would be size-at-age data; that is, individual-level data. Few studies use size at age; notable exceptions include

studies of fish populations in the North Sea (Daufresne et al. 2009, Baudron et al. 2014), but disentangling the covarying effects of fisheries and warming temperatures is problematic.

Many studies that demonstrate reductions in ectotherm body size coincident with local warming trends use size-frequency distributions (or their summary statistics) at multiple points in time; that is, population-level data (Caruso et al. 2014, Fenberg et al. 2016). This is an important point because the size-frequency distribution of a population is an emergent property affected by a variety of individual-level processes (e.g., ecophysiological variation in growth rates, reproductive investment), population-level processes (e.g., recruitment variability, intraspecific competition), and community-level processes (e.g., interspecific competition, predation, density-independent mortality) (Ohlberger 2013). Therefore, ascribing historical changes in size-frequency distributions to a single cause (e.g., climate warming in the context of the temperature–size rule) without considering other processes explicitly is fraught with difficulties (Grant 2015, Elahi et al. 2016, Wilson-Brodie et al. 2017). Perhaps it is not surprising that historical studies over the past century reveal considerable variability in the magnitude and direction of body-size change (Gardner et al. 2011). Some of this variability

Manuscript received 14 November 2019; revised 1 April 2020; accepted 14 April 2020. Corresponding Editor: Geerat J. Vermeij.

⁴E-mail: elahi@stanford.edu

likely reflects ecological context (Wilson et al. 2019), lacking in many historical studies.

Museum specimens have been invaluable in understanding ecological change over longer periods of time than most contemporary ecological studies (Suarez and Tsutsui 2004, Pyke and Ehrlich 2010), and they have contributed to the discussion of climate-associated changes in body size. The use of museum specimens requires an awareness of their well-known limitations (Pyke and Ehrlich 2010, Grant 2015), some of which are specific to understanding reductions in body size coincident with climate warming. In particular, museum specimens typically lack any ecological context beyond the collection site and date. One ecologically relevant omission in museum-based studies of body size is population density. Because of the negative effects of crowding and food limitation, body size is often correlated negatively with local abundance (Underwood 1978, White et al. 2007). Second, individuals are often distributed across local abiotic and biotic gradients that can modify growth and survival and, ultimately, the size-frequency distribution of the population (Vermeij 1972). Such small-scale habitat variation is well appreciated in contemporary studies of body-size distributions (Mittelbach 1981, Hacker and Steneck 1990), but is often missing from museum-based studies. In addition to lacking ecological context, museum specimens often lack details on the sampling protocol. Without this information, it is impossible to determine whether the sample is representative of the population—a fundamental tenet necessary for inference. Consequently, samples may be biased toward the most unusual, brightest, or biggest individuals, depending on the collector's preference (Pyke and Ehrlich 2010). With respect to understanding historical changes in body size, minimum size thresholds have been used to circumvent potential biases by focusing attention on reductions in maximum body size (Roy et al. 2003, Wilson-Brodie et al. 2017), or the removal of juveniles to focus on adult body size (Caruso et al. 2014). It is unclear if and how inferences about historical body-size change are sensitive to local population density, abiotic conditions, and the use of size thresholds (i.e., data availability). Here we address these three issues with the use of a comparative-historical approach with field-contextualized ecological records, rather than museum specimens, in a rocky intertidal ecosystem.

The rocky intertidal zone is a useful arena to examine the ecological consequences of climate warming (Helmuth et al. 2006). Long-term monitoring efforts and resurveys of historical studies have demonstrated changes in the abundance (Southward 1991, Southward et al. 1995), composition (Sagarin et al. 1999, Burrows et al. 2020), and phenology (Moore et al. 2011, Poloczanska et al. 2013) of intertidal plants and animals associated with recent warming trends. Moreover, the long history of manipulative experiments facilitates the discussion of ecological processes relevant to observational studies. Finally, abiotic stress (e.g., temperature, desiccation) increases from lower to upper positions

along intertidal shores, and invertebrates display distinct, and sometimes contrasting, patterns of body size along this abiotic gradient. For example, lower-shore gastropod species (i.e., species that are predominantly found at lower tidal heights) tend to be larger at lower tidal heights (Vermeij 1972), which may be related to greater food supply (Bertness 1977). In contrast, upper-shore gastropod species tend to be larger at higher tidal heights because size-related differences in the tolerance of desiccation stress may restrict juveniles to lower tidal heights because of their inability to withstand longer bouts of emersion (Vermeij 1972). Small limpets are indeed more susceptible to water loss because of their disproportionately large surface area to volume ratio (Branch 1975). Under conditions of decadal-scale air and seawater warming, we would expect reductions in body size along the entire intertidal gradient, but desiccation-related mortality of small animals only on upper shores where aerial exposure is frequent. We also predict larger reductions in body size when local abundances are high. At high population densities, the growth of intertidal gastropods can be limited by food scarcity due to interspecific competition (Sutherland 1970, Underwood 1978). Consequently, population density can be inversely correlated with body size (Shanks et al. 2014).

We tested these predictions on a rocky shore in central California, USA because these communities have already undergone assemblage shifts consistent with climate warming (Sagarin et al. 1999). Specifically, we examined the consistency of body-size change across a suite of species that span an intertidal range of environmental variability by resurveying gastropod populations four to six decades after the original studies. In general, our observations demonstrate reductions in body size, but we highlight the sensitivity of our inferences in the context of population density, spatial variation in environmental temperatures, and data availability.

METHODS

We searched old (1919–1970) theses, dissertations, and class papers archived at the Hopkins Marine Station of Stanford University with the goal of finding a set of studies that met the following criteria: (1) size-frequency data were available, (2) maps and/or written descriptions enabled relocation of sampling sites, and (3) the set of studies were focused on species that represented a single functional group. We found three repeatable studies on different intertidal gastropods whose sampling locations spanned a large intertidal gradient (~7 m in tidal height; Appendix S1: Fig. S1). These sampling locations were all located within the Hopkins Marine Life Refuge, which has been protected from recreational and commercial harvesting of invertebrates and algae since 1931. The three gastropods graze upon macroscopic and microscopic algae, and in this sense represent a single functional group. However, they differ somewhat in morphology and life history.

The black turban snail (*Tegula funebris*) lives in the low to mid-intertidal zone, and its geographic distribution ranges from Vancouver Island to central Baja California (Morris et al. 1980). The periwinkle snail (*Littorina keenae*; formerly *L. planaxis*) lives high on the uppermost parts of rocky shores, and it ranges from Oregon to central Baja California (Morris et al. 1980). Both *T. funebris* and *L. keenae* were considered to be coastwide species in Sagarin et al. (1999). The third gastropod, a ribbed limpet (formerly *Acmaea digitalis* and *Collisella digitalis*, now *Lottia digitalis*), lives on rock walls in the mid to high intertidal zone, and, prior to 1978, was considered to be a single species (but with two different ecotypes; Giesel 1970) that ranged from the Aleutian Islands to Baja California. The ribbed limpet was eventually split into a pair of cryptic sibling species with northern (*L. digitalis*) and southern (*L. austrodigitalis*) geographic affinities (Murphy 1978). Throughout the manuscript, we use both names in tandem, *L. digitalis/L. austrodigitalis*, to reflect the uncertainty in species identification based on exterior shell morphology alone. However, we assessed the relative composition of the two sibling species using a genetic fingerprint (16S ribosomal RNA) and found about twice as many *L. austrodigitalis* (69%) than *L. digitalis* (31%) in samples collected between December 2012 and April 2013 within tens to hundreds of meters from the original sampling locations (Appendix S1: Fig. S2). *Lottia digitalis/L. austrodigitalis* and *T. funebris* spawn gametes into the water column, where they undergo development into nonfeeding veliger larvae prior to settlement; *L. keenae* releases pelagic egg capsules from which feeding veligers emerge (Strathmann 1992). In the supporting information (Appendix S1: Section S1), we describe the methods used to quantify historical shifts in gastropod body size in the context of local population density and tidal height, as well as spatial variability in temperature at the sampling locations.

Model specification

We constructed a pair of statistical models (“field-agnostic” and “field-contextualized”) relevant to comparisons of body-size change in the context of museum specimens. The response variable was individual body size (mm). The field-agnostic models had a categorical effect of era but lacked the relevant ecological covariates (i.e., population density, tidal height), and treated each gastropod as an individual replicate (i.e., ignored sampling design). The field-contextualized models were appropriate to the sampling designs for each of the three study species, but the common goal was to determine whether incorporating uncertainty at the scale of tens or hundreds of meters (a higher resolution than typical museum studies) would affect our inferences about body-size change. The models of individual body size for *L. digitalis/L. austrodigitalis* and *L. keenae* included interactive effects of era \times density and era \times tidal

height. Because of the nested nature of the sampling designs (unlike *T. funebris*), these models included group-level intercepts for sampling units unique to each era ($n = 34$ and 12; *L. digitalis/L. austrodigitalis* and *L. keenae*, respectively). We did not include higher group-level intercepts (e.g., for sampling area or site), because we did not wish to constrain the intercepts because of the lengthy time intervals between sampling (>50 yr). The study design for *T. funebris* included only two sampling areas (exposed area and sheltered area), and thus estimating a group-level intercept was not possible. Instead, the model for individual body size included an interaction between era and sampling area.

Each pair of models was run for varying levels of data availability, because analyses of body size from museum specimens are often on truncated size distributions. We varied data availability by truncating the size-frequency data according to the past size distribution at 0.05 quantile intervals from 0 to 0.5. In other words, at minimum we removed all individuals smaller than the smallest one observed in the historic study, and at most we removed all individuals smaller than the median gastropod observed in the historic study.

The model of individual body size for *T. funebris* did not include an effect of population density or tidal height because estimating the effect of either continuous covariate with only two estimates of density was minimally informative. Instead we used a different source of data for a second analysis of mean body size, population density, and tidal height for *T. funebris* (Appendix S1: Section S1). In this analysis, we included effects of era, population density, and tidal height, as well as the following interactions to test our hypotheses: era \times density and era \times tidal height. We fit a separate intercept for each sampling area (exposed and sheltered areas).

We assessed multicollinearity among the covariates (era, density, tidal height) using variance inflation factors and Pearson correlation coefficients. All variance inflation factors were <1.6 and correlations were <0.42, indicating the multicollinearity was not a concern. Body length was natural log transformed to facilitate the interpretation of the main effect of interest (era) as a proportional change in body size. We incorporated weakly informative normal priors on the global intercept (mean = 2, SD = 2) and slope parameters (mean = 0, SD = 1). For *T. funebris* and *L. digitalis/L. austrodigitalis*, we modeled the response variable, size, with a normal distribution. For individual body size in *L. keenae*, we instead chose to use a Student's t distribution to accommodate outliers and estimated v (degrees of freedom) using a gamma distribution. We fit the models with 8,000 iterations across four chains and discarded the first 1,000 iterations of each chain as warm-up, resulting in a posterior sample of 4,000 for each response. We inspected visually the chains for convergence, confirmed that the scale-reduction factor (R_{hat}) was less than 1.05, and ensured that the minimum effective sample size (n_{eff}) was greater than 1,000

for all the parameters (Gelman et al. 2013). To assess model fit, we used posterior predictive checks, calculated Bayesian P values for the discrepancy between observed or simulated data and their expected values (Gelman et al. 2013), and calculated Bayesian R^2 (Gelman et al. 2019). We also plotted model residuals against fitted values to determine whether heterogeneity was a problem. For *T. funebris*, model residuals did not display heterogeneity. For *L. digitalis/L. austrodigitalis*, residuals displayed some evidence of heterogeneity when quantile thresholds of 0.4–0.5 were used for the field-agnostic models, and when a threshold of 0 was used for the field-contextualized model. For *L. keenae*, residuals displayed some evidence of heterogeneity when quantile thresholds of 0.35–0.5 were used for the field-agnostic models. However, these departures from homogeneity were not deemed serious enough to warrant reparameterizing the models. All models were fit with Stan (Carpenter et al. 2017) using the package “brms” (Bürkner 2017) in R 3.2.2 (R Core Team 2018). A permanent clone of the data and code is available in the Stanford Digital Repository (<https://purl.stanford.edu/bs528mw1630>).

Long-term trends in air and seawater temperature

We used long-term seawater and air temperature time-series data to place the decadal-scale changes in gastropod body size in a climate context (Appendix S1: Section S1). In brief, we used seawater temperature

data (1937–2015) collected from a beach at Hopkins Marine Station and air temperature data (1951–2015) from a nearby weather station in Monterey (5 km southeast of the sampling sites; 117 m above sea level). Temperature data were summarized to characterize average interannual variation across each year (mean), the three hottest months within a year (maximum), and the three coldest months (minimum). We tested for linear temporal trends in air and seawater temperature using a regression incorporating a continuous autocorrelation structure of order 1. Model fit was assessed using plots of residuals and observed values against fitted values.

RESULTS

In general, the size-frequency distribution for all three gastropods displayed a shift towards smaller sizes (Fig. 1) over the study period of 61.0 ± 8.7 yr (mean \pm SD, $n = 3$). For example, median body size decreased by 41% in *L. keenae* and decreased by 23–24% in *L. digitalis/L. austrodigitalis* and *T. funebris*. However, maximum size increased by 36% in modern *L. keenae*, and the size-frequency distribution became positively skewed in 2014. The consequences of bimodality became apparent when we removed progressively more data (represented by the vertical lines in Fig. 1) prior to analysis. Our inferences about body-size change were sensitive not only to data availability, but also ecological context (i.e., sampling design, covariates).

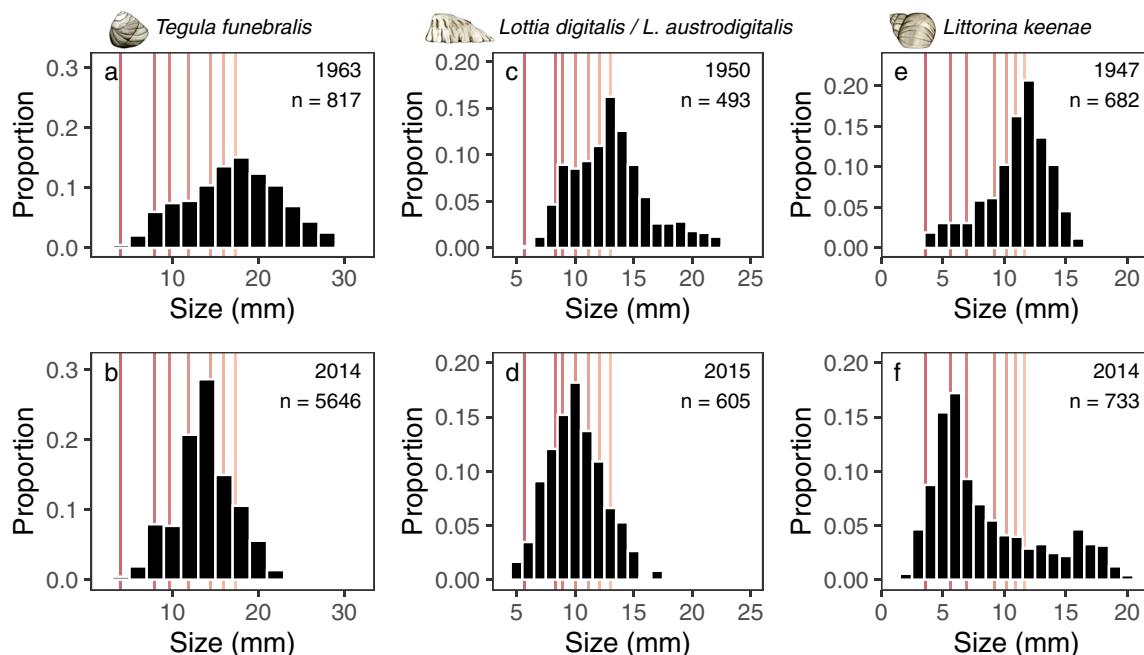


FIG. 1. Size-frequency distributions of three intertidal gastropods sampled in the past (a, c, e) and present (b, d, f), pooled across all sampling locations. The vertical lines indicate the i th quantile of size for each species in the past (where $i = 0, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5$), used as minimal size thresholds for inclusion in the analysis. That is, the darkest (leftmost) vertical line represents 0, and the lightest (rightmost) vertical line represents 0.5.

In turban snails (*T. funebris*), we compared a field-agnostic model (Fig. 2a; Bayesian $R^2 = 0.05\text{--}0.23$) to one that included a fixed effect of sampling area (Fig. 2a; Bayesian $R^2 = 0.08\text{--}0.23$) across different size thresholds for inclusion (i.e., data availability). Snails at the exposed transect displayed smaller declines in body size (7–15% declines) than at the protected transect (11–22% declines). As the size-threshold for inclusion increased, these differences became less apparent and the effect was dominated by snails at the sheltered transect (Fig. 2a). The field-contextualized models for limpets and periwinkles included hierarchical random effects and thus did not have separate red symbols for each sampling unit (Fig. 2b,c). Bayesian R^2 was higher for field-contextualized models (0.48–0.51 and 0.35–0.58 for *L. digitalis*/*L. austrodigitalis* and *L. keenae*, respectively) than field-agnostic (0.06–0.21 and 0.00–0.35 for *L. digitalis*/*L. austrodigitalis* and *L. keenae*, respectively) models. The field-contextualized models resulted in larger uncertainty around the estimated proportional change in size. For *L. digitalis*/*L. austrodigitalis*, the decline in body size inferred from field-contextualized models became weaker as more data were removed (–18% to –4%; Fig. 2b), but for *L. keenae*, the magnitude and sign changed (Fig. 2c). That is, the historical change in body size switched from a 37% decline to a 13% increase as the size threshold increased. This pattern is a consequence of the observed bimodality of the snail size distribution in 2014 (Fig. 1f). In summary, the proportional change in body size depended on whether pertinent field information and the entire size distribution was included in the analysis. None of the field-agnostic (Bayesian $P = 0.47\text{--}0.55$) nor field-contextualized

(Bayesian $P = 0.47\text{--}0.56$) models across all three species suffered from a lack of fit.

In addition to the effect of history (era), the field-contextualized models revealed that population density and tidal height influenced body size in different ways for each of the gastropods (Appendix S1: Fig. S3). For example, there was a strong negative relationship between mean body size and snail density in *T. funebris* in 2014, but this relationship was absent in historical samples (Fig. 3). In general, turban snails were larger at lower tidal heights, but this effect was stronger in the past (Fig. 3). The inclusion of population density and tidal height for the model of mean body size in *T. funebris* explained more than half the variance (Bayesian $R^2 = 0.54$). Individual body size was also correlated negatively with population density in the two other species, but in *L. digitalis*/*L. austrodigitalis*, the effect was stronger in the past. Tidal height did not affect the individual body size of *L. digitalis*/*L. austrodigitalis*, but was correlated weakly with individual body size of *L. keenae* in the past (Fig. 3).

Between 1951 and 2010, air temperature in Monterey displayed considerable variability (Fig. 4a). Maximum air temperatures declined, albeit nonsignificantly, by $0.02^\circ\text{C}/\text{yr}$ ($t_{1,58} = -1.6$, $P = 0.12$) while minimum air temperatures increased by $0.02^\circ\text{C}/\text{yr}$ ($t_{1,58} = 2.1$, $P < 0.05$). Annual mean air temperatures did not change ($t_{1,58} = -0.4$, $P = 0.7$) over this period. In contrast, seawater temperature at Hopkins Marine Station between 1938 and 2015 displayed less variability than air temperature, and maximum seawater temperatures increased by $0.01^\circ\text{C}/\text{yr}$ ($t_{1,76} = 2.8$, $P < 0.01$) (Fig. 4b). Minimum seawater temperatures

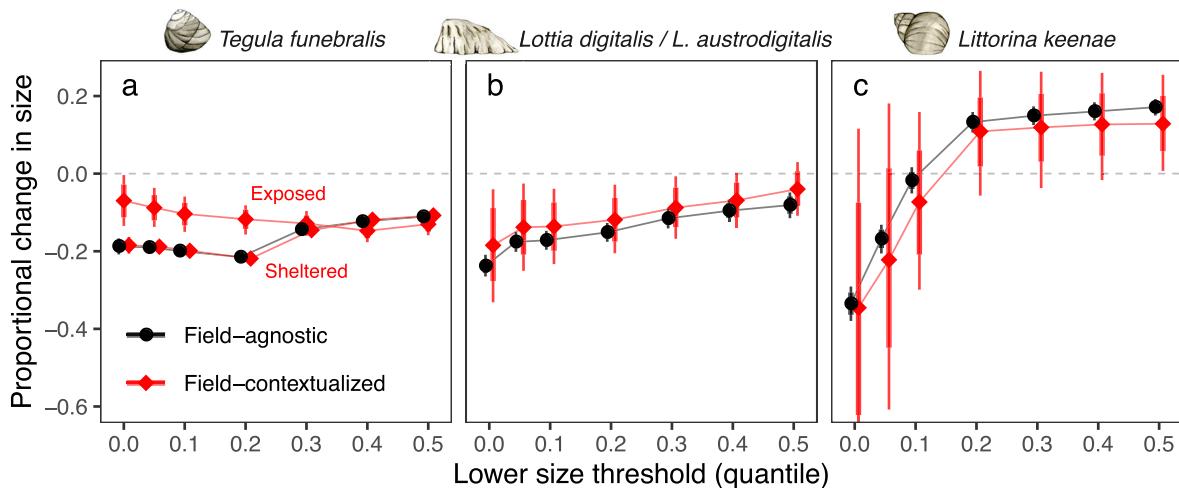


FIG. 2. Proportional change in gastropod body size derived from field-agnostic (black points) and field-contextualized (red diamonds) models. For *Tegula funebris* (a), the field-contextualized models included a fixed effect of sampling area (exposed vs. sheltered). For *Lottia digitalis*/*L. austrodigitalis* (b) and *Littorina keenae* (c), the field-contextualized models were hierarchical and included a group-level intercept for each sampling area. The field-agnostic models ignored the sampling areas for all three species. The x-axis represents the size threshold (i.e., minimum) for inclusion in the analysis. In other words, we removed all individuals smaller than the size quantile i ($i = 0, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5$) in the historical population. Error bars represent 80% and 95% Bayesian credible intervals.

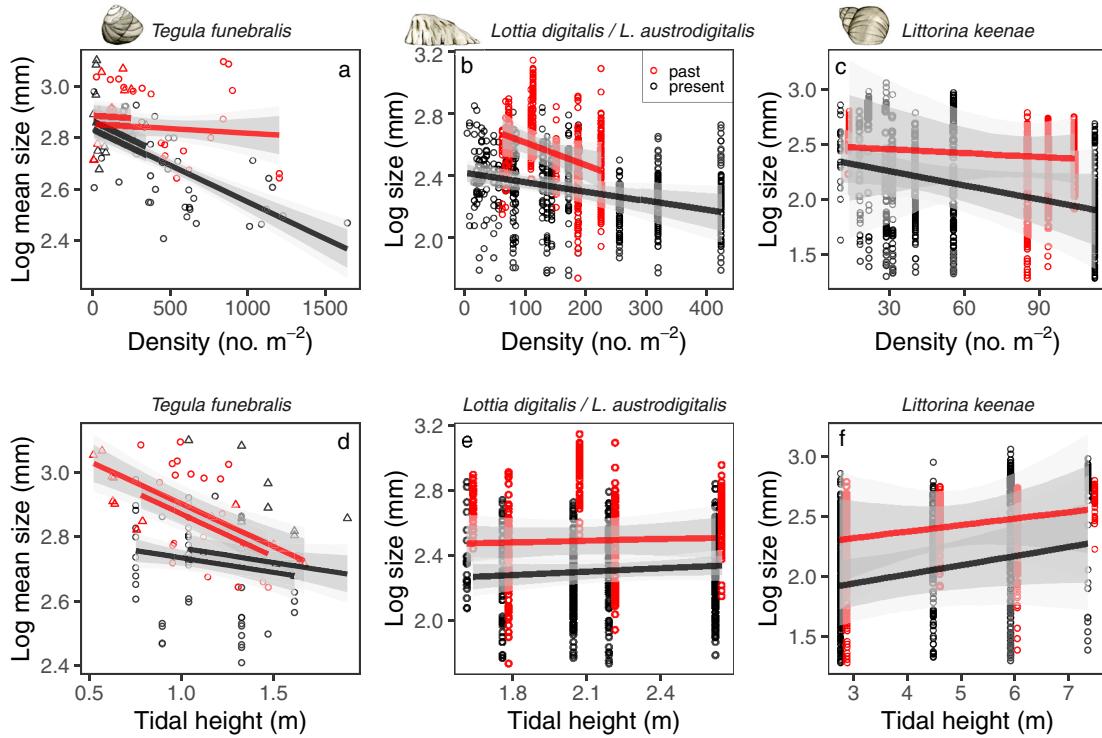


FIG. 3. Gastropod size (log mm) plotted against population density and tidal height for *Tegula funebralis* (a, d), *Lottia digitalis*/*L. austrodigitalis* (b, e), and *Littorina keenae* (c, f). For *T. funebralis*, we plot mean size for a sampling unit; for the other two species we plot individual size. Fitted lines are derived from linear models with 80% and 95% Bayesian credible intervals; coefficients from these models are plotted in Appendix S1: Fig. S3.

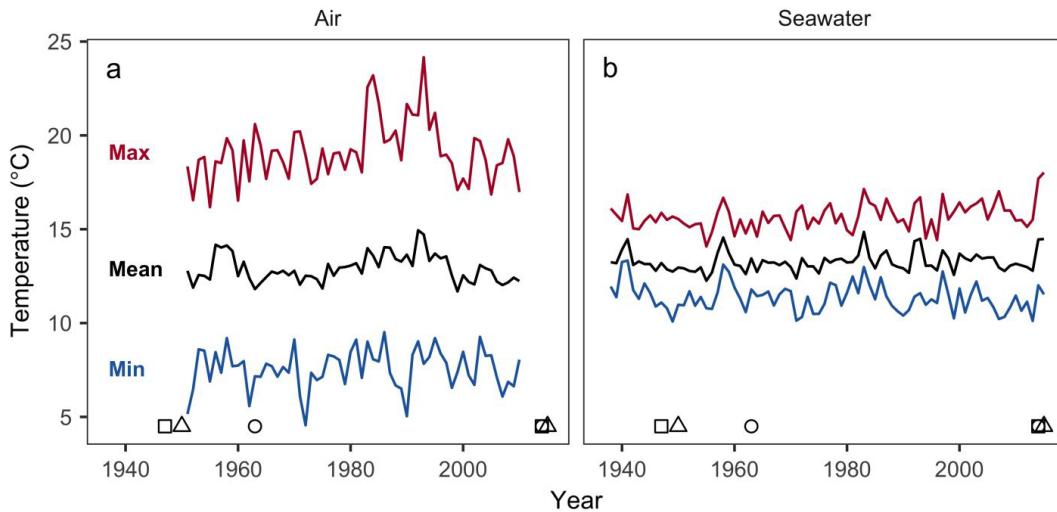


FIG. 4. (a) Air temperatures from a weather station in Monterey, California and (b) seawater temperatures from Hopkins Marine Station, Pacific Grove, California. Symbols next to the x-axis represent the years during which gastropods were sampled (*Tegula funebralis*, circles; *Lottia digitalis*/*Lottia austrodigitalis*, triangles; *Littorina keenae*, squares).

declined by 0.01°C/yr, but this trend was marginally significant ($t_{1,76} = -1.7$, $P = 0.09$). Mean seawater temperatures did not change ($t_{1,76} = 1.2$, $P = 0.24$) over this period.

DISCUSSION

Our case study using intertidal gastropods demonstrates that the direction, magnitude, and uncertainty of body-size change is contingent upon pertinent field

details and the amount of data available for analysis. These contingencies became apparent only because we could choose to ignore them or incorporate them appropriately in our analysis, but this choice is often not available in historical comparisons of body size (or any other biological attribute) that rely on archival data. Sources of archival data include archaeological middens, museum specimens, photographs, and documents; their creative and careful integration offer a longer perspective on environmental change than contemporary approaches in ecology (McClenachan et al. 2015). The use of archival data is typically opportunistic and thus the central tenet of statistical inference, random sampling, must be evaluated with care (Grant 2015).

Many historical studies of body size rely on archived museum specimens that lack information on sampling methods, and there is a well-appreciated risk that collectors chose the biggest or most unusual specimens (Pyke and Ehrlich 2010). Comparisons of body size based on museum specimens have addressed the potential bias by removing small or juvenile individuals to truncate size distributions for analysis (Roy et al. 2003, Caruso et al. 2014, Wilson-Brodie et al. 2017). Moreover, museum specimens are typically associated only with a collector, date, and a coarse site location. Despite the well-known fact that organisms display gradients in size over fine spatial scales and environmental gradients (Vermeij 1972), relevant ecological covariates are usually lacking in museum-based comparisons, and more generally, in archival studies. We discuss the potential consequences of these limitations below.

The spatial scale of a field site can vary and depends on the organism of interest, but often ranges from meters to hundreds of meters for ecological studies. Even over these short distances, sites can encompass enough environmental variation that result in distinct populations and communities. For example, the spatial extent of our study site (Point Cabrillo) is 180×80 m. Within the site, there is considerable variation in the physical habitat and environmental covariates. These details must be taken into account when studying present-day patterns in populations and communities, and thus are also relevant for making historical comparisons. Indeed, our inferences regarding body-size decline were tempered when the variation between sampling units was taken into consideration, resulting in greater uncertainty around the estimate of proportional change in body size (for *L. digitalis*/*L. austrodigitalis* and *L. keenae*). In the case when a hierarchical model was not possible, declines in the body size of *T. funebris* were more apparent in the sheltered sample than the exposed sample, despite being only 180 m apart. Some of the variation in gastropod body size was predictable. Smaller individuals were associated with higher population densities, particularly in the present-day samples. Larger snails were found at lower tidal heights for *T. funebris* (a low intertidal species), but the opposite was true for *L. keenae* (a high intertidal species). At worst, ignoring relevant

covariates could result in erroneous inferences about body-size change, if for example historical samples were collected at different tidal heights or in populations with different densities. Instead, we have generated hypotheses about the context dependence of body-size change; for example, is the density dependence of body size stronger under present environmental conditions?

In addition to ecological context, our inferences were sensitive to data availability. One limitation of museum-based studies of body-size change is the potential bias towards larger size classes. A strength of our approach, based on historical reports, is that we were able to test the consequences of different size thresholds on our interpretations of body-size change. For two gastropods (*T. funebris*, *L. digitalis*/*L. austrodigitalis*), the magnitude of the observed decline became smaller as a larger size threshold was imposed on the data. In *L. keenae*, the direction of change switched. There was a large decline (-35%) in body size when considering the entire size distribution, but the inferred change in body size became positive ($+20\%$) when the smallest size classes were excluded from analysis. These results highlight an unsurprising, yet undiscussed, feature of historical comparisons of body size that are unable to consider more than one summary statistic of a size-frequency distribution. The use of a minimum size threshold in museum-based comparisons of body size alleviates the potential preference towards large specimens, which is an important consideration. But another oft-stated justification of arbitrary size thresholds is the desire to focus on maximum body size. By necessity, the observed maximum (e.g., the upper quantile of a size distribution) is subject to the vagaries of chance because the largest individuals are necessarily rare. For this reason, although we observed the largest periwinkle snails in 2014, we view the large (37%) overall decline in body size as an equally important result.

We have observed a pattern of decline in average gastropod body size over the past 4–6 decades, but identifying the mechanism for the decline, or understanding variability in the response, is not straightforward. Previous studies have associated declines in body size with climate warming and the temperature–size rule. In our study, the three gastropods were distributed along an intertidal gradient and thus varied in their exposure to seawater and air temperatures. We observed the most consistent declines in *T. funebris*, which lives primarily in the low intertidal and is most affected by seawater temperatures. For *L. digitalis*/*L. austrodigitalis* living in the mid to upper intertidal, the populations generally exhibited declines in body size. We saw the most variable change in *L. keenae*, which lives in the high intertidal and is primarily affected by air, rather than seawater, temperatures. Over the study period, maximum seawater temperatures increased, and minimum air temperatures increased. Mean air and seawater temperatures did not change appreciably. Minimum seawater temperatures declined, but this trend was marginally significant. Determining which aspects of temperature (e.g., mean or maximum, air or seawater) are relevant for the

relative speed of development and growth, and thus the concordance of these body-size declines with the temperature–size rule, will require detailed investigations of the environmental conditions during the ontogeny of each species. Moreover, without size-at-age data, it is difficult to exclude other mechanisms for the observed declines in body size.

The estimated linear trends for air and seawater temperature were punctuated by considerable interannual fluctuations, particularly for air temperature. Such interannual variability in air and seawater temperature, as well as other climatic variables (e.g., northerly winds, oceanic transport, and fog), is a well-appreciated feature of the upwelling environments that characterize central and northern California (García-Reyes and Largier 2010, Johnstone and Dawson 2010). Interannual variation in upwelling influences the supply of invertebrate larvae to rocky shores with downstream consequences for recruitment and ecological dynamics (Roughgarden et al. 1988, Menge et al. 2004). Relevant to our study, changes in body size between any two points in time can simply reflect naturally variable recruitment during the years preceding the sampling events. For example, the bimodal size-frequency distribution of *L. keenae* suggests a recent recruitment event coupled with survival of a few long-lived individuals. Variable recruitment and survival may also influence the relative composition of the cryptic limpet species pair, *L. digitalis* and *L. austrodigitalis*. Between 1977 and 1998–1999, the proportion of the northern species (*L. digitalis*) declined (from 34% to 7% on rocky habitat), but the proportion of the southern species (*L. austrodigitalis*), increased (from 66% to 93%) on the Monterey Peninsula (Murphy 1978, Crummett and Eernisse 2007). By 2013 (our data), the relative composition had reverted back to 69% *L. austrodigitalis*, suggesting that the temporary reduction of the northern species on the Monterey Peninsula was related to the warm El Niño phase in 1998. These observed changes in species composition are consistent with the thermal physiology of *L. digitalis*/*L. austrodigitalis* and *L. austrodigitalis* (Dong and Somero 2009). Therefore, the relative composition of *Lottia* limpets in 2015 (during the resampling of *Lottia* size-frequency distributions) was likely to be similar to that in 1977, but it is impossible to know their relative composition in 1950 (during the original sampling of *Lottia* size-frequency distributions). However, it is also unclear whether these congeners differ in size in their zone of sympatry (e.g., on Point Cabrillo), where they would be exposed to similar environmental conditions. In short, we caution that inferences regarding body-size change may be complicated by potential shifts in the relative frequencies of these two cryptic sister species.

Thus far we have focused primarily on temperature as a mechanism to influence the size distributions of intertidal gastropods. However, reductions in the body size of any shelled marine invertebrate may also be caused by ocean acidification, because declines in the saturation state of aragonite makes calcification more energetically expensive (Gazeau et al. 2010). Species interactions can

also influence body size. In particular, sea otters recolonized the Monterey Peninsula in the early 1960s (Lubina and Levin 1988), and therefore we would expect a decline in the body size of their prey. This specific trophic interaction likely applies only to the turban snails (*Tegula funebris*; Estes et al. 2003) and highlights the potential for different mechanisms to cause the same observed response.

Museum specimens have been used to demonstrate both declines (Roy et al. 2003) and increases (Fisher et al. 2009) in the size distributions of intertidal gastropods. In heavily populated Southern California (northeast Pacific Ocean), size declines in one species (*Lottia gigantea*) were readily attributable to human harvesting, but the causes of decline in three other species were less clear (Roy et al. 2003). Considerable increases (23%) in the body size of an intertidal predatory whelk (*Nucella lapillus*) were observed in Maine, USA (northwest Atlantic Ocean), but Fisher et al. (2009) were unable to identify the cause of this directional change in shell length. It is impossible to know if and how the issues we have raised here, namely, sampling methods and pertinent ecological covariates (tidal height, population density), would have changed inferences about body-size change in these and other previous studies that are based on archived collections (Gardner et al. 2011). Moving forward, we propose that incorporating relevant ecological details will help resolve the observed variation in the direction and magnitude of ectotherm body-size change over the past century.

ACKNOWLEDGMENTS

We thank W. Sano and L. Howitt for logistical support, D. Kohrs with archived materials at Hopkins' Miller Library, and S. Palumbi and E. Sheets for the molecular identification of limpets. Snails were illustrated by M. Mach. Comments from C. Baxter, J. Carlton, M. Denny, A. Galloway, H. Hayford, F. Micheli, J. Pearse, V. Pearse, and J. Watanabe improved an early version of the manuscript. We thank two anonymous referees and M. Vermeij for constructive reviews. RE was supported by a National Science Foundation postdoctoral fellowship (DBI 1308719), LPM was supported by National Science Foundation grant OCE 1130095, and SYL was supported by the Marine Life Observatory Program at Hopkins Marine Station.

LITERATURE CITED

- Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* 25:1–58.
- Baudron, A. R., C. L. Needle, A. D. Rijnsdorp, and C. Tara Marshall. 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology* 20:1023–1031.
- Bertness, M. D. 1977. Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. *Ecology* 58:86–97.
- Branch, G. 1975. Ecology of *Patella* species from the Cape Peninsula, South Africa. IV. Desiccation. *Marine Biology* 32:179–188.
- Bürkner, P.-C. 2017. brms: an R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* 80:1–28.

- Burrows, M. T., S. J. Hawkins, J. J. Moore, L. Adams, H. Sugden, L. Firth, and N. Mieszkowska. 2020. Global-scale species distributions predict temperature-related changes in species composition of rocky shore communities in Britain. *Global Change Biology* 26:2093–2105.
- Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. *Journal of Statistical Software* 76:1–32.
- Caruso, N. M., M. W. Sears, D. C. Adams, and K. R. Lips. 2014. Widespread rapid reductions in body size of adult salamanders in response to climate change. *Global Change Biology* 20:1751–1759.
- Crummett, L. T., and D. J. Eernisse. 2007. Genetic evidence for the cryptic species pair, *Lottia digitalis* and *Lottia austrodigitalis* and microhabitat partitioning in sympatry. *Marine Biology* 152:1–13.
- Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences USA* 106:12788–12793.
- Dong, Y., and G. N. Somero. 2009. Temperature adaptation of cytosolic malate dehydrogenases of limpets (genus *Lottia*): differences in stability and function due to minor changes in sequence correlate with biogeographic and vertical distributions. *Journal of Experimental Biology* 212:169–177.
- Elahi, R., K. P. Sebens, and G. A. De Leo. 2016. Ocean warming and the demography of declines in coral body size. *Marine Ecology Progress Series* 560:147–158.
- Estes, J., M. Riedman, M. Staedler, M. Tinker, and B. Lyon. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology* 72:144–155.
- Fenberg, P. B., A. Self, J. R. Stewart, R. J. Wilson, and S. J. Brooks. 2016. Exploring the universal ecological responses to climate change in a univoltine butterfly. *Journal of Animal Ecology* 85:739–748.
- Fisher, J. A., E. C. Rhile, H. Liu, and P. S. Petraitis. 2009. An intertidal snail shows a dramatic size increase over the past century. *Proceedings of the National Academy of Sciences USA* 106:5209–5212.
- García-Reyes, M., and J. Largier. 2010. Observations of increased wind-driven coastal upwelling off central California. *Journal of Geophysical Research: Oceans* 115:1–8.
- Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? *Trends in Ecology & Evolution* 26:285–291.
- Gazeau, F., J.-P. Gattuso, C. Dawber, A. Pronker, F. Peene, J. Peene, C. Heip, and J. Middelburg. 2010. Effect of ocean acidification on the early life stages of the blue mussel *Mytilus edulis*. *Biogeosciences* 7:2051–2060.
- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2013. *Bayesian data analysis*. Chapman and Hall, Boca Raton, Florida, USA.
- Gelman, A., B. Goodrich, J. Gabry, and A. Vehtari. 2019. R-squared for Bayesian regression models. *American Statistician* 73:307–309.
- Giesel, J. T. 1970. On the maintenance of a shell pattern and behavior polymorphism in *Acmaea digitalis*, a limpet. *Evolution* 24:98–119.
- Grant, E. H. 2015. Please don't misuse the museum: 'declines' may be statistical. *Global Change Biology* 21:1018–1024.
- Hacker, S. D., and R. S. Steneck. 1990. Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71:2269–2285.
- Helmuth, B., N. Mieszkowska, P. Moore, and S. J. Hawkins. 2006. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology Evolution and Systematics* 37:373–404.
- Hochachka, P. W., and G. N. Somero. 1984. *Biochemical adaptation*. Princeton University Press, Princeton, New Jersey, USA.
- Johnstone, J. A., and T. E. Dawson. 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. *Proceedings of the National Academy of Sciences USA* 107:4533–4538.
- Lubina, J. A., and S. A. Levin. 1988. The spread of a reinvading species: range expansion in the California sea otter. *American Naturalist* 131:526–543.
- McClenachan, L., A. B. Cooper, M. G. McKenzie, and J. A. Drew. 2015. The importance of surprising results and best practices in historical ecology. *BioScience* 65:932–939.
- Menge, B. A., C. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecological Monographs* 74:663–684.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.
- Moore, P. J., R. C. Thompson, and S. J. Hawkins. 2011. Phenological changes in intertidal con-specific gastropods in response to climate warming. *Global Change Biology* 17:709–719.
- Morris, R., D. Abbott, and E. Haderlie. 1980. *Intertidal invertebrates of California*. Stanford University Press, Palo Alto, California, USA.
- Murphy, P. 1978. *Collisella austrodigitalis* sp. nov.: a sibling species of limpet (Acmaeidae) discovered by electrophoresis. *Biological Bulletin* 155:193–206.
- Ohlberger, J. 2013. Climate warming and ectotherm body size—from individual physiology to community ecology. *Functional Ecology* 27:991–1001.
- Poloczanska, E. S., et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3:919–925.
- Pyke, G. H., and P. R. Ehrlich. 2010. Biological collections and ecological/environmental research: a review, some observations and a look to the future. *Biological Reviews* 85:247–266.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology* 106:85–108.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics of complex life cycles. *Science* 241:1460–1466.
- Roy, K., A. G. Collins, B. J. Becker, E. Begovic, and J. M. Engle. 2003. Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California. *Ecology Letters* 6:205–211.
- Sagarin, R. D., J. P. Barry, S. E. Gilman, and C. H. Baxter. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* 69:465–490.
- Schmidt-Nielsen, K. 1984. *Scaling: Why is animal size so important?* Cambridge University Press, Cambridge, UK.
- Shanks, A. L., A. Walsler, and L. Shanks. 2014. Population structure, northern range limit, and recruitment variation in the intertidal limpet *Lottia scabra*. *Marine Biology* 161:1073–1086.

- Sheridan, J. A., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. *Nature Climate Change* 1:401–406.
- Southward, A. 1991. Forty years of changes in species composition and population density of barnacles on a rocky shore near Plymouth. *Journal of the Marine Biological Association of the United Kingdom* 71:495–513.
- Strathmann, A., S. Hawkins, and M. Burrows. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology* 20:127–155.
- Strathmann, M. F. 1992. Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. University of Washington Press, Seattle, Washington, USA.
- Suarez, A. V., and N. D. Tsutsui. 2004. The value of museum collections for research and society. *BioScience* 54:66–74.
- Sutherland, J. P. 1970. Dynamics of high and low populations of the limpet, *Acmaea scabra* (Gould). *Ecological Monographs* 40:169–188.
- Underwood, A. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* 33:185–202.
- Vermeij, G. J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology* 53:693–700.
- White, E. P., S. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution* 22:323–330.
- Wilson, R. J., S. J. Brooks, and P. B. Fenberg. 2019. The influence of ecological and life history factors on ectothermic temperature–size responses: Analysis of three Lycaenidae butterflies (Lepidoptera). *Ecology and Evolution* 9:10305–10316.
- Wilson-Brodie, R. J., M. A. MacLean, and P. B. Fenberg. 2017. Historical shell size reduction of the dogwhelk (*Nucella lapillus*) across the southern UK. *Marine Biology* 164:190.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3101/supinfo>

DATA AVAILABILITY

Data and code are available in the Stanford Digital Repository: <https://purl.stanford.edu/bs528mw1630>.