RESEARCH ARTICLE

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Temperature-mediated variation in selection on offspring size: A multi-cohort field study

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Abstract

1. Offspring size is a key life-history trait that often covaries negatively with temperature. Most studies focus on how temperature alters selection on offspring size during early life-history stages such as embryos or larvae. The degree to which temperature alters the relationship between offspring size and post-metamorphic performance remains unclear as field studies across multiple temperature regimes are rare.

2. I deployed over 6,000 individuals of known offspring size, into the field across 28 cohorts spanning 4 years for the model marine invertebrate, *Bugula neritina* and monitored their survival, growth and reproduction.

3. Offspring size closely tracked the local environmental temperature across cohorts. This offspring size–temperature covariance appeared to be adaptive, at least from the perspective of mothers. When temperatures were warmer, the relationship between offspring size and performance was weak; when temperatures were cooler, the relationship was strongly positive.

4. The estimates of selection based on maternal fitness differed from those based on offspring fitness, suggesting temperature-mediated parent–offspring conflict over offspring provisioning exists. I also found evidence for temporal autocorrelation in temperature and selection on offspring size.

5. The fact that temperature affects the relationship between offspring size and post-metamorphic performance further complicates the challenge in understanding the ubiquitous covariance between offspring size and temperature.

KEYWORDS

egg size, maternal effect, offspring size, seed size

1 | INTRODUCTION

Offspring size varies enormously. Orchids produce millions of dust-like seeds while double coconuts weigh kilograms (Moles et al., 2005). Unlike body size, which tends to vary strongly with phylogeny, offspring size can differ massively between very closely related taxa (Marshall & Keough, 2008). Offspring can also vary in size among conspecifics, populations and even siblings from same clutch offspring can differ by more than twofold (Cameron et al., 2017; Marshall et al., 2018). Understanding variation in offspring size at all scales has long been a goal of life-history theoreticians (Stearns, 1992).

Offspring size is an interesting and confusing trait because it affects the fitness of both mothers and offspring simultaneously, so selection acts on both (Hadfield, 2012; Wolf & Wade, 2001). Because maternal resources are not infinite, mothers can either make a few large offspring that perform relatively well or many offspring that perform poorly but are inexpensive to produce (Smith & Fretwell, 1974; Vance, 1973). Mothers and offspring may be in conflict over the amount of provisioning that each offspring

receives—selection on offspring typically favours larger offspring sizes, while selection on mothers may favour less investment per individual offspring. The resolution of this conflict depends on accurate estimates of the heritability of offspring size—a logistically challenging parameter to estimate and data are lacking (Wolf & Wade, 2001). However, exploring covariation between selection on offspring size from the perspective of both offspring and mother and observed offspring size distributions may shed light on who 'wins' this parent–offspring conflict. For example, if offspring size covaries with estimates of selection based on offspring fitness, then this implies that offspring 'win' the conflict over provisioning. If, on the other hand, offspring size covaries with estimates of selection based on maternal fitness, then this implies that mothers 'win'. To date, few studies have explored the correlation between temporal variation in selection on offspring size and phenotypic distributions in nature (but see Kingsolver et al., 2001; Sinervo et al., 2000; Wilson et al., 2009).

One of the more reliable patterns in offspring size variation is the relationship with temperature. Offspring size strongly covaries with temperature at all scales of organisation, from among broods, to among populations and even species (Marshall et al., 2018; Pettersen et al., 2019). In almost all taxa, higher temperatures are associated with smaller offspring (though there are exceptions Marshall et al., 2018), implying that there may be a universal explanation for this pattern.

Most studies seeking to understand the relationship between offspring size and temperature focus on early life-history stages. These studies invoke different mechanisms by which temperature affects selection on offspring size but they are not mutually exclusive. Anderson and Gillooly (2020) argue that temperature-dependent changes in larval growth and mortality shape maternal investment, and show strong support for their theory using latitudinal variation in fish life histories. Meanwhile, others have focused on temperature-dependent changes in developmental costs (Kamler, 1992, 2005), such that development tends to be less costly in warmer conditions. Again, there is reasonable support for this theory across a range of taxa (Kamler, 2005; Marshall et al., 2020; Pettersen et al., 2019). Importantly, both these branches of theory focus on embryo/larval phase and imply that selection at this stage drives temperature-dependent selection on offspring size overall. Such a focus seems reasonable—selection on offspring size during this early phase can be strong and temperature-dependent (Bownds et al., 2010; Burgess & Marshall, 2011; Fischer et al., 2003; Kamler et al., 1998). However, it is worth remembering that offspring size can affect performance across the entire life history, and can even permeate multiple generations (Marshall et al., 2003; Plaistow et al., 2006). How the relationship between offspring size and post-larval performance changes with temperature remains unclear, particularly under field conditions.

The rarity of field studies that explore the relationships among temperature, offspring size and adult performance is understandable, given the formidable logistical challenges associated with such studies. In order to reliably determine whether the relationship between offspring size and adult performance varies with natural fluctuations in temperatures, repeated measures of selection across multiple seasons and years are necessary to avoid confounding (assuming that such experiments cannot be done across spatial temperature gradients). Thus, there is a dearth of field studies that examine the relationship between offspring size and adult performance for multiple cohorts across multiple years sampling a range of environmental temperatures, particularly outside a few classic systems of large vertebrates (Wilson et al., 2009). I sought to address this knowledge gap by conducting a field experiment whereby I deployed over 6,000 individuals of known offspring size, across 28 different experimental cohorts spanning 4 years. I monitored the survival, growth and reproduction of these individuals to examine how the relationship between offspring size and adult performance changes with environmental temperature in the field. I used these estimates of performance to parameterise a simple optimality model to examine how selection on offspring size changes with temperature from the perspective of mothers (for development of the modelling approach, see Marshall et al., 2006; Marshall & Keough, 2006) and compared to estimates of selection based on offspring fitness alone.

The degree to which selection varies over time in nature remains a long-standing and controversial topic in evolutionary ecology (Arnold, 2014; Kingsolver & Diamond, 2011; Kingsolver et al., 2016; Morrissey, 2016; Morrissey & Hadfield, 2012). Thus, an additional long-term and ongoing goal of this study is to estimate temporal variability in selection in a marine invertebrate. Such measures are lacking outside the studies of model field organisms, in which vertebrates tend to be over-represented (Kingsolver & Diamond, 2011). Furthermore, studies of temporal variation in selection in marine systems are extremely rare, and yet environmental variation shows very different temporal patterns in marine systems (Vasseur & Yodzis, 2004). Thus, I also used my 28 consecutive estimates of selection on offspring size to formally estimate the temporal autocorrelation of this parameter across cohorts. The cohorts correspond roughly with the generation time of my study species and therefore provide a rare insight into how selection varies over time in the field for an invertebrate.

2 | MATERIALS AND METHODS

2.1 | Experimental set-up and sites

I used well-established methods to collect, measure and deploy offspring of known size into the field (Cameron et al., 2016; Marshall et al., 2003). Reproductively mature *Bugula neritina* colonies were collected from the Royal Brighton Yacht Squadron in Port Phillip Bay, Victoria Australia (37°54′19.08″S, 144°58′51.94″E). I collected between five and 10 colonies from the field, with care taken to ensure they were around the same size. Colonies were maintained in insulated aquaria for between 24 and 48 hr before being exposed to bright light, whereupon they released their brooded larvae. Note that multiple colonies were spawned in the same container,

so I could not distinguish which larvae came from which colony. I collected larvae, measured their length to the nearest micron using a digital camera attached to a dissecting microscope and then settled them onto individual, pre-roughened PVC settlement plates (11 cm × 11 cm × 8 mm). Because I could not trace which larvae came from which colony, both among- and within-colony variation in offspring size contributed to the variation that I observed. Based on previous studies, I expect that most of the variation in offspring size was driven by within-colony variation (Marshall et al., 2008).

Larvae were allowed to settle for 1 hr before any that had not settled were discarded. The metamorphosing settlers were given 24–36 hr to undergo metamorphosis before being transported in insulated aquaria to the field site for deployment. Temperatures during settlement and metamorphosis were kept constant at 18°C (±0.5) throughout the entire experimental period. Note that after settlement, *Bugula* sp. is sessile for the rest of its life.

I deployed the experiment at Blairgowrie Yacht Squadron (38°21′20.2′S, 144°46′22.8′E), approximately 60 km south of my source population (Brighton). While using one site for collections of brood stock, and another for field deployment of the experiment is not ideal, it was unavoidable in this instance. Brighton provides one of the few sites in Port Phillip Bay that has a reasonable population of reproductive individuals year-round, but unfortunately, experiments deployed here during the summer typically experience mass die-offs. In contrast, *Bugula neritina* is harder to collect at Blairgowrie, where it appears to be strongly out-competed by the native, *Bugula dentata*, but experiments deployed here experience relatively less severe mortality events during summer. Importantly, temperature regimes between the two sites are extremely similar, and show the same temporal trends—indeed, exploration of temperature data for the two sites revealed a correlation of >0.99 in the years 2008–2014. Blairgowrie has slightly more water movement (Lagos et al., 2017), and a greater proportion of the sessile invertebrate community is native relative to Brighton, but the sites are very similar in most other respects. Though the use of two different sites for sourcing larvae and deploying the experiment is imperfect, I saw no other option that allowed me to collect reproductive material and conduct these experiments year-round.

I deployed the settlement plates (bearing offspring of known size) into the field by attaching them to the undersides of PVC backing panels (50 × 50 cm; 16 plates per panel) suspended at a depth of ~1 m. Over 4 years (January 2016 to January 2020), cohorts were deployed approximately every 6–8 weeks, with 28 cohorts (experimental cohorts) deployed in total. Within each cohort, I deployed between 210 and 240 larvae of known offspring size, with the exception of two cohorts where I could only deploy 160 and 54 larvae (due to unusually low numbers of reproductive colonies in the source population for those cohorts). Because each panel received 16 experimental plates (individuals), for any one cohort there were between four and 15 backing panels, but the density of experimental plates was the same on each panel across all cohorts. Overall then, I estimated the offspring size–performance relationship for over 6,000 individuals, which were deployed in the field across 28 cohorts

that spanned four austral summers and three winters. Experiments have paused due to the disruption of the COVID-19 pandemic.

2.2 | Estimating offspring performance in the field

Individuals of known offspring size were censused weekly for a total of 4 weeks in the field. In warmer months, 4 weeks is sufficient time for individuals to become reproductive but in cooler months, individuals grow much more slowly and are not yet reproductive after this time (though many are approaching the size at which reproduction occurs). I refer to post-metamorphic individuals as 'adults' throughout because, with their colonial form, *Bugula neritina* have the same body plan throughout post-metamorphic life and so it seems inappropriate to refer to pre-reproductive colonies as 'juveniles'. Nevertheless, it should be noted that not all the colonies I refer to as adults were necessarily reproductive.

Individuals were recorded as alive if they were present and >10% of their zooids were healthy, or dead if they were missing or >90% of zooids were pale and empty. *Bugula neritina* grows via the budding of zooids at regular intervals and I used the standard metric of counting the number of bifurcating branches in an individual to estimate size (a good proxy for biomass). I monitored individuals for signs of reproduction—individuals begin sexually reproducing by producing specialised zooids (ovicells) that contain a single brooded larva. When individuals became reproductive, I counted the total number of ovicells on that individual. Previous experiments show that individuals can live for up to 9 months in the field (though most do not live this long, see Pettersen et al., 2016) and so ideally, each cohort should have lasted at least this long. However, my goal was to estimate the performance of different cohorts at regular intervals across the year, so if I had left each experimental cohort in the field until all of the individuals had died in every cohort, I would have quickly been overwhelmed by the task of monitoring multiple cohorts simultaneously. In an effort to keep the monitoring manageable, I therefore ended every cohort after the same amount of time. Importantly, most mortality occurs in the first 2 weeks after deployment in this system and size at 4 weeks successfully predicts around 80% of variation in lifetime reproductive output in *Bugula* (Pettersen et al., 2016). Specifically, data from the study by Pettersen et al. (2016) showed a strong, positive relationship between size at 4 weeks and lifetime reproductive output, and the study was conducted at the same field site, spanning March to November in 2014. My performance metrics were imperfect but represent a pragmatic compromise that allowed me to estimate the offspring size–performance relationship repeatedly across multiple cohorts.

2.3 | Temperature data

Temperature data for calculations of temporal autocorrelations during the experiments were sourced from Integrated Marine Observatory System (IMOS-SOOP-TMV 2008–2013: Lat −38.2,

144.8 to Lat/Lon −38.154, 144.944). This dataset has the highest spatial and temporal resolution data I could access with the longest contiguous set of data for as close as possible to my locations of interest. I used daily mean temperature as my response variable and used standard autocorrelation analysis to determine how correlations in temperature decayed with increasing lags between time points. To analyse how temperature during the experiments covaried with various life-history traits, I used mean temperature for the month in which that cohort was deployed at the site. Spatial variation in temperature also exists but it is likely to be trivial relative to temporal variation—my experimental panels were distributed only a few metres from each other and deployed to the same, constant depth (temperature varies with depth at my field site).

2.4 | Analytical methods

Offspring size was a fixed continuous variable in all analyses. To analyse the effect of offspring size on subsequent survival after 4 weeks in the field, I used logistic ANCOVA where survival was a binomial response, and Cohort and Panel (Cohort) were categorical effects. To analyse the effect of offspring size on growth and reproduction, I used a mixed-effects linear model, estimated using REML. I was also interested in estimating how temperature altered the relationship between offspring size and performance, so I replaced cohort with the mean temperature of the water when that cohort was deployed as a continuous factor. In other words, temperature and cohort were synonymous with each other.

2.5 | Temperature and selection on offspring size from the perspective of mothers

To estimate how temperature alters post-metamorphic selection on offspring size at the level of cohorts, I parameterised a simple optimality model based on the relationship between offspring size and performance (survival and growth) for each cohort, after 4 weeks in the field (see Marshall et al., 2006 for details). The relationship between offspring size and survival for each cohort is described by a logistic regression, and the relationship between size and offspring size is described by a simple linear regression. The coefficients for both the survival function and the growth function were conditioned on temperature. Because larger offspring are costlier than smaller offspring, I then calculated maternal fitness as the product of offspring performance divided by offspring size (volume). I plotted the relationship between offspring size and predicted maternal fitness for a range of offspring sizes.

I was therefore able to generate the estimates of how selection on offspring size from the perspective of mothers varied as a function of the temperature a cohort experienced. To estimate selection from the perspective of offspring and how this varied as a function of temperature, I used the same parameters as above but did not include the offspring size number trade-off. Finally, I also used

standard temporal autocorrelation analyses to examine variation in selection at the level of cohorts.

3 | RESULTS

3.1 | General patterns

Of the 6,362 individuals of known offspring size deployed into the field, 4,262 (66%) survived to the final census date within each cohort. Survival and growth of adult colonies varied substantially among experimental cohorts (Table 1). Growth showed very little variation in space (panels) within cohorts, whereas survival was more spatially variable. Some cohorts had over 90% survival while others had less than 10%. Offspring size varied between 152 and 355 microns, with a mean of 249 and standard deviation of 19.08 (Figure 1, CV = 7%).

3.2 | Temperature variation

Temperature varied between ~10.5 and 22.5°C during the experimental period (Figure 1). Temperature was strongly autocorrelated

TABLE 1 Variance partitioning in survival and growth of *Bugula neritina* colonies across 28 experimental cohorts. Time refers to variance attributable to cohort effects, space refers to experimental panels deployed across the field site

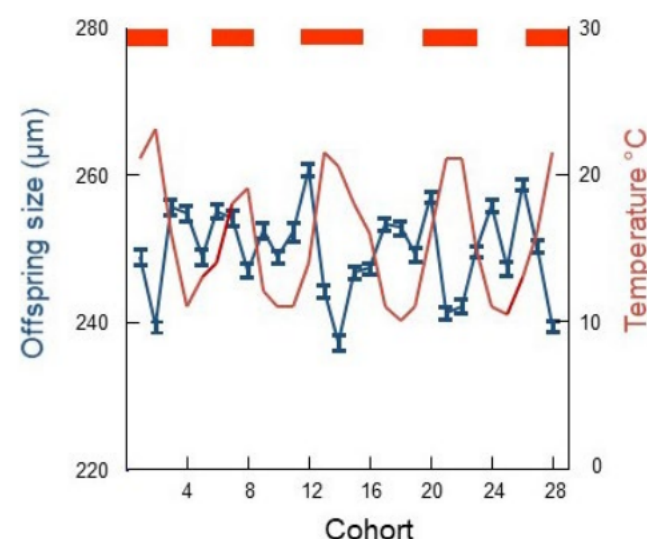| Source	Survival	Growth
Time	22	35
Space	15	6
Residual	63	59

FIGURE 1 Plot of mean offspring size (shown in blue; ±*SE*) and mean temperature (shown in red) across the experimental period. Red bars indicate summer periods
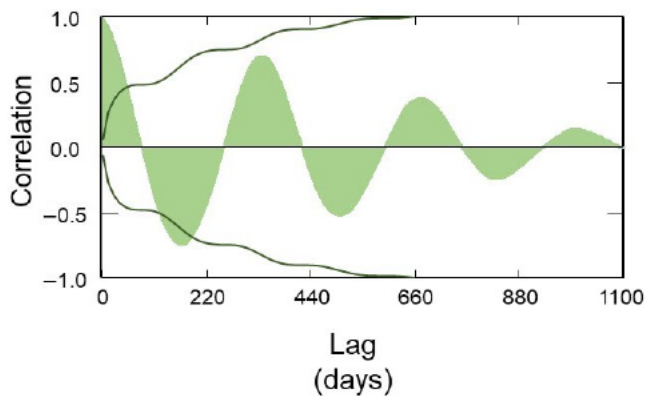
FIGURE 2 Autocorrelation plot of daily temperatures from 2008 to 2012 in Port Phillip Bay, Australia. Green bars represent correlation coefficient for each lag period. Dark green lines indicate the estimate of error of correlation coefficient. Correlations are no longer significantly positive after lags of >54 days. Note that there is also a significant negative correlation between temperatures 122 days apart

from one day to the next, such that temperature on any one day was significantly positively correlated with the temperature up to 59 days into the future (Figure 2). For an interval of 6 weeks (the average frequency at which cohorts were deployed), the temperature at the start of the period had a correlation coefficient of ~0.62 with temperature at the end the period.

3.3 | Offspring size effects within and across cohorts

Overall, individuals that came from larger offspring survived better ($\chi^2 = 6.395$, $p = 0.011$) and were larger ($F_{1,4,040} = 15.17$, $p < 0.001$) after 4 weeks in the field, compared to individuals that were smaller as offspring. Individuals from the largest offspring had, on average, a 91% chance of surviving, whereas the smallest offspring had only a 33% chance of surviving. On average across all cohorts, after 4 weeks in the field, the smallest offspring formed colonies of ~360 zooids, while the largest offspring grow to ~620 zooids—a 72% difference in colony size.

The effects of offspring size on survival varied in space (Offspring size × Panel (Cohort): $\chi^2 = 21.71$, $p < 0.001$) within cohorts, but the effects of offspring size on growth was more spatially consistent (Offspring size × Panel (Cohort): $F_{211,3,799} = 0.826$, $p = 0.966$). In contrast, I detected temporal variation in the effects of offspring size on both survival ($\chi^2 = 47.66$, $p < 0.001$) and growth (Offspring size × Cohort: $F_{28,4,012}$ 1.528, $p = 0.037$), though the effect for growth was relatively minor. Looking across cohorts (time), the relationship between offspring size and growth varied from essentially flat to significantly positive (Figure 3). The relationship between offspring size and survival varied much more among cohorts in both sign and strength. For example, in two cohorts, there was a significant negative relationship between offspring size and survival, while for most others there was either a flat or significantly
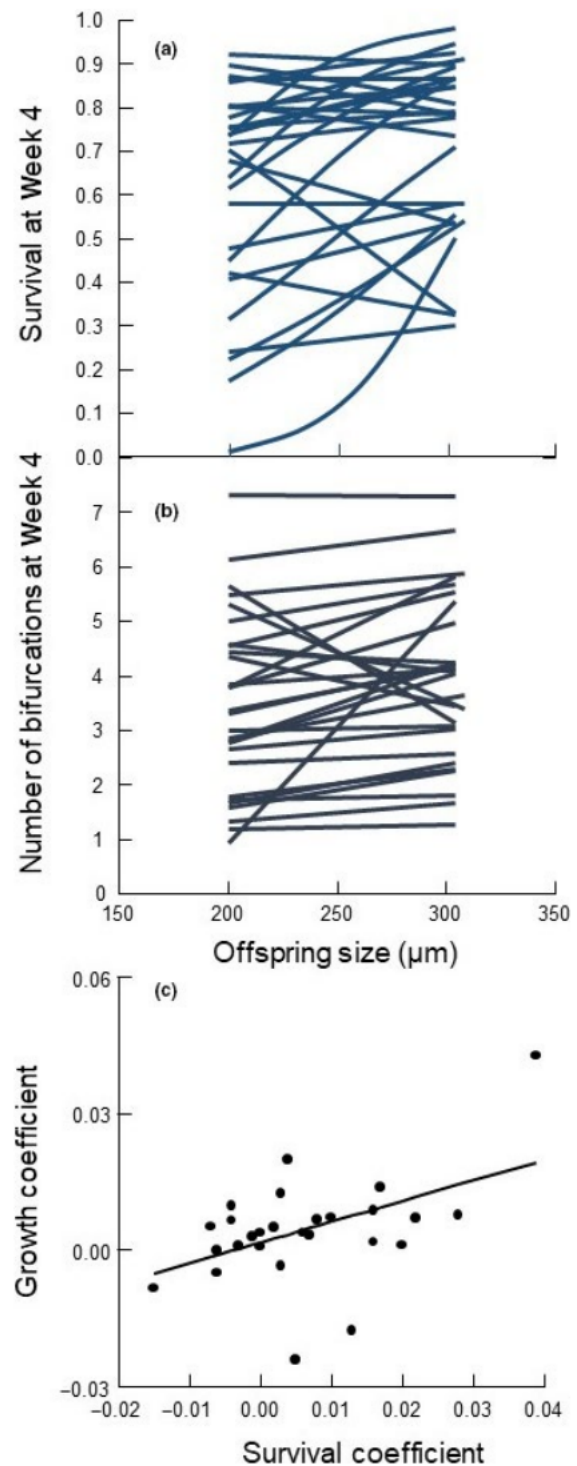

FIGURE 3 Projected relationships between offspring size and survival (panel a) and growth (panel b) after 4 weeks in the field for *Bugula neritina*. Each line represents an individual cohort and is generated based on the regression equations (logistic for survival, linear for growth) for that particular cohort. Note the axis for growth is in colony bifurcations, zooid number relates to colony bifurcations according to the formula Zooids = 2^{2+n}, where *n* is the number of zooids. Panel (c) shows the relationship between the coefficient linking offspring size to survival and the coefficient linking offspring size to growth—in cohorts where there was a strong positive relationship between offspring size and survival, there was also a strong positive relationship between offspring size and growth

positive relationship between offspring size and survival (Figure 3). The relationship between offspring size and survival positively co-varied with the slope of the relationship between offspring size and growth (Figure 3). In other words, in cohorts where the relationship between offspring size and survival was strongly positive, so was the relationship between offspring size and growth. Conversely, when the relationship between offspring size and survival was weak or negative, the relationship between offspring size and survival was similarly weak or negative.

Reproduction only occurred in eight cohorts, but there was a positive relationship between offspring size and fecundity ($F_{1,3,984} = 18.48$, $p < 0.001$), and there was no significant variation in this relationship among cohorts ($F_{28,3,984} = 1.15$, $p = 0.263$).

3.4 | (Co)Variation between life-history traits and temperature among cohorts

At the cohort level, offspring size, growth and survival were all correlated with each other and with temperature (Figure 4). Average survival and growth of the cohort was strongly correlated with temperature, as higher temperatures were associated with higher rates of growth ($F_{1,26} = 11.29$, $p = 0.002$, $R^2 = 0.276$) and lower rates of survival ($F_{1,26} = 20.06$, $p < 0.001$, $R^2 = 0.436$) across all years.

Offspring size was highly variable among cohorts and covaried with temperature (Figure 4c). Mean offspring sizes were smaller at higher temperatures across all years (Temperature: $t_{26} = 3.68$, $p = 0.001$; Figure 3c). The relationship between offspring size and temperature was unaffected by year (Year × Temperature: $t_{25} = -1.45$, $p = 0.306$; Year: $t_{26} = 0.966$, $p = 0.343$).

Temperature strongly mediated the relationship between offspring size and performance (Figure 5). At moderate to warmer temperatures, the relationship between offspring size and post-metamorphic survival was flat, or even slightly negative at the highest temperatures, where all offspring had relatively low performance. In contrast, at cooler temperatures, there was a strongly positive relationship between offspring size and survival—with larger offspring surviving better. Similarly, for growth, the relationship between offspring size was weak to non-existent at warmer temperatures, despite growth being higher overall. At cooler temperatures, the effect of offspring size on growth was again positive and strong (Figure 5). In contrast to patterns for survival and growth, the relationship between offspring size and fecundity was steepest (and positive) at highest temperatures, but relatively weak at lower temperatures.

3.5 | How does temperature affect selection on offspring size from the perspective of mothers and offspring?

The estimates of selection on offspring size were strongly related to temperature and differed depending on whether the fitness of
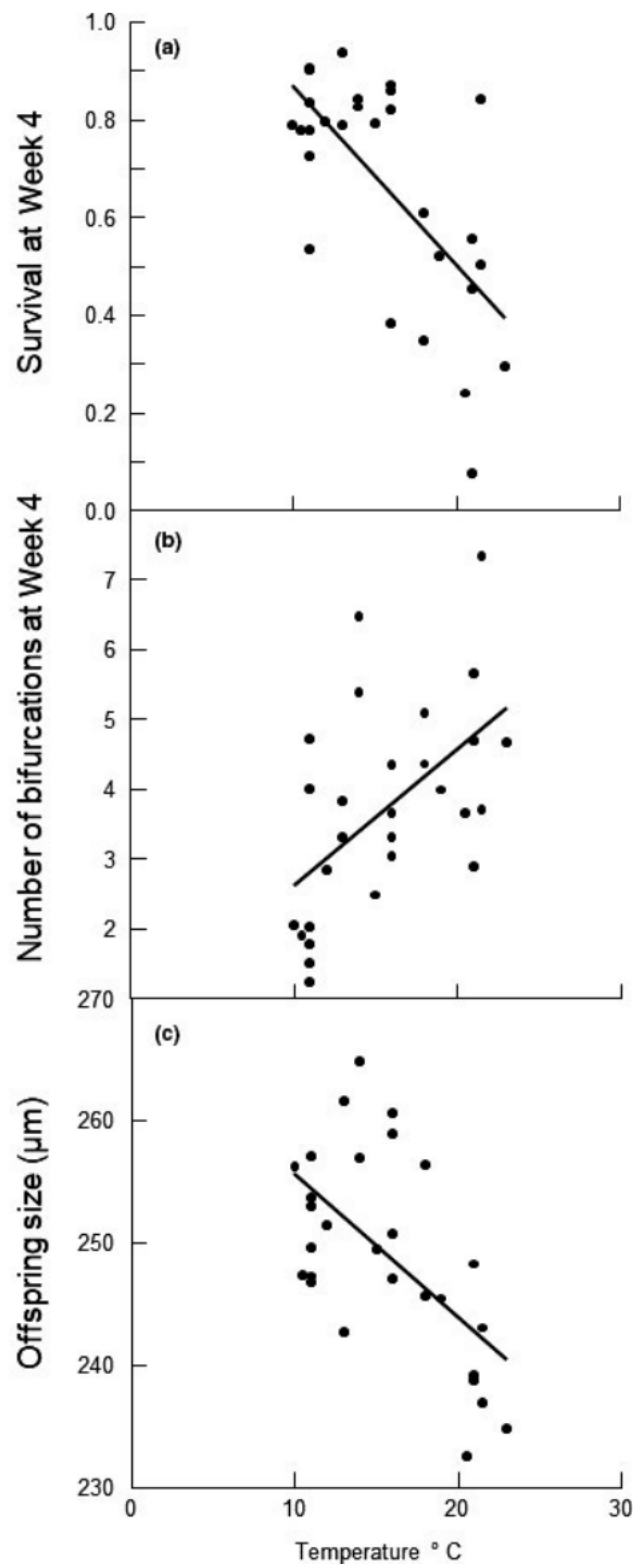

FIGURE 4 Relationship between mean environmental temperature and (a) mean survival, (b) mean growth and (c) mean offspring size of 28 experimental cohorts for *Bugula neritina*. Each dot represents the mean for a single cohort and the line is the line of best fit

offspring or mothers was considered (Figure 6). There was a significant negative correlation between cohort temperature and selection on offspring size from the perspective of both mothers ($R^2 = 0.933$,
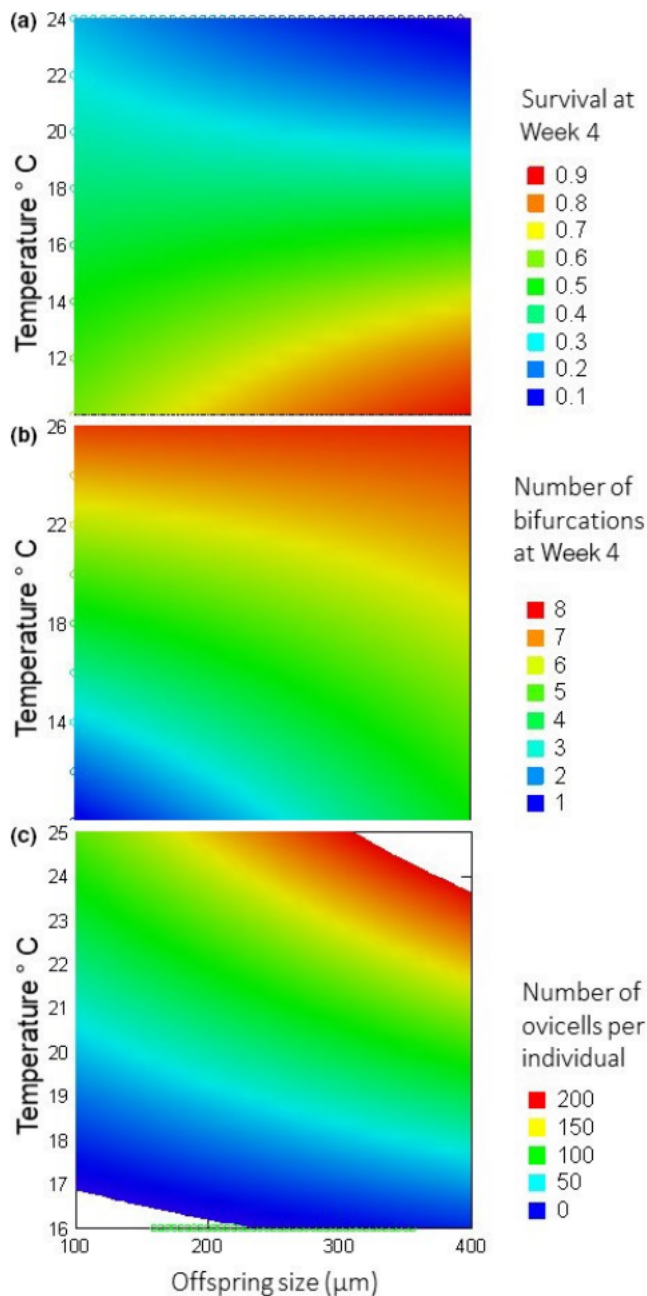
FIGURE 5 Projected relationship between various performance metrics of *Bugula neritina* and environmental temperature (*y* axis) and offspring size (*x* axis) across cohorts. Warmer colours indicate higher values of performance. Panel (a) shows projected survival, panel (b) shows projected growth (in bifurcations) and panel (c) shows reproductive output. Projections are based on the coefficients of the analysis of offspring size and temperature on the various performance metrics

$F_{1,26} = 362.7$, $p < 0.001$) and offspring ($R^2 = 0.614$, $F_{1,26} = 41.4$, $p < 0.001$). While higher temperatures generally resulted in smaller, or even negative selection coefficients, the precise form varied depending on how fitness was evaluated (Figure 6).

At temperatures cooler than ~17°C, selection on both mothers and offspring favoured larger offspring. At the hottest temperature (24°C), selection on both mothers and offspring favoured smaller
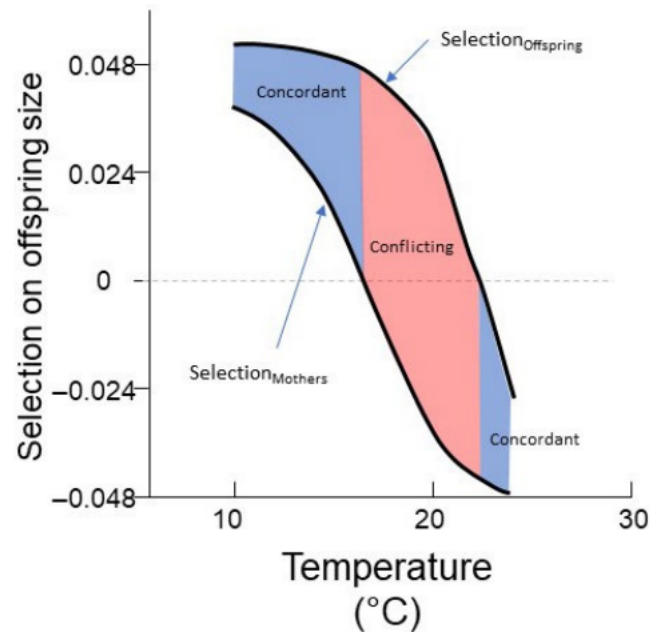

FIGURE 6 Summary of selection coefficients on offspring size as a function of environmental temperature in the field. Top line represents selection measured as a function of offspring fitness, and bottom line represents selection measured as a function of maternal fitness, which incorporates a trade-off between offspring size and number. Blue shading indicates temperatures where selection is in the same direction for both measures (qualitatively concordant) and red shading indicates temperatures where selection favours smaller offspring from the maternal perspective and larger offspring from the offspring's perspective (qualitatively conflicting)

offspring. However, between these two temperatures (~18–22°C), selection on offspring favoured larger offspring sizes but selection on mothers favoured smaller offspring sizes. In terms of numbers of cohorts, 25% of cohorts (7 of 28) experienced a mismatch between selection on maternal and selection on offspring. However, in terms of percentage of the year occupying the temperature range in which selection was mismatched, temperatures sit between these values for around ~40% (149 days per year) of the year on average. The qualitative predictions of selection on mothers matched the observed temporal variation in offspring sizes among cohorts (cf. Figures 4 and 6)—the observed offspring sizes in a particular cohort matched the offspring size that was predicted to be optimal from the perspective of mothers, rather than offspring.

3.5.1 | Temporal autocorrelation in selection on offspring size

Selection on offspring size in one cohort is significantly positively correlated with selection in the subsequent cohort (Figure 7). Selection is also significantly negatively correlated with selection on offspring size two cohorts later. The pattern of autocorrelation after this follows a clear seasonal trend with alternating positive and
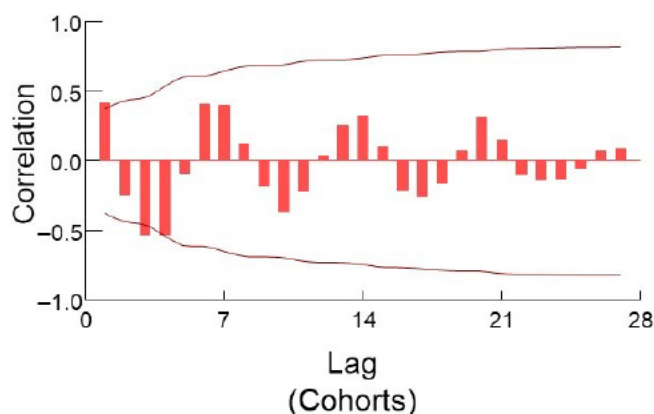
FIGURE 7 Autocorrelation plot of selection on offspring size. Red bars represent correlation coefficient for each lag period. Dark red lines indicate the estimate of error of correlation coefficient. Correlations are no longer significantly positive after lags of >1 cohort. Note that there is also a significant negative correlation between selection estimates two cohorts apart

negative correlations (though none significant) as the intervals align with the different seasons. A similar pattern appears for the much better replicated autocorrelation plot of environmental temperature (see Figure 2).

4 | DISCUSSION

The relationship between offspring size and adult performance varied in time and was strongly correlated with temperature. In some cohorts, offspring size had no effect on subsequent performance but in most cohorts, larger offspring survived and grew more than smaller offspring. For those cohorts in which reproduction occurred, those individuals from larger offspring had higher fecundity. Generally, the relationship between offspring size and performance was strongest and most positive under cooler conditions. Most surprisingly, I found that in cohorts growing in the warmest temperatures, offspring size had little to no effect on growth but there was a weak but significant, negative relationship between offspring size and survival—larger offspring poorly relative to smaller offspring in higher temperatures. The strong covariance between temperature and offspring size effects occurred independently of conditions during metamorphosis—across all cohorts, offspring developed in the same thermal environment and only experienced different temperatures as juveniles. It seems therefore that temperature affects the offspring size–performance relationship throughout the entire life history, not just during development (Anderson & Gillooly, 2020; Pettersen et al., 2019). That offspring size effects are temperature dependent from the larval stage, and through adult life to reproduction illustrates the complex web of selection acting on this trait.

Offspring size is a plastic trait in *Bugula* (Allen et al., 2008; Burgess & Marshall, 2011). I found offspring sizes from field-collected colonies varied both within and among cohorts. Comparing cohort mean offspring sizes in terms of volume, there was an ~1.5-fold difference

in size between the cohort with the smallest mean size and the cohort with the largest mean size. Offspring size in any one cohort tracked environment temperature closely—under cooler conditions, offspring were much larger. This temperature effect on offspring size matches previous studies in *Bugula* (Burgess & Marshall, 2011) and studies across ectotherms more broadly (Pettersen et al., 2019). The among-cohort covariation between offspring size and temperature strongly matched the covariance between selection on offspring size and temperature—implying this variation was adaptive. It is worth noting that my estimates of selection ranged between −0.05 and 0.05, which compared to other studies, are relatively weak (median reported values are ~0.16 from a meta-analysis of linear selection coefficients; Kingsolver et al., 2001), but these (subtle) changes in selection are closely tracked by changes in offspring size.

The covariance between offspring size and temperature appears to be adaptive from the perspective of mothers, though not always from the perspective of offspring. When temperatures were cooler, the relationship between offspring size and performance was generally steep and positive—a small increase in offspring size therefore yielded a larger increase in performance. When temperatures were warmer, larger offspring survived slightly less well and grew around the same rate at smaller offspring, such that increases in offspring size yielded little to no increase in offspring performance. Given larger offspring are costlier to produce than smaller offspring, mothers should produce larger offspring when they achieve much higher performance than smaller offspring (Smith & Fretwell, 1974). Accordingly, a simple optimality model parameterised with the data predicted that mothers that produce larger offspring are favoured when temperatures are cooler and smaller offspring when temperatures are warmer. Importantly, offspring size plasticity in response to temperature will only be adaptive if the temperature experienced by mothers is a reasonable indicator of the temperature experienced by offspring (Burgess & Marshall, 2014). At my study site, the temperature on any one day significantly, positively correlated with the temperature up around 60 days into the future which covers most of the typical life span of my study species.

I found evidence for temperature-mediated conflicting selection acting on mothers and offspring. The optimality model predicted that for some temperatures, maternal and offspring selection coefficients are qualitatively similar, in essence their interests are aligned. At the coolest temperatures observed, selection from the perspective of both mothers and offspring favours larger sizes; similarly, at the warmest temperatures, selection (from both perspectives) favours smaller sizes, but at intermediate temperatures, conflict emerges. From around 18 to 22 degrees, it is still better to be larger from the offspring's perspective. Larger offspring had higher survival and growth than smaller offspring, but these benefits are insufficient to offset the fecundity costs—across these temperatures, mothers are better off producing smaller offspring. In other words, at intermediate to warmer temperatures, conflict over offspring size emerges and different offspring sizes are predicted to be favoured, depending on which perspective is taken. Temperature data indicate temperatures that generate this conflict occur around 40%

of year, and the cohort data indicate it occurs at least 25%—either way this conflicting selection is not particularly rare. The observed patterns of offspring size (co)variation imply that mothers 'win' this conflict—offspring size declines with increasing temperatures across the range of 18–22 degrees suggesting that selection on maternal fitness drives the plastic response in offspring size. In the absence of the estimates of heritability of offspring, however, definitive answers regarding conflict over provisioning are premature (Wolf & Wade, 2001). Regardless, this study joins those demonstrates that incorporating the costs of producing larger offspring alters the estimates of selection on offspring size dramatically (Cameron et al., 2021; Einum & Fleming, 2000; Larios & Venable, 2018).

I estimated the temporal autocorrelation of selection on offspring size among cohorts—such measures are exceedingly rare for invertebrates and marine species more generally (Kingsolver & Diamond, 2011). Estimating temporal autocorrelation is a notoriously data-hungry exercise, a problem that is exacerbated when one is interested in a cohort-level parameter such as selection (even after measuring thousands of individuals, I only have estimates for 28 cohorts). Thus, any analysis of temporal correlation in selection based on so few cohorts must be regarded as preliminary and underpowered. Nevertheless, when I apply a simple autocorrelation analysis to my estimate of selection on offspring size, I find that the correlation from one cohort to the next is significantly positive. Perhaps more surprising, I find a significant negative correlation at a lag of three cohorts, such that selection during one generation negatively covaries with selection two cohorts later. While I will resume estimating selection on offspring size once COVID-19-related impediments end, selection already shows some autocorrelation patterns. Theory suggests that variation and the degree to which selection is autocorrelated strongly determines the pace of evolution (Travis, 2001). It would therefore be valuable to generate other such estimates for more species other than vertebrates. Regardless, it seems that selection varies from generation to generation, but this variation is not entirely random. It will be interesting to see whether these trends continue once more data can be collected.

The drivers of why temperature alters the relationship between offspring size are unclear. In particular, that larger offspring actually have poorer survival than smaller offspring in very high temperatures is hard to explain—these effects were consistent across multiple years. Yet such temperature × offspring size interactions for survival are not without precedent—larger offspring suffered higher rates of predation than smaller offspring when temperatures were warm in the fire-bellied toad (Kaplan, 1992). Whether larger *Bugula* offspring are also more susceptible to predation in warmer temperatures is unclear. It is worth noting that temperature itself may not be directly responsible for temporal changes I observed—productivity, interspecific competition and predation are all likely to covary with temperature as well. For now, I suspect that temperature itself drives the effects I observed, but this requires more exploration testing. I also found that the relationship between offspring size and subsequent colony growth was much steeper in cooler conditions relative to warmer conditions. In essence, it seems that growth approaches maximal levels at the highest temperatures regardless of offspring size, and offspring size only conveys an advantage under cooler, slower growing conditions.

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CONFLICT OF INTEREST

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DATA AVAILABILITY STATEMENT

The raw data used for these analyses can be accessed at http://dx.doi.org/10.5061/dryad.k3j9kd57f (Marshall, 2021).

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