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PRIMARY RESEARCH PAPER

Transgenerational effects influence acclimation to varying temperatures in *Aurelia aurita* polyps (Cnidaria: Scyphozoa)

Alexandra Loveridge · Cathy H. Lucas

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Abstract Temperature is one of the most important drivers to affect marine ectotherms in the context of anthropogenic climate change modifying seasonal cycles in temperate regions. To reliably predict the impact of climate variability on marine ectotherms, their capacity to adapt to rapid change needs to be understood. Due to fast transmission between generations, transgenerational effects may enable populations to moderate stressors. We examined reproduction across three temperature scenarios and three generations of asexual *Aurelia aurita* polyps: transgenerational warming, transgenerational cooling, and stable temperatures. Polyps were incubated at three temperatures (15, 17, 19°C) encountered in summertime in Southampton Water. In the first two polyps generations, temperature remained the main driver of polyp reproduction. However, in the third generation parental and grandparental temperature influenced offspring production. These effects appeared most strongly in cooling scenarios: polyps who experienced rapid cooling between generations displayed an immediate drop in reproductive output as opposed to polyps who remained at the same temperature as their parents. Our results highlight that transgenerational effects may require more extreme temperatures or increased numbers of generations to have a measurable impact on a population, highlighting the vulnerability of these organisms to continued climate change.

Keywords Jellyfish · Temperature · Asexual reproduction · Transgenerational effects · *Aurelia aurita*

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A. Loveridge (✉) · C. H. Lucas
Ocean and Earth Science, University of Southampton, Southampton, UK
e-mail: al2g14@soton.ac.uk

Introduction

Rising air and ocean temperatures are two indicators of global climate change currently taking place (IPCC, 2019). This warming has profound effects on most ecosystems and the animals living within them: increasing the frequency of marine heatwaves (IPCC, 2019; Shanks et al., 2019); encouraging ocean acidification (Byrne et al., 2010; Klein et al., 2014, 2017); and forcing species to shift their ranges (Poloczanska et al., 2013). In marine ecosystems, several species of scyphozoan jellyfish form large blooms in coastal regions, often interfering with human industry and recreation, from forcing beach closures to clogging power station intake valves (Dong et al., 2010; Kingsford et al., 2018). These transient blooms typically show large interannual variations in both abundance and phenology (Condon et al., 2012; Schnedler-Meyer et al., 2018a) although due to the scarcity of reliable baseline data and a complex life cycle it is unclear how

continued changes to the ocean system will affect scyphozoan populations in the future.

Further investigation of jellyfish life histories has revealed natural cycles spanning multiple spatial and temporal levels (Brodeur et al., 2008; Gibbons & Richardson, 2013; Schnedler-Meyer et al., 2018a). Scyphozoan jellyfish such as the frequently studied *Aurelia* spp. have life cycles composed of both a mobile, pelagic medusa and a sedentary, benthic polyp (Lucas et al., 2012). This flexible life history enables them to take advantage of rapidly changing environments, such as changes to the seasonal temperature cycle experienced by a population (Bayha & Graham, 2014). Polyps are now known to be one of the key determinants of the longevity, magnitude and timing of scyphozoan blooms, by maintaining the benthic population across the year and producing ephyrae under appropriate environmental conditions (Lucas et al., 2012; Schnedler-Meyer et al., 2018b).

As a cosmopolitan species containing multiple different lineages and cryptic sister species (Dawson & Jacobs, 2001), how *Aurelia* spp. populations respond to seasonal environmental stimuli in the short term and the effects of climate variability on this cycle will vary depending on the population and life stage in question (Gambill & Peck, 2014; Hubot et al., 2017). As sedentary benthic organisms, polyp health and reproductive rates are largely determined by in situ environmental conditions and temperature is a key variable dictating growth, survival (Chi et al., 2019) and reproduction (Lucas, 2001; Willcox et al., 2007; Pascual et al., 2015). The thermal optima reflects the seasonal temperature range experienced by a population (Riascos et al., 2013; Höhn et al., 2017) and temperatures above, or below this optima will negatively affect survivorship and growth, even if temperatures are within the survivable temperature range (Purcell et al., 2012; Gambill & Peck, 2014; Loveridge et al., 2021). Asexual reproduction rates increase with increasing temperature as temperatures reach the thermal optima, and in temperate areas, the warmer months are key to increasing the size of the benthic population before reproductive rates decrease as temperatures decline (Purcell et al., 2012). In the context of increased instability in the ocean sphere due to continued climate warming, it is crucial to understand how populations will respond to changes in their thermal environment during these warmer months.

To mitigate the effects of temperatures above or below the thermal optima, the conditions experienced by a polyp may partly determine the performance of its offspring via non-genetic parental effects, or epigenetic processes (Klein et al., 2017; Lu et al., 2020). To date, despite careful study of polyps and their role in perpetuating jellyfish populations, very few studies distinguish between different polyp generations (Lu et al., 2020; Chi et al., 2022). Transgenerational acclimation encompass previous generations' influences on offspring phenotype (Mousseau & Fox, 1998; Zhang et al., 2006; Youngson & Whitelaw, 2008; Wolf & Wade, 2009), resulting in the phenotypic modification of physiological and behavioural offspring traits by the parent in response to a permanent or temporary stimulus (Mousseau & Fox, 1998; Youngson & Whitelaw, 2008). These effects play a critical role in moderating the response of individuals to stressors such as temperature, acting as a buffer against rapid environmental change, providing time for adaptation and genetic change to catch up (Tucić & Avramov, 1996; Mousseau & Fox, 1998; Marshall et al., 2010). This phenomena, also referred to as 'transgenerational plasticity' is generally reserved for sexual reproduction, although there is mounting evidence for similar processes occurring across asexual generations (Garbutt et al., 2014; Norouzitallab et al., 2014). Following Lu et al. (2020), here we define a generation by individuals, i.e. an individual bud is considered the offspring of the individual parent from which it was produced.

In scyphozoan jellyfish, we are only just starting to identify how much of polyp response to environmental change is driven by the in situ external environment or by offspring internal phenotype (Klein et al., 2017; Lu et al., 2020). Transgenerational effects of temperature on reproduction and fitness have been identified in several species across multiple taxa such as the waterflea *Daphnia* sp. and a number of fish species (Wolf & Wade, 2009; Veilleux et al., 2015; Donelson et al., 2016), but remain largely unexplored in scyphozoan jellyfish (Chi et al., 2022). Due to the exclusive asexual reproduction in polyps, these effects may be important in governing population acclimation to changing environmental conditions.

In this study, we aimed to understand how transgenerational effects modify the response of polyps to climate variability in the warmer months of the year. In particular, we examined asexual reproductive

across three polyp generations of the scyphozoan *Aurelia aurita* (Linnaeus, 1758) collected from UK temperate coastal waters. We examined three temperature scenarios: transgenerational warming, transgenerational cooling, and stable temperatures. We tested the following hypotheses:

i. The exposure of parent polyps to different temperatures affects (a) the number of offspring produced per polyp; (b) offspring reproductive mode; and (c) reproductive timing.
ii. Offspring of polyps experiencing stable temperature across multiple generations will differ in terms of (a) the number of offspring produced per polyp; (b) offspring reproductive mode; and (c) reproductive timing, compared with offspring of polyps that experienced transgenerational warming or cooling.

Methods

Medusa collection and establishment of polyp cultures

Polyps of *Aurelia aurita* were settled from planula larvae taken from mature female medusae collected on 18th January 2018 from Horsea Lake, UK (50° 49′ 58.8; − 1° 05′ 36.9), when the ambient surface temperature was 6.3°C and salinity was 21.9. Horsea Lake is a brackish, semi-enclosed, man-made body of water connected to Portsmouth Harbour via a controlled pipe and valve, and the mean bottom (6 m) water temperature ranges from 6.8 (± 1.82 S.D.) °C in February to 19.3 (± 1.36 S.D.) °C in August, remaining below 10°C from December to March (CEFAS, 2018).

Medusae were maintained in a kreisel at the National Oceanography Centre Southampton aquarium. Fully developed polyps that settled on the glass surface were removed using a scalpel and Pasteur pipette and 90 polyps were individually reattached in 60 ml clear polystyrene pots.

Polyp maintenance

Generation 0 (G0) replicates were maintained in individual 60 ml microcosms at 15°C for 14 days before the start of the experiment. Only G0 polyps that reattached were used in the experiment. Prior to the start of the experiment, over 21 days, thirty replicates per group were either maintained at experimental temperatures (15°C), or gradually transitioned at a constant rate to experimental temperatures prior to the start of the experiment (17, 19°C). All replicates were maintained at their experimental temperatures for an additional week before the start of the experiment. Any offspring produced by asexual reproduction before the start of the experiment were removed.

Food was supplied at non-limiting quantities 3 days a week, directly on to polyp tentacles using a Pasteur pipette to minimise uneaten food remaining in the water. Due to suggestions that *Artemia* nauplii are not of sufficient quality to sustain polyps (Lesniowski et al., 2015), a combination of ZM100 (80–200 µm dried zooplankton) mixed with 1 day-old *Artemia* nauplii were fed to the polyps. Salinity was maintained at 31 following a week-long transition from the collection salinity. Seawater was sourced from Southampton Water and passed through pressurised sand filters, a UV steriliser, a protein skimmer and a de-nitrifier before use. When required, reduced salinity water was created by adding reverse osmosis water to seawater until the desired salinity was achieved. Polyp cultures were maintained in darkened temperature-controlled incubators apart from when measurements were being taken (< 1 min) or when being fed (< 1 min) to minimise algal growth and to remove any confounding effects of the dark/light cycle on asexual reproduction (Holst & Jarms, 2007; Liu et al., 2009).

Experimental set up and measurements

Three successive polyp generations (G0, G1, G2) were exposed one of three temperatures representing the potential range of temperatures encountered in summertime in Southampton Water (Fig. 1, 15°C = cold summer; 17°C = typical summer; 19°C = hot summer) (Lucas et al., 1997; Lucas & Lawes, 1998). Successive generations were moved to different temperature conditions in the order outlined in Fig. 1 in order to examine transgenerational warming, transgenerational cooling, and stable temperature scenarios. Temperature cycles in Horsea Lake and Southampton Water are very similar (Lucas et al., 1997), and temperature data from Southampton Water were used because the estuary has longer data records (1984–2012) revealing more

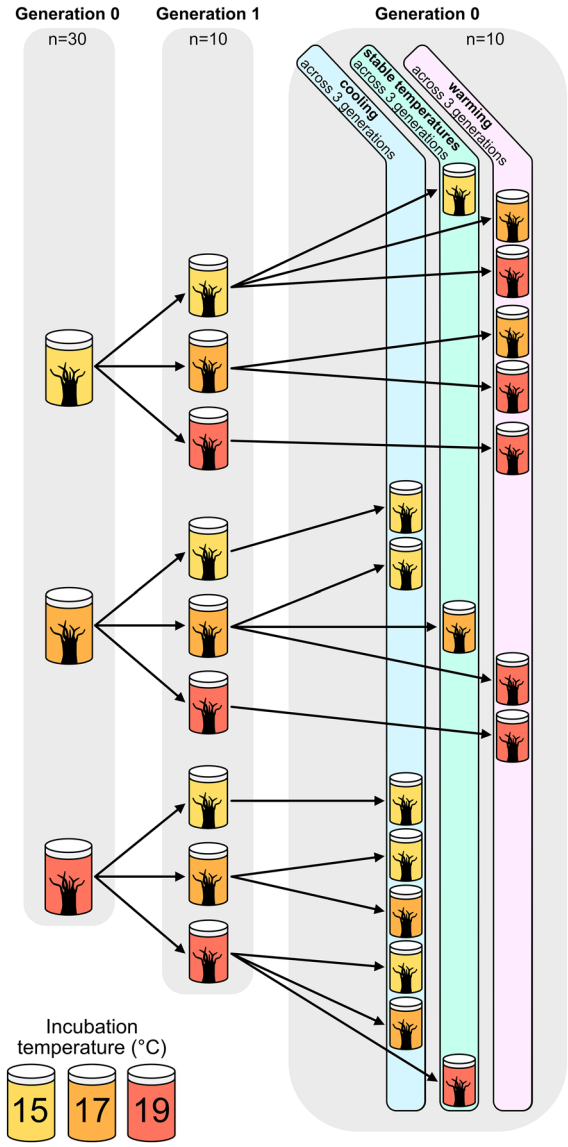

Fig. 1 Experimental design. Three successive generations of asexually reproducing polyps were exposed to three summer temperatures (cold, average, hot) for 49 days to examine the transgenerational effect of cooling, warming and stable temeprature scenarios on reproduction

of the inter-annual variability (CEFAS, 2018). Offspring of G0 and G1 replicated were removed from parent polyps using a Pasteur pipette and placed in individual 60 ml clear polystyrene pots to supply the next experimental generation. Each experiment lasted for 49 days from the introduction of the polyp into its individual microcosm and each replicate was followed individually.

Reproductive output (number of stolonal, directly budded polyps and podocysts, Adler & Jarms, 2009) and whether the polyp was attached, were recorded on a weekly basis.

Data analysis

Each generation was analysed independently from the others. Data were tested for normality and assumptions of statistical models were tested with *q*–*q* plots, Levene's and Shapiro–Wilk's test. Appropriate statistical tests were selected for each analysis based on the results of these tests:

G0: A one-way parametric ANOVA was used to examine the effects of temperature on average total reproductive output and mode (directly, stolonally budded polyp, podocyst) followed by a post hoc Tukey test.

G1: The effect of parental and current temperature on average offspring production for total reproductive output and by reproductive mode in G1, as well as on the number of days taken by G1 polyps to produce offspring was analysed using a negative binomial regression model due to over-dispersed count data. As this was non-significant, the interaction term was dropped, and an additive model was created, followed by post hoc Tukey contrasts. Too few podocysts were produced to enable robust statistical analysis.

G2: The effect of grandparental, parental, and current temperature on average total offspring production for all outputs, and separated by mode (stolonally budded polyps, directly budded polyps, podocysts), in G2 was analysed using a negative binomial regression model. The data were subset by grandparental temperature and each dataset was reanalysed using a negative binomial regression model to further uncover the effects of parental and current temperature on average offspring production. Too few podocysts were produced to enable robust statistical analysis. As there was no significant interactive effect between parental and current incubation temperature the interaction term was dropped when examining replicates whose grandparents were incubated at 15°C (all), and 17°C (stolonal budding), and an additive negative binomial regression model was created.

The effect of grandparental, parental, and current temperature on the number of days taken by G2 polyps to produce offspring was analysed using an additive negative binomial regression model.

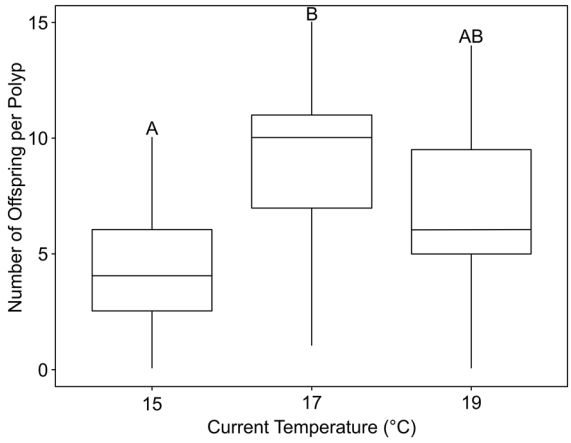

Fig. 2 Number of offspring produced across the three G0 temperature treatments. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and solid vertical lines denote the range. Letters above data points indicate similarities (e.g. A, A), and differences (e.g. A, B) between treatments at single time points, as determined by post hoc tests

Results

Generation 0 (G0)

In the G0 generation, ≥ 95% of polyps survived to the end of the experiment in each of the three temperature treatments. Asexual reproduction via the production of direct and stolonal buds, as well as the production of podocysts occurred in all three temperature treatments. No strobilation was observed in any treatment. Temperature had a significant effect on the number of total offspring produced by G0 ($F_{(2,\ 54)} = 7.906$, $P < 0.001$), with G0 polyps incubated at 15°C producing significantly fewer buds than those incubated at 17 and 19°C ($P < 0.001$, Fig. 2).

There were no significant differences in the number of podocysts or directly budded polyps produced across the three temperature treatments, however temperature influenced the number of stolonally budded polyps produced ($F_{(2,\ 54)} = 14.47$, $P < 0.001$), with polyps incubated at 17°C producing significantly more stolonally budded polyps than those at 15°C or 19°C ($P < 0.001$).

Generation 1 (G1)

A higher number of offspring were produced by polyps incubated at higher incubation temperatures, regardless of the temperature at which their parents were incubated ($Z = 8.55$, $P < 0.001$; Fig. 3). On average 2.5 additional offspring were produced for every 2°C increase in replicate incubation temperature.

There were no significant transgenerational effects of temperature affecting the production of different reproductive modes in G1 polyps. Only their current incubation temperature affected the number of direct buds ($Z = 8.287$, $P < 0.001$) and stolonal buds ($Z = 3.608$, $P < 0.001$), with polyps incubated at warmer temperatures producing more of each type no matter their parental temperature ($P < 0.001$, Fig. 4).

There were no significant transgenerational effects of temperature affecting the number of days to first bud in G1 polyps. Polyps incubated at average and warmer temperatures produced their first offspring more rapidly than those incubated at a cooler temperature, no matter their parental temperature ($Z = -5.648$, $P < 0.001$, Fig. 5). Out of the G1 polyps incubated at 15°C, 19 polyps did not produce any buds across the experimental period.

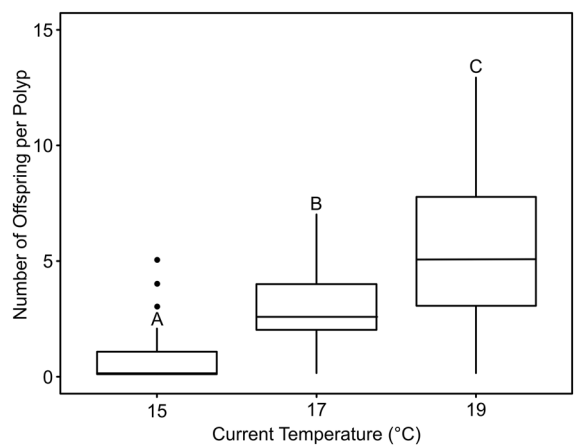

Fig. 3 Number of offspring produced across the three G1 temperature treatments. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the solid vertical lines denote the range. Any points beyond the solid vertical line are outliers. Letters above data points indicate similarities (e.g. A, A), and differences (e.g. A, B) between treatments at single time points, as determined by post hoc tests

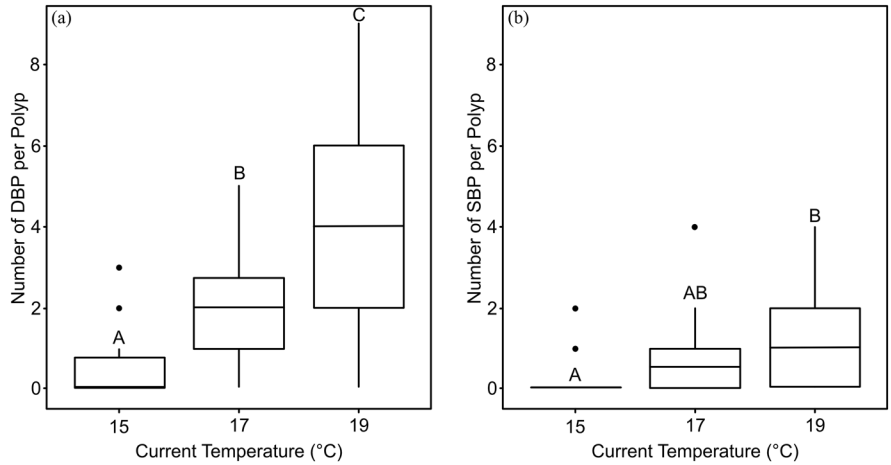

Fig. 4 Number of **a** directly budded polyps (DBP) and **b** stolonally budded polyps (SBP) produced across the three G1 temperature treatments. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the solid vertical lines denote the range. Any points beyond the solid vertical lines are outliers. Letters above data points indicate similarities (e.g. A, A), and differences (e.g. A, B) between treatments at single time points, as determined by post hoc tests

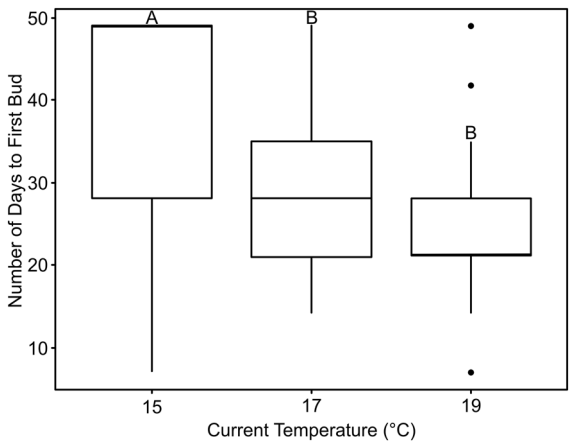

Fig. 5 Number of days taken for G1 polyps to produce offspring by temperature. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the solid vertical lines denote the range. Any points beyond the solid vertical lines are outliers. Letters above data points indicate similarities (e.g. A, A), and differences (e.g. A, B) between treatments at single time points, as determined by post hoc tests

Transgenerational effects in Generation 2 (G2)

In G2, ≥ 95% of polyps survived to the end of the experiment in each temperature treatment.

The effect of parental (i.e. G1) temperature on a replicate's offspring production (i.e. G2) was significant, but its effect depended on the replicate's current incubation temperature. As well as this, the interaction between parental and current temperature differed depending on the replicate's grandparental (i.e. G0) temperature ($Z = 3.416$, $P < 0.001$, Fig. 6).

Amongst polyps whose grandparents were incubated at 15°C, there was no significant interactive effect between parental and current incubation temperature influencing offspring production ($P < 0.05$, Fig. 6a). Current temperature had a significant effect on offspring production, with more offspring being produced at higher temperatures ($Z = 2.523$, $P < 0.05$).

Amongst polyps whose grandparents were incubated at 17°C, offspring production increased with increasing parental incubation temperature, but the strength of this effect depended on the polyp's current temperature ($Z = 2.523$, $P < 0.05$, Fig. 6b).

Finally, there was a strong effect of parental temperature on polyps whose grandparents were incubated at 19°C, although the strength of the effect also depended on the current incubation temperature of the polyp ($Z = 3.350$, $P < 0.001$, Fig. 6c). G2 polyps whole parents were incubated at 17°C produced fewer than 1 offspring on average. G2 polyps who were themselves incubated at 15°C produced over twice as

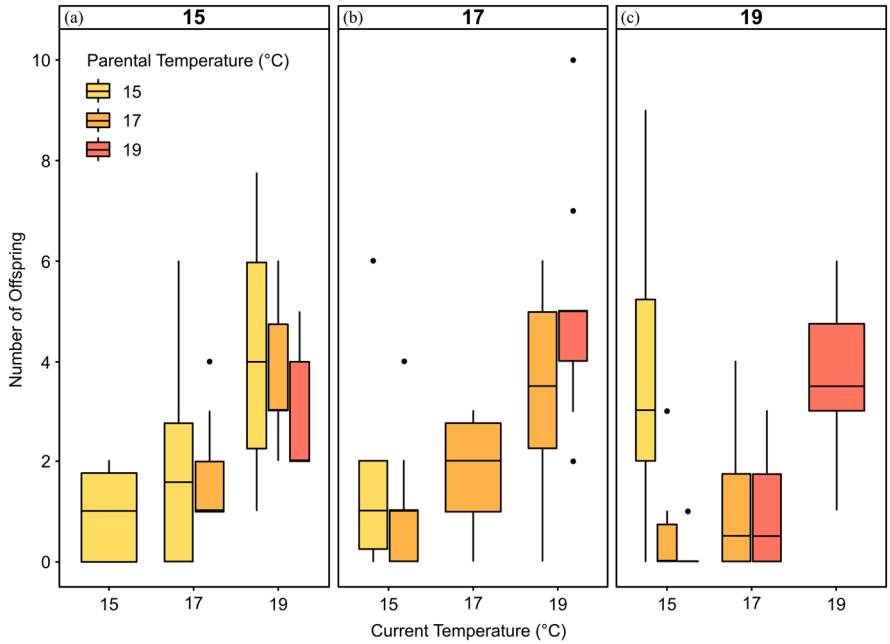

Fig. 6 Number of offspring produced across the G2 temperature treatments, split according to grandparental (G0) temperature, i.e. **a** G0 temperature 15°C, **b** 17°C, and **c** 19°C. Colour indicates parental (G1) temperature. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the solid vertical lines denote the range. Any points beyond the solid vertical lines are outliers

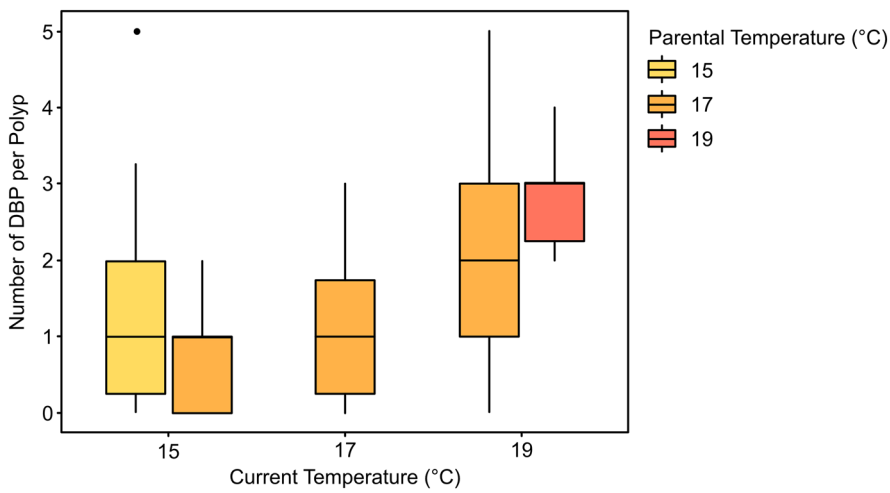

Fig. 7 Number of directly budded polyps produced by G2 polyps whose grandparents were incubated at 17°C. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the solid vertical lines denote the range. Any points beyond the solid vertical lines are outliers

many offspring when their parent was also incubated at 15°C, as opposed to 17 or 19°C.

The effect of parental temperature on polyps' directly budded polyp and stolonally budded polyp production was significant, but the effect depended on the replicate's current incubation temperature. As well as this, the interaction between parental and current incubation temperature differed depending on the replicate's grandparental temperature for directly budded polyps ($Z=2.768$, $P<0.01$) and stolonally budded polyps ($Z=2.538$, $P<0.05$).

Amongst replicates whose grandparents were incubated at 15°C, only current temperature significantly influenced the production of directly budded polyps ($Z=3.462$, $P<0.001$) and stolonal budded polyps ($Z=3.736$, $P<0.001$), with more direct buds and stolonal buds produced at current warmer temperatures.

Amongst replicates whose grandparents were incubated at 17°C, directly budded polyp production was affected by parental incubation temperature, but the strength of this effect depended on the replicate's current temperature ($Z=2.151$, $P<0.05$, Fig. 7).

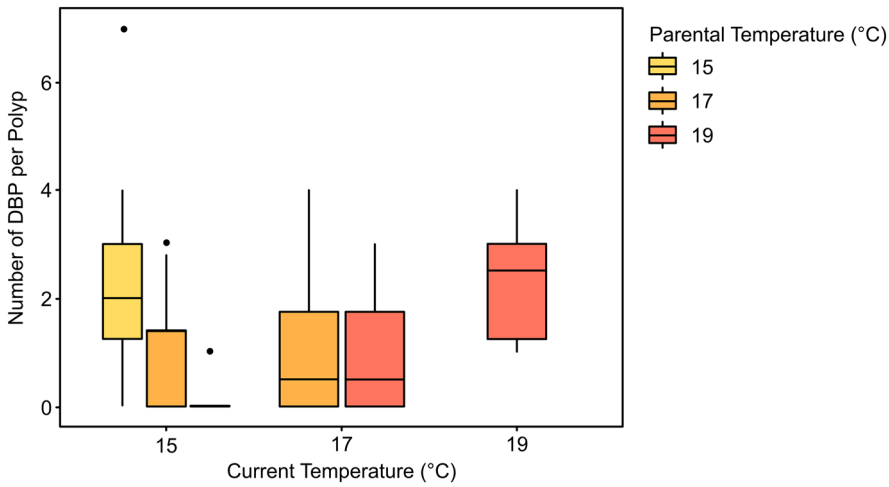

Fig. 8 Number of directly budded polyps produced by G2 polyps whose grandparents were incubated at 19°C. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the solid vertical lines denote the range. Any points beyond the solid vertical lines are outliers

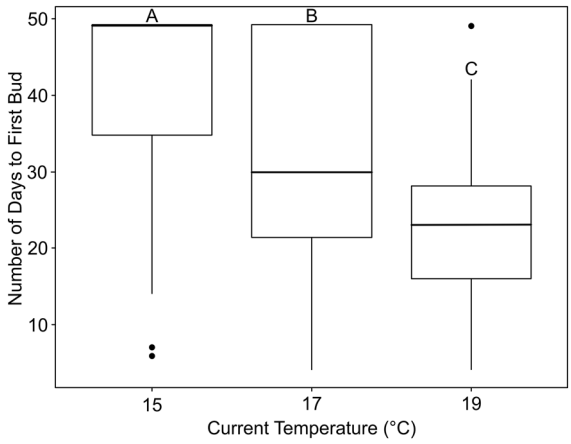

Fig. 9 Number of days taken for G2 polyps to produce offspring by temperature group. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the solid vertical lines denote the range. Any points beyond the solid vertical lines are outliers. Letters above data points indicate similarities (e.g. A, A), and differences (e.g. A, B) between treatments at single time points, as determined by post hoc tests

Stolonal bud production was only affected by polyps' current incubation temperature ($Z = 2.151$, $P < 0.05$).

Amongst replicates whose grandparents were incubated at 19°C, directly budded polyp production was affected by parental incubation temperature, but the strength of this effect depended on the replicate's current temperature ($Z = 2.422$, $P < 0.05$, Fig. 8). Too few podocysts were produced to enable robust statistical analysis.

The preparatory period needed prior to initial offspring production was reduced in G2 with increasing current incubation temperature ($Z = -6.128$, $P < 0.001$, Fig. 9) and there were no observed transgenerational effects of temperature on reproductive timing. At 19°C, G2 polyps took on average 23 days to produce their first bud, as opposed to 30 days at 17°C and approximately 49 days at 15°C degrees.

Discussion

To reliably predict the impact of climate variability on ecosystems, the capacity of organisms to adapt to rapid thermal change needs to be understood. Despite a wide tolerance to variable environmental conditions, increasing instability in the ocean sphere threatens to modify the timing and abundance of seasonal temperate jellyfish blooms, which can be highly disruptive to human activity. Across the 4°C temperature range used in this experiment, we characterised the complex effects of a range of potential summer temperatures on three polyp generations of the scyphozoan *Aurelia aurita*. In all generations, the temperature experienced by the polyp was the main variable driving polyp reproductive activity. However transgenerational effects did affect polyps' reproductive activity in certain scenarios.

Thermal regimes are a key determinant of polyp's reproductive output: thermal windows are as narrow as possible to minimise maintenance costs and increase efficiency. Steep declines in respiration

rates occur at temperatures beyond thermal limits, likely leading to a loss of function (Höhn et al., 2017). This may explain why the widely distributed scyphozoan *A. aurita* is known to have a wide tolerance to environmental conditions as temperate populations are well adapted to UK coastal waters that undergo large seasonal variations in temperature. In our experiment, G1 and G2 polyps produced more offspring at warmer temperatures, indicating that our highest experimental temperature (19°C) was within this population's thermal limits. As well as this, the number of days taken by polyps to produce their first offspring was lower at warmer temperatures. Producing more offspring more rapidly at warmer summer temperatures will prove advantageous to polyp colonies, both in maintaining the benthic population across the year, as well as when producing ephyrae following suitable environmental cues (Han & Uye, 2010). Provided this reproductive growth is sustained with sufficient food resources, increased reproductive output may compensate for mortality caused by predation, inter- and intra-specific competition for space and food and physiological stress experienced across the year (Lucas et al., 2012).

Transgenerational effects of temperature have been observed in a range of taxa (Burgess & Marshall, 2011; Donelson et al., 2012; Groot et al., 2017). In parthenogenetic *Daphnia magna* Straus, 1820, females, maternal incubation temperature affects offspring resistance to bacterial parasites and other pathogens (Garbutt et al., 2014), as well as increasing resistance to toxic cyanobacteria at high temperatures (Lyu et al., 2017). In the coral *Acropora tenuis* (Dana, 1846) parental effects account for variations in larval settlement success and associated *Symbiodinium* communities (Quigley et al., 2016). Effects are most likely to be environmentally adaptive if the offspring are faced with the same stressors and environment as the previous generation (Salinas & Munch, 2012; Mousseau & Fox, 2014). For example, a strong adaptive response was observed in Sheepshead minnows where offspring from high and low temperature parents grew best at their parental temperatures, provided sufficient exposure time (Mousseau & Fox, 1998; Salinas & Munch, 2012). Similarly, Putnam and Gates (2015) observed that when adults of the reef building coral *Pocillopora damicornis* (Linnaeus, 1758) were exposed to warmer, more acidic conditions, larvae were able to better respond to similar post-release conditions.

We examined three scenarios across three generations of asexual polyps: transgenerational warming, transgenerational cooling, and stable temperatures. Polyps that remained at the same temperature as their parent produced more offspring than those that experienced transgenerational cooling. This could indicate that within the 4°C range examined in our experiment, transgenerational effects of temperature could offer an advantage to polyps that experience the same conditions as their parents. However, in regions with large seasonal variations in temperature, such as in UK coastal waters, these effects may not prove beneficial. Similar to Lu et al. (2020), we observed significant inhibition of budding activity in cooling scenarios. In the winter and at colder experimental temperatures, bud production slows and can reduce to almost zero (Willcox et al., 2007). Seasonal cooling in the autumn and winter may therefore dampen polyp colony growth in the winter period partly due to a mismatch between parental and offspring thermal conditions. In temperate areas where polyp colonies maintain the population through the winter, colony expansion is likely to occur in the warmer months of the year, and significant losses in colony size that occur in the cooling and colder months of the year which are unlikely to be recouped until springtime, leaving the colony vulnerable to overgrowth and predation events.

An increasingly unstable ocean sphere due to global climate change poses significant threats to marine organisms, through changes to phenology (Parmesan 2007) and range (Zhang et al., 2020). For example, likely in response to increasing sea surface temperatures *Calanus* spp. copepods have shifted their range further north in the NE Atlantic (Beaugrand, 2003). For species dependent on spring plankton blooms, such as *Aurelia* spp. these changes could potentially cause a large disruption to reproduction and growth. As well as this, with some regions experiencing rapid warming, and increased occurrences of marine heatwaves (Belkin, 2009; IPCC, 2019), populations are likely to be vulnerable to continued warming beyond their thermal limits (Höhn et al., 2017). Thermal transgenerational plasticity may provide a buffer against the effects of warming in the short term (Bellantuono et al., 2012). However, it is still unclear how evolution, phenotypic plasticity and

transgenerational plasticity interact to generate long-term responses (Salinas & Munch, 2012). For example, in the tropical Irukandji jellyfish *Alatina alata* (Reynaud, 1830), pre-exposure of parent polyps to elevated temperatures and reduced pH did not confer any advantage on to offspring polyps and both parent and offspring polyps responded similarly to the treatments (Klein et al., 2017).

In our experiment we did not uncover any effects of transgenerational warming increasing the fitness or resilience of offspring in the face of increase temperature instability due to continued climate warming. Parental temperature did not affect G1 reproductive output and in G2 reproductive timing was only driven by the current incubation temperature. Polyps who experienced transgenerational warming across subsequent generations did not produce significantly different numbers of offspring than polyps who were maintained at constant warm temperatures across multiple generations. Our results indicate that, at our temperature range of 15–19°C, transgenerational effects did not significantly benefit polyp reproductive output. Our results indicate that the environmental temperature that polyps directly experience likely plays a much larger role in driving reproduction. If temperatures increase past population thermal limits, polyps are likely to experience a sharp decline in reproductive activity (Höhn et al., 2017). Consequently, determining the thermal limits of different populations with the aim of highlighting potentially vulnerable regions is critical to understanding how continued ocean warming will affect scyphozoan jellyfish populations.

The extent to which a stressor modifies an offspring phenotype depends on the amplitude, predictability, and length of the fluctuation (Mousseau & Fox, 1998; Klein et al., 2017). As such, how an effect is expressed, either visibly in an organism's reproductive output, or in the offspring's phenotype, will vary depending on the environment and genotype in question. Responses to environmental drivers are therefore highly contextual to the spatio-temporal scale of the stressor (Mousseau & Fox, 2014). Across smaller temperature ranges, such as the 4°C range examined in this study, transgenerational effects are subtle, and may require an increased number of generations to become fully apparent. For example, in our experiment, only the third generation of polyps (G2) presented visible influences of past generations on offspring production, whereas across the 8°C range used by Lu et al. (2020), effects became visible in the second generation of polyps. Examining larger temperature ranges is likely to result in more visible effects that may become apparent in fewer generations (Lu et al., 2020). Nevertheless, despite observing no visible response in G1, it is possible that phenotypic modification of offspring traits was occurring at the molecular level. Pespeni et al. (2013) examined the response of the purple sea urchin *Strongylocentrotus purpuratus* (Stimpson, 1857) to elevated CO_2. No visible signs of change were recognised, although changes across hundreds of loci were detected, suggesting that there was potential for change (Pespeni et al., 2013). Consequently, a molecular component to experiments is key to understanding transgenerational effects.

In conclusion, where polyps experience temperatures above or below their thermal optima, our results indicate that transgenerational effects may require more extreme temperatures or increased numbers of generations to have a measurable impact on a population. Our experiment benefitted from taking place over three clearly defined generations of asexual polyps, providing further insights into the characterisation of transgenerational acclimation in the scyphozoan jellyfish *Aurelia aurita* and the thermal drivers of asexual reproduction. Future investigations should investigate population-specific responses to environmental change to understand how transgenerational effects may affect populations in the context of future environmental change.

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Data availability The datasets during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have declared that no competing interests exist.

Ethical approval The moon jellyfish *Aurelia aurita* is not a protected species in the area of study. Permission was obtained

from the Royal Navy to access Horsea Lake, UK (50° 49′ 58.8; − 1° 05′ 36.9) to collect *A. aurita* specimens. All international, national, and/or institutional guidelines for the care and use of animals were followed where applicable.

References

Adler, L. & G. Jarms, 2009. New insights into reproductive traits of scyphozoans: Special methods of propagation in *Sanderia malayensis* GOETTE, 1886 (Pelagiidae, Semaeostomeae) enable establishing a new classification of asexual reproduction in the class Scyphozoa. Marine Biology 156: 1411–1420.

Bayha, K. M. & W. M. Graham, 2014. Nonindigenous marine jellyfish: invasiveness, invasibility, and impacts. In Pitt, K. A. & C. H. Lucas (eds), Jellyfish Blooms. Dordrecht: Springer.

Beaugrand, G., 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fisheries Oceanography 12: 270–283.

Belkin, I. M., 2009. Rapid warming of large marine ecosystems. Progress in Oceanography 81: 207–213.

Bellantuono, A. J., C. G. Granados-Cifuentes, D. J. Miller, O. Hoegh-Guldberg & M. Rodriguez-Lanetty, 2012. Coral thermal tolerance: tuning gene expression to resist thermal stress. PLoS ONE 8: e50685.

Brodeur, R. D., M. B. Decker, L. Ciannelli, J. E. Purcell, N. A. Bond, P. J. Stabeno, E. Acuna & G. L. Hunt Jr., 2008. Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Progress in Oceanography 77: 103–111.

Burgess, S. C. & D. J. Marshall, 2011. Temperature-induced maternal effects and environmental predictability. Journal of Experimental Biology 214: 2329–2336.

Byrne, M., N. Soars, P. Selvakumaraswamy, S. A. Dworjanyn & A. R. Davis, 2010. Sea urchin fertilization in a warm, acidified and high pCO_2 ocean across a range of sperm densities. Marine Environmental Research 69: 234–239.

CEFAS, 2018. Station 22: Fawley PS. Accessed 16 August 2018. https://www.cefas.co.uk/cefas-data-hub/sea-temperature-and-salinity-trends/presentation-of-results/station-22-fawley-ps/

Chi, X., D. C. Muller-Navarra, S. Hylander, U. Sommer & J. Javidpour, 2019. Food quality matters: interplay among food quality, food quantity and temperature affecting life history traits of *Aurelia aurita* (Cnidaria: Scyphozoa) polyps. Science of the Total Environment 656: 1280–1288.

Chi, X., F. Zhang & S. Sun, 2022. Transgenerational effects and temperature variation alter life history traits of the moon jellyfish. Frontiers in Marine Science 9: 913654.

Condon, R. H., W. M. Graham, C. M. Duarte, K. A. Pitt, C. H. Lucas, S. H. D. Haddock, K. R. Sutherland, K. L. Robinson, M. N. Dawson, M. B. Decker, C. E. Mills, J. E. Purcell, A. Malej, H. Mianzan, S. Uye, S. Gelcich & L. P. Madin, 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. BioScience 62: 160–169.

Dawson, M. N. & D. K. Jacobs, 2001. Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). Biological Bulletin 200: 92–96.

Donelson, J. M., P. L. Monday, M. I. McCormick & C. R. Pitcher, 2012. Rapid transgenerational acclimation of a tropical reef fish to climate change. Nature Climate Change 2: 30–32.

Donelson, J. M., M. Wong, D. J. Booth & P. L. Munday, 2016. Transgenerational plasticity of reproduction depends on rate of warming across generations. Evolutionary Applications 9: 1072–1081.

Dong, Z., D. Liu & J. K. Keesing, 2010. Jellyfish blooms in China: dominant species, causes and consequences. Marine Pollution Bulletin 60: 954–963.

Gambill, M. & M. A. Peck, 2014. Respiration rates of the polyps of four jellyfish species: potential thermal triggers and limits. Journal of Experimental Marine Biology and Ecology 459: 17–22.

Garbutt, J. S., J. A. Scholefield, P. F. Vale & T. J. Little, 2014. Elevated maternal temperature enhances offspring disease resistance in *Daphnia magna*. Functional Ecology 28: 424–431.

Gibbons, M. J. & A. J. Richardson, 2013. Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. Journal of Plankton Research 35: 929–938.

Groot, M. P., A. Kubisch, J. O. Ouborg, J. Pagel, K. J. Schmid, P. Vergeer & C. Lampei, 2017. Transgenerational effects of mild heat in *Arabidopsis thaliana* show strong genotype specificity that is explained by climate at origin. New Phytologist 215: 1221–1234.

Han, C. H. & S. Uye, 2010. Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* s.l. Plankton and Benthos Research 5: 98–105.

Höhn, P. H., C. H. Lucas & S. Thatje, 2017. Respiratory response to temperature of three populations of *Aurelia aurita* polyps in Northern Europe. PLoS ONE 12: 1–13.

Holst, S. & G. Jarms, 2007. Substrate choice and settlement preferences of planula larvae of five Schyphozoa (Cnidaria) from German Bight, North Sea. Marine Biology 151: 863–871.

Hubot, N., C. H. Lucas & S. Piraino, 2017. Environmental control of asexual reproduction and somatic growth of *Aurelia* spp. (Cnidaria, Scyphozoa) polyps from the Adriatic Sea. PLoS ONE 12: e0178482.

IPCC (2019) Special report on the ocean and cryosphere in a changing climate. In: Pörtner, H.-O., Roberts, D. C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N. M. (eds)

Kingsford, M. J., S. Becken, C. Bordehore, V. L. Fuentes, K. A. Pitt & A. A. Yangihara, 2018. Empowering stakeholders to manage stinging jellyfish: a perspective. Coastal Management 46: 1–18.

Klein, S. G., K. Pitt, K. A. Rathjen & J. E. Seymour, 2014. Irukandji jellyfish polyps exhibit tolerance to interacting climate change stressors. Global Change Biology 20: 28–37.

Klein, S. G., K. A. Pitt & A. R. Carroll, 2017. Pre-exposure to simultaneous, but not individual, climate change stressors limits acclimation capacity of Irukandji jellyfish polyps to predicted climate scenarios. Coral Reefs 36: 987–1000.

Lesniowski, T. J., M. Gambill, S. Holst, M. A. Peck, M. Algueró-Muñiz, M. Haunost, A. M. Malzahn & M. Boersma, 2015. Effects of food and CO_2 on growth dynamics of polyps of two scyphozoan species (*Cyanea capillata* and *Chrysaora hysoscella*). Marine Biology 162: 1371–1382.

Liu, W. C., W. T. Lo, J. E. Purcell & H. H. Chang, 2009. Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. Hydrobiologia 616: 247–258.

Loveridge, A., C. H. Lucas & K. A. Pitt, 2021. Shorter, warmer winters may inhibit production of ephyrae in a population of the moon jellyfish *Aurelia aurita*. Hydrobiologia 848: 739–749.

Lu, Y., C. H. Lucas & A. Loveridge, 2020. Transgenerational acclimation influences asexual reproduction in *Aurelia aurita* jellyfish polyps in response to temperature. Marine Ecology Progress Series 656: 35–50.

Lucas, C. H., 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita,* in relation to its ambient environment. Hydrobiologia 451: 229–246.

Lucas, C. H. & S. Lawes, 1998. Sexual reproduction of the scyphomedusa *Aurelia aurita* in relation to temperature and variable food supply. Marine Biology 131: 629–638.

Lucas, C. H., A. G. Hirst & J. A. Williams, 1997. Plankton dynamics and *Aurelia aurita* production from two contrasting ecosystems: comparisons and consequences. Estuarine, Coastal and Shelf Science 45: 209–219.

Lucas, C. H., W. M. Graham & C. Widmer, 2012. Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Advances in Marine Biology 63: 133–196.

Lyu, K., L. Zhang, L. Gu, X. Zhu, A. E. Wilson & Z. Yang, 2017. Cladoceran offspring tolerance to toxic M*icrocystis* is promoted by maternal warming. Environmental Pollution 227: 451–459.

Marshall, D. J., S. S. Heppell, S. B. Munch & R. R. Warner, 2010. The relationship between maternal phenotype and offspring quality: do older mothers really produce the best offspring? Ecology 91: 2862–2873.

Mousseau, T. A. & C. W. Fox, 1998. The adaptive significance of maternal effects. Trends in Ecology and Evolution 13: 403–407.

Mousseau, T. A. & C. W. Fox, 2014. Maternal effects as adaptations, Oxford University Press, Oxford:

Norouzitallab, P. L., R. R. Warner, K. Monro, J. M. Pandolfi, G. Van Stappen, F. Catania, J. Vanden Bussche, L. Vanhaecke, P. Sorgeloos & P. Bossier, 2014. Environmental heat stress induces epigenetic transgenerational inheritance of robustness in parthenogenetic *Artemia* model. FASEB J 28: 3552–3563.

Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13: 1860-1872.

Pascual, M., V. Fuentes, A. Canepa, D. Atienza, J.-M. Gili & J. E. Purcell, 2015. Temperature effects on asexual reproduction of the scyphozoan *Aurelia aurita* S.l.: differences between exotic (Baltic and Red seas) and native (Mediterranean Sea) populations. Marine Ecology 36: 994–1002.

Pespeni, M. H., E. Sanford, B. Gaylord, T. M. Hill, J. D. Hosfelt, H. K. Jaris, M. LaVigue, E. A. Lenz, A. D. Russell, M. K. Young & S. R. Palumbi, 2013. Evolutionary change during experimental ocean acidification. Proceedings of the National Academy of Sciences of the United States of America 110: 6937–6942.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. Schwing, S. A. Thompson & A. J. Richardson, 2013. Global imprint of climate change on marine life. Nature Climate Change 3: 919–925.

Purcell, J. E., D. Atienza, V. Fuentes, A. Olariaga, U. Tilves, C. Colahan & J.-M. Gili, 2012. Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. Hydrobiologia 690: 169–180.

Putnam, H. M. & R. D. Gates, 2015. Preconditioning in the reef-building coral *Pocillopora damicornis* and the potential for transgenerational acclimatization in coral larvae under future climate change conditions. The Journal of Experimental Biology 218: 2365–2372.

Quigley, K. M., B. L. Willis & L. K. Bay, 2016. Maternal effects and Symbiodinium community composition drive differential patterns in juvenile survival in the coral *Acropora tenuis*. Royal Society Open Science 3: 160471.

Riascos, J. M., L. Paredes, K. González, I. Cáceres & A. S. Pacheco, 2013. The larval and benthic stages of the scyphozoan medusa *Chrysaora plocamia* under El Niño–La Niña thermal regimes. Journal of Experimental Marine Biology and Ecology 446: 95–101.

Salinas, S. & S. B. Munch, 2012. Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. Ecology Letters 15: 159–163.

Schnedler-Meyer, N. A., T. Kiørboe & P. Mariani, 2018a. Boom and bust: life history, environmental noise, and the (un)predictability of jellyfish blooms. Frontiers in Marine Science 5: 257.

Schnedler-Meyer, N. A., S. Pigolotti & P. Mariani, 2018b. Evolution of complex asexual reproductive strategies in jellyfish. The American Naturalist 192: 72–80.

Shanks, A. L., L. K. Rasmuson, J. R. Valley, M. A. Jarvis, C. Salant, D. A. Sutherland, E. I. Lamont, M. A. H. Hainey & R. B. Emlet, 2019. Marine heat waves, climate change,

and failed spawning by coastal invertebrates. Limnology and Oceanography 65: 627–636.

Tucić, B. & S. Avramov, 1996. Maternal effects on early juvenile traits in *Iris pumila* (*Iridaceae*). Plant Systematics and Evolution 201: 179–197.

Veilleux, H. D., T. Ryu, J. M. Donelson, L. van Herwerden, L. Seridi, Y. Ghosheh, M. L. Berumen, W. Leggat, T. Ravasi & P. L. Munday, 2015. Molecular processes of transgenerational acclimation to a warming ocean. Nature Climate Change 5: 1074–1078.

Willcox, S., N. A. Moltschaniwiskyj & C. Crawford, 2007. Asexual reproduction in scyphistomae of *Aurelia* sp.: effects of temperature and salinity in an experimental study. Journal of Experimental Marine Biology and Ecology 353: 107–114.

Wolf, J. B. & M. J. Wade, 2009. What are maternal effects (and what are they not)? Philosophical Transactions of the Royal Society B 364: 1107–1115.

Youngson, N. A. & E. Whitelaw, 2008. Transgenerational epigenetic effects. Annual Review of Genomics and Human Genetics 9: 233–257.

Zhang, T. Y. B., R. Bagot, C. Parent, C. Nesbitt, T. W. Bredy, C. Caldji, E. Fish, H. Anisman, M. Szyf & M. J. Meaney, 2006. Maternal programming of defensive responses through sustained effects on gene expression. Biological Psychology 73: 72–89.

Zhang, Z., C. Caphina, D. N. Karger, X. Turon, H. J. Maclsaaz & A. Zhan, 2020. Impacts of climate change on geographical distributions of invasive ascidians. Marine Environmental Research 159: 104993.