



Shorter, warmer winters may inhibit production of ephyrae in a population of the moon jellyfish *Aurelia aurita*

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Abstract Scyphozoan jellyfish blooms display high interannual variability in terms of timing of appearance and size of the bloom. To understand the causes of this variability, the conditions experienced by the polyps prior to the production of ephyrae in the spring were examined. Polyps reared from planula larvae of *Aurelia aurita* medusae collected from southern England (50°49'58.8; – 1°05'36.9) were incubated under orthogonal combinations of temperature (4, 7, 10 °C) and duration (2, 4, 6, 8 weeks), representing the range of winter conditions in that region, before experiencing an increase to 13 °C. Timing and success of strobilation were recorded. No significant production of ephyrae was observed in any of the 2- and 4-week incubations, or in any 10 °C incubation. Time to first ephyra release decreased with longer winter

incubations, and more ephyrae were produced following longer and colder winter simulations. This experiment indicates that *A. aurita* requires a minimum period of cooler temperatures to strobilate, and contradicts claims that jellyfish populations will be more prevalent in warming oceans, specifically in the context of warmer winter conditions. Such investigations on population-specific ontogeny highlights the need to examine each life stage separately as well as in the context of its environment.

Keywords Jellyfish bloom · Polyp · Asexual reproduction · Temperature

Introduction

Scyphozoan medusae are key components of marine ecosystems (Richardson et al., 2009), providing essential ecosystem services (Doyle et al., 2014; Yusuf et al., 2018) despite their frequent portrayal as trophic dead ends, or in the media as dangerous nuisances (Lunney & Moon, 2008). Whilst there is still much debate surrounding the extent of the anthropogenic influence on jellyfish population dynamics (Purcell, 2012; Pitt et al., 2018), if present in large numbers jellyfish blooms can cause problems for human coastal services (Lynam et al., 2006; Roux et al., 2013; Remigante et al., 2018).

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One of the most frequent blooming species along the south coast of England is *Aurelia aurita* (Linnaeus, 1758) (Pikesley et al., 2014; Dawson et al., 2015). *Aurelia* is a cosmopolitan genus of Scyphozoa (Russell, 1970) comprising multiple cryptic species living in coastal and shelf sea environments between 70°N and 40°S (Dawson & Jacobs, 2001). Like many scyphozoans, it has a complex life cycle comprising a pelagic sexual medusa and a benthic asexual polyp (Lucas, 2001; Fuchs et al., 2014). Through the production of ephyrae via strobilation, polyps directly and indirectly influence where medusa populations occur, the seasonal and interannual variability in medusa abundance, and may even be key to the success or failure of a jellyfish bloom (Gröndahl, 1988; Feng et al., 2018; Schnedler-Meyer et al., 2018).

Strobilation in *Aurelia aurita* has been studied in a variety of populations in the laboratory (Holst, 2012; Fuchs et al., 2014; Sukhoputova & Kraus, 2017). In situ, most populations strobilate following the seasonal cooling and subsequent warming of the water (Brewer, 1989; Feng et al., 2018), alongside changes in other variables such as salinity (Holst & Jarms, 2010), light (Custance, 1964; Purcell et al., 2009), oxygen (Condon et al., 2001), tidal rhythms (Calder, 1974) and food supply (Lucas & Williams, 1994). Different polyp populations vary widely in their response to forcing variables and authors have suggested varied and sometimes contradicting triggers (Sukhoputova & Kraus, 2017). For example, in many temperate locations ephyrae are typically released in spring (Lucas, 1996; Schnedler-Meyer et al., 2018), or following ice-out in late February in the Niantic River, USA (Brewer, 1989). However, some populations, such as those in the Suez Canal, strobilate when they reach the winter minimum temperature (Hamed & Khaled, 2011; Sukhoputova & Kraus, 2017). Others follow tidal rather than temperature cues: in Roscoe Bay, Canada, strobilation occurs in June and July coinciding with the lowest summer tides (Albert & Walsh, 2014). Finally, in Horsea Lake, UK, from where the current study animals originate, most *A. aurita* ephyrae appear in early spring around February and March (Lucas, 1996).

Despite the range of responses to a number of forcing variables, temperature consistently appears as one of the main triggers of strobilation, although the magnitude and direction of temperature change (i.e. cooling vs. warming) is inconsistent between studies

(Holst, 2012; Treible & Condon, 2019). Thermal windows constrain polyps' latitudinal distributions, and temperature determines the rate at which physiological processes occur (Gambill & Peck, 2014; Höhn et al., 2017). The gene CL390 is a temperature-dependent molecular timer that interacts with the RxR transcription factor to distinguish between short-term temperature fluctuations and seasonal changes, regulating the polyp-to-jellyfish transition in *Aurelia* spp. (Fuchs et al., 2014; Shi et al., 2018). It is produced gradually at low temperatures, initiating metamorphosis once an activation threshold is reached. This results in the initiation of strobilation only after a sufficient period of time at low temperatures (Fuchs et al., 2014). Purcell et al. (2009) showed that *Aurelia* spp. polyps strobilated earlier when the pre-strobilation temperature was higher. However, a number of other studies propose that a period at colder temperatures is necessary to ensure that ephyral growth and development occurs in spring, when temperate species can take advantage of the spring bloom (Lucas, 2001; Widmer et al., 2016).

Alongside increased food availability, warmer winter periods may promote the production of certain temperate scyphozoan medusae (Purcell et al., 2012; Goldstein & Steiner, 2020). However, large-scale climatic variability has the potential to modify the timing and abundance of phytoplankton blooms, and to directly change zooplankton community structure (Edwards and Richardson, 2004; Hays et al., 2005). In such regions, certain scyphozoan jellyfish, such as *A. aurita*, can act as indicators of ecosystem variability (Lynam et al., 2004). For example, across the North Atlantic, the North Sea and Europe, the North Atlantic Oscillation (NAO) influences the variability of weather systems, both directly and indirectly affecting marine ecosystems (Beaugrand, 2003). The NAO has a strong positive correlation with sea surface temperature in areas such as the North Sea, where it is at its strongest in spring and winter. This period coincides with *A. aurita* ephyra release in early spring (Lucas, 2001; Lynam et al., 2004). A strong inverse relationship exists between the winter NAOI and the median abundance of *A. aurita* medusae in this region, suggesting that especially in the winter and spring months, increased sea surface temperatures during high NAOI phases may contribute to poor strobilation and ephyral development, resulting in smaller populations of medusae in the summer (Lynam et al.,

2004). To add to these observations and further elucidate this link between the hydroclimatic environment and *A. aurita* populations, it is necessary to understand to what extent variable winter temperatures influence *A. aurita* polyp reproduction.

Despite being mentioned in Treible & Condon (2019) as a determining factor of the phenology in strobilation, duration of the winter period has not been examined as a factor influencing strobilation in the spring, even though the gene CL390 necessitates a certain period at cooler temperatures to initiate strobilation (Fuchs et al., 2014). To predict the timing and magnitude of ephyra release, it is essential to understand how the conditions preceding strobilation influences a population, from triggering the strobilation process, to the final number of ephyrae produced. Here we report on a laboratory experiment investigating the effects of different winter temperatures and durations on the production of ephyrae by scyphistomae originating from Horsea Lake in the UK. The following hypotheses were tested: differences in the duration and temperature of the winter period would significantly affect (i) the time from the temperature increase to strobilation, (ii) the proportion of polyps strobilating, and (iii) total numbers of ephyrae produced.

Methods

Establishment of polyp cultures

Polyps of *Aurelia aurita* were settled from planula larvae taken from three mature female medusae collected from Horsea Lake, UK (50°49'58.8; –1°05'36.9) on 28th June 2018, when the ambient surface temperature was 23 °C and the salinity 23.5 (Dawson et al., 2015). Horsea Lake is a brackish, semi-enclosed, man-made body of water connected to Portsmouth Harbour via a controlled pipe and valve, and the bottom (6 m) water temperature typically ranges from 5.5 °C in February to 23.0 °C in July, remaining below 10 °C from November to March (Lucas, 1996; CEFAS, 2018). The winter minimum usually occurs in February at 7 °C but has ranged from 10 °C in 2008 to 3.7 °C in 1986 (CEFAS, 2018).

Medusae and released larvae that settled into polyps were maintained for 3 months 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 reattached by placing polyps directly on the bottom of individual 60 ml clear polystyrene pots filled with water at the same salinity, maintained in darkness. The pots had been preconditioned by filling them with seawater 24 h before the procedure.

Polyp maintenance

One hundred and sixty reattached polyps were maintained in individual 60 ml microcosms at 15 °C for 14 days before the start of the experiment. Any offspring (podocysts, directly and stolonally budded polyps or ephyrae) produced before the start of the experiment were removed using a scalpel and Pasteur pipette after naturally separating from the parent polyp. Over 7 days (sensu Widmer et al., 2016; Treible & Condon, 2019) replicates were transitioned to experimental temperatures (4 °C, 1.5 °C day⁻¹; 7 °C, 1.1 °C day⁻¹; 10 °C, 0.7 °C day⁻¹; and 13 °C, 0.2 °C day⁻¹).

Salinity was maintained at 23.5 and seawater was completely exchanged once a week. 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. Food was supplied at non-limiting quantities once 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 (Lesniowsky et al., 2015), a combination of ZM100 (80-200 micron dried zooplankton) mixed with 1-day-old *Artemia* nauplii were fed to the polyps. 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). Any offspring (podocysts, directly and stolonally budded polyps or ephyrae) produced during the experiment were recorded and removed using a scalpel and Pasteur pipette after naturally separating from the parent polyp.

Experimental setup

The experiment consisted of two orthogonal factors: temperature (three levels: 4, 7 and 10 °C) and duration (four levels: 2, 4, 6, 8 weeks; Fig. 1). Controls were maintained at a constant temperature (4, 7, 10 or 13 °C) for 12 weeks. Each treatment had 10 replicates, each comprising a single polyp in a 60 ml microcosm. Following each incubation period, all treatments were moved to 13 °C (average springtime temperature) for 4 weeks. If after 4 weeks there was no evidence of strobilation (i.e. lateral constrictions of the polyp, darkened colour, retraction of tentacles or presence of ephyrae) the treatment was terminated. If any polyps were about to strobilate or were still strobilating then they were maintained at 13 °C until they released all ephyrae. Controls were not moved to 13 °C and remained at a constant temperature for 12 weeks to demonstrate that a temperature change is necessary to initiate strobilation. Reproductive output (number of stolonal, directly budded polyps, podocysts, and ephyrae), survival and attachment were recorded weekly.

Temperature cycles in Horsea Lake and Southampton Water are very similar (Lucas et al., 1997), and temperature data from Southampton Water were used because it has longer data records (1984–2012; Fig. 2) revealing more of the interannual variability (CEFAS, 2018).

Data analyses

No ephyrae were produced in the 2- or 12-week treatments, and only 2 ephyrae were produced in the 4-week treatment so these data were excluded from all following analyses. Time from the end of the winter simulation to first ephyra release was analysed using a two-way ANOVA. The factors were Duration (two levels; 6 and 8 weeks) and Temperature (three levels: 4, 7 and 10 °C). As no significant interaction occurred between temperature and duration, the interaction term was removed and an additive analysis was carried out. The number of replicates that strobilated within each treatment was analysed using a logistic regression model (family: binomial; $n = 10$). As no significant interaction occurred between temperature and

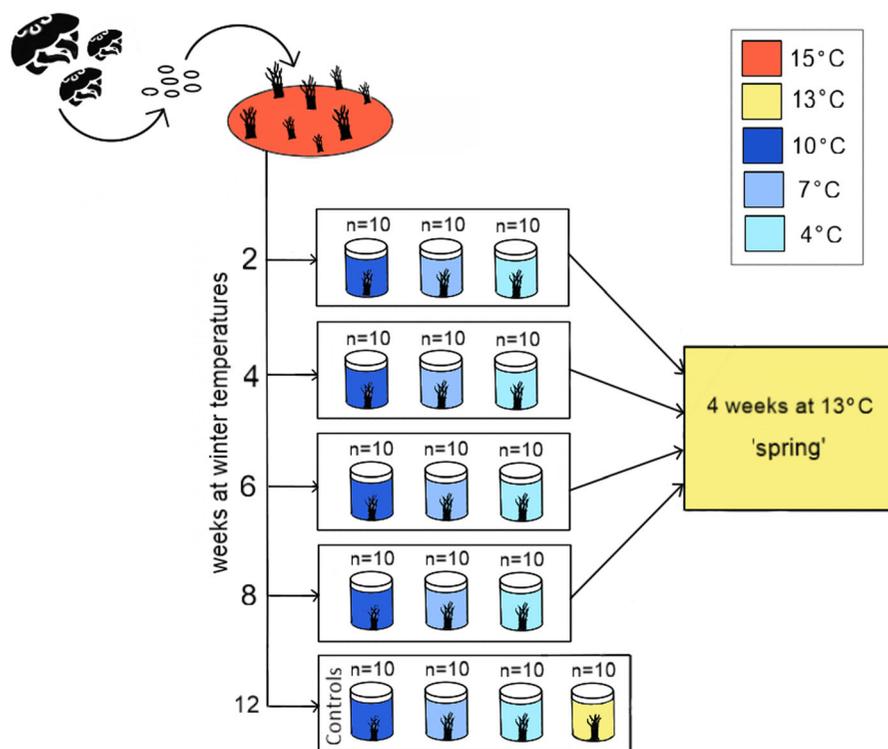


Fig. 1 Experimental design

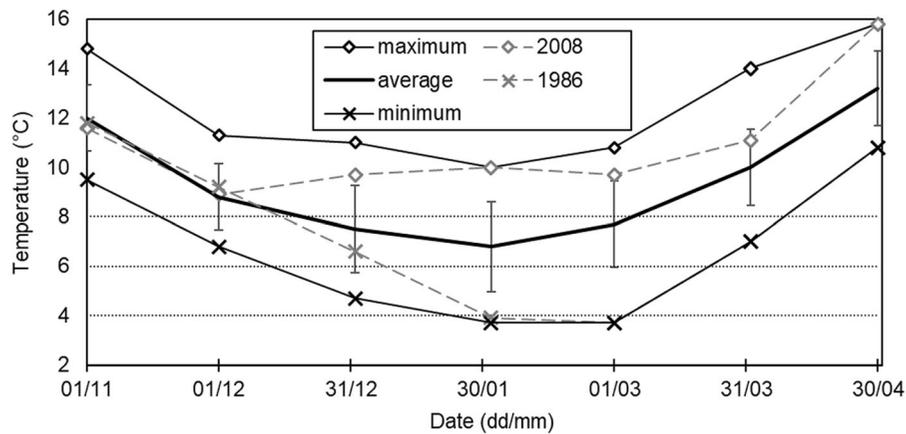


Fig. 2 Average monthly winter sea surface temperature in Southampton Water from November to May 1984–2012. Original data obtained from CEFAS (2018)

duration, the interaction term was removed and an additive analysis was carried out. Post hoc tests were consequently conducted separately within temperature (4, 7, 10 °C; $n = 40/\text{temperature}$) and duration (2, 4, 6, 8 weeks; $n = 30/\text{duration}$) groups. Finally, since the dataset on number of ephyrae produced was zero-inflated, a negative binomial regression model was created to analyse the influence of temperature and duration on the total number of ephyrae produced per replicate ($n = 10$).

Prior to analysis, data were tested for normality (Shapiro–Wilk test) and homogeneity of variance (Bartlett test). If variances could not be stabilised by transformation, α was reduced to 0.01 to reduce the risk of Type I error. Best fitting models were chosen based on Akaike Information Criterion (AIC). When significant differences were detected post hoc multiple comparisons of means (Tukey contrasts) determined which treatments differed.

Results

Survival and budding

All replicates survived to the end of the experiment except for a single replicate in each of the 4 weeks/10 °C and 8 weeks/4 °C treatments that died (disintegration of polyp body) before the temperature was increased to 13 °C. Minimal budding and podocyst production was observed in all treatments (See appendices 1–3 for further details).

Days from temperature increase to first ephyrae release

Time to first ephyra release decreased significantly with increasing winter duration, with replicates incubated for 8 weeks at winter temperatures releasing ephyrae on average 10 days earlier than those incubated for 6 weeks (Table 1; Fig. 3). Temperature of incubation did not influence the average number of days to first ephyra release ($P > 0.05$).

Number of replicates strobilating

More replicates strobilated in treatments incubated at cooler or average winter temperatures (Table 2). Approximately one quarter of replicates incubated at 4 and 7 °C strobilated, whilst only 4% strobilated at 10 °C (Fig. 4a). Duration also affected the number of replicates that strobilated (Table 2), with more than 5 times as many polyps strobilating when incubated at winter temperatures for eight weeks than for 4 weeks (Fig. 4b).

Table 1 Two-way ANOVA model results comparing the number of days to first ephyra release between treatments

Day to first ephyra release	Mean Sq	df	F	P value
Duration	0.759	1	15.404	< 0.001
Temperature	0.066	1	1.348	0.259

Values in bold are significant at $P < 0.05$. df = degrees of freedom

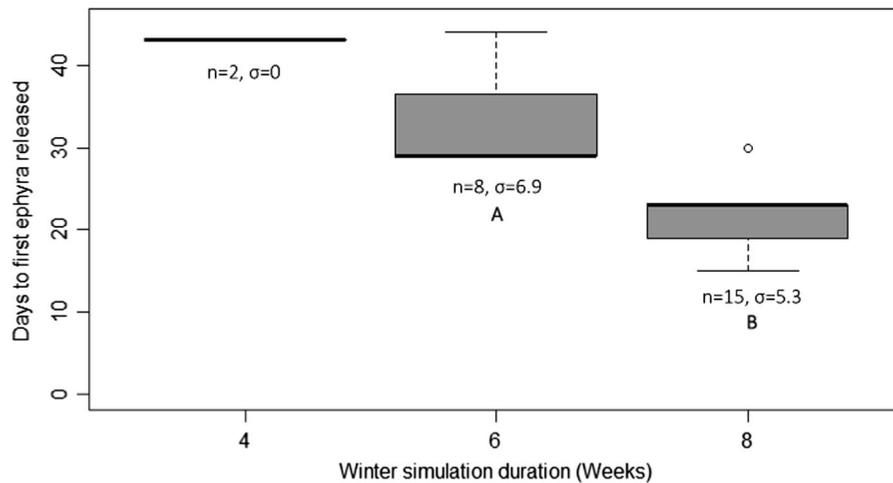


Fig. 3 Number of days from the end of the winter simulation to first ephyra release. Only replicates that produced at least one ephyra are included. A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the dotted lines denote the range.

Any points beyond the dotted line are outliers. Letters below each box indicates differences (e.g. A, B) between treatments, as determined by post hoc tests. Note the 4-week treatment was excluded from the analysis

Table 2 Logistic regression model (family = binomial) test results comparing the influence of duration and temperature on the number of replicates strobilating within each treatment

% replicates strobilating within each treatment	Estimate	SE	<i>P</i> value
Duration	0.778	0.178	< 0.001
Temperature	− 0.378	0.125	0.002

Values in bold are significant at $P < 0.05$. df = degrees of freedom

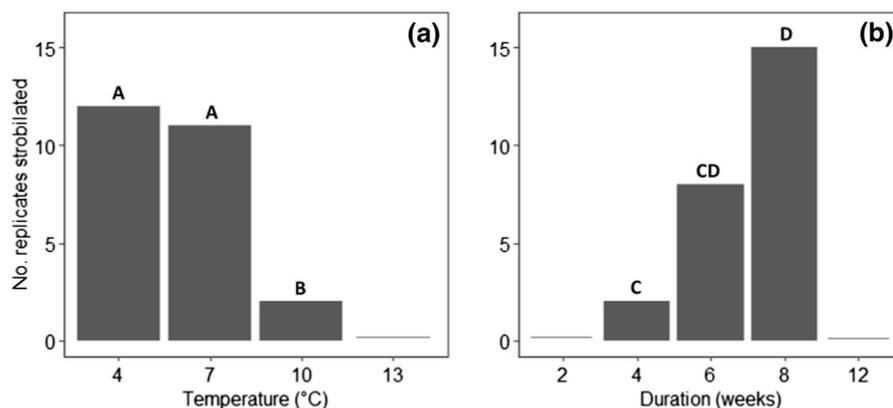


Fig. 4 Number of replicates that strobilated at each (a) temperature and (b) duration. The two graphs refer to separate groupings and contain 120 experimental replicates and 40 control replicates, giving a total of 160 replicates each. Letters

above data points indicate similarities (e.g. A, A) and differences (e.g. A, B) between treatments, as determined by post hoc tests

Ephyra production

The number of ephyrae produced varied among duration treatments, but patterns differed depending on the temperature at which polyps were incubated (Table 3). For example, in the 6-week treatments more ephyrae were produced when incubated at cold or average temperatures, whereas those incubated at 10 °C only produced ephyrae when incubated for 8 weeks (Fig. 5). The most ephyrae were produced in the 8-week treatment when incubated at 7 °C (with a maximum of 21 ephyrae produced by a single polyp).

Discussion

How changes in sea surface temperature may influence marine organisms, especially ectotherms (Pinsky et al., 2019) such as fishes (Moyano et al. 2017; Dahlke et al., 2020) and zooplankton (Edwards and Richardson, 2004; Kvile et al., 2016), has been one of the key focuses of research efforts over the past two decades. Whilst numerous studies have now examined temperature effects on jellyfish and especially on polyps (Shi et al., 2018; Purcell et al., 2012; Lu et al., 2020), none have examined potential interactions between temperature and duration of temperature on strobilation. Within this context, we show for the first time how the temperature and duration of the winter period influences reproduction in the spring. Polyps were more productive (i.e. more polyps strobilated and more ephyrae were produced) when incubated for longer periods of time at cold (4 °C) and average (7 °C) winter temperatures. Furthermore, polyps began strobilating sooner following longer (8 week) incubations. Consequently, the shorter, warmer winters predicted under climate change (IPCC, 2013, 2018) are likely to produce fewer ephyrae and, potentially, to lead to

smaller populations of medusae in temperate coastal regions. In the shortest incubation (2 weeks), no polyps strobilated and very few of those incubated at the warmest temperature (10 °C) strobilated and only when incubated for 8 weeks. This indicates that polyps are likely to have a limited thermal window in which they can successfully strobilate.

Thermal windows constrain ectothermic animal distributions and limit the geographic range within which they can live and reproduce (Höhn et al., 2017; Dahlke et al., 2020). Each population's thermal window differs and this may contribute to the population-specific timings of reproduction, and to their variable responses to different minimum winter temperatures (Kroiher et al., 2000; Pascual et al., 2015; Kvile et al., 2016). Some studies report that warmer temperatures result in more ephyrae (e.g. Holst, 2012) and others report that cooler temperatures increase productivity (e.g. Kroiher et al., 2000; Purcell et al., 2012; Widmer et al., 2016). Such inconsistencies may exist because the *Aurelia* genus is highly plastic and the species *Aurelia aurita* comprises numerous cryptic species (Dawson et al., 2015). Our results from Horsea Lake on the south coast of the UK provide evidence that cooler winter temperatures could enhance strobilation in temperate populations of *A. aurita* polyps.

Interannual variations in timing of strobilation result partly from differences in winter duration and temperature. In the laboratory, the 'preconditioning period', experienced by polyps prior to the induction of strobilation, mimics this preparatory period and influences how polyps respond to cues. Differences in preconditioning between experiments may explain variations in response time and production of ephyrae between these studies (Kroiher et al., 2000; Purcell et al., 2012; Fuchs et al., 2014). However, due to large differences in experimental setups and procedures, separating this influence from other environmental

Table 3 Negative binomial regression model results comparing the total number of ephyrae produced per polyp between treatments ($n = 10$)

Total ephyrae produced per polyp	Estimate	SE	<i>P</i> value
Duration	− 1.291	0.914	0.158
Temperature	− 2.323	0.934	0.013
Duration:Temperature	0.277	0.129	0.032

Values in bold are significant at $P < 0.05$. df = degrees of freedom

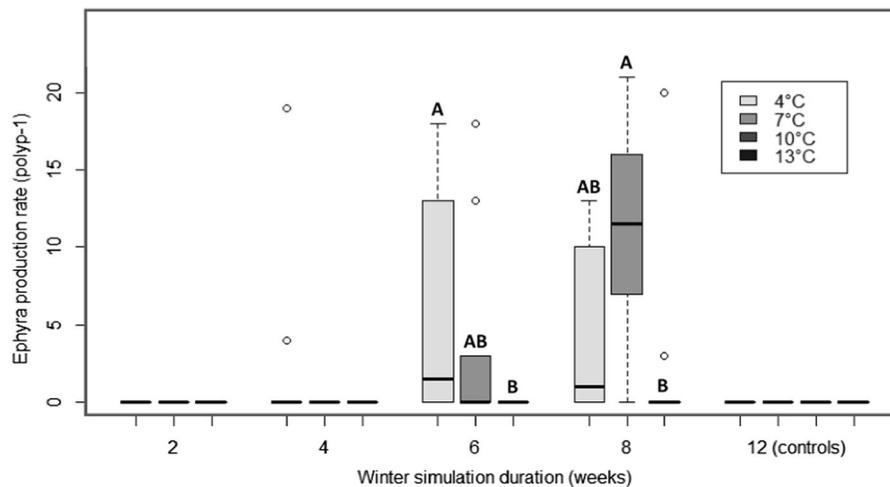


Fig. 5 Median number of ephyrae produced per polyp in each treatment ($n = 10$ replicates/treatment). A bold line inside each box and whisker plot marks the median. The extremities of the box denote the first and the third quartile and the dotted lines

denote the range. Points beyond the dotted line are outliers. Letters indicate similarities (e.g. A, A) and differences (e.g. A, B) between temperature treatments within each duration, as determined by post hoc tests

factors in past studies is very challenging (Hubot et al., 2017). In situ, the trend of delayed ephyrae appearance after cold winters observed in Southampton Water by Lucas (2001) can be partly explained by the duration of the winter period and, in particular, the timing of the winter minimum. Shorter, sharper winters, whilst increasing the final number of ephyrae produced, may delay their production as compared to longer winters where ephyrae respond more rapidly to the eventual warming of the water in the spring.

A key finding of our study was that minimal strobilation was observed following incubation at warmer-than-average winter temperatures. The interaction of the RxR transcription factor and the *Aurelia* spp. specific protein CL390, a likely candidate for the strobilation hormone, provides insight into the molecular processes behind the lack of strobilation in the warmer treatments (Fuchs et al., 2014). Specifically, the above-average winter temperature may not have reached the critical low threshold needed to induce upregulation of the CL390 transcript. Alternatively, a longer incubation at these temperatures was needed to produce enough transcript to reach the activation threshold and initiate strobilation. This lack of strobilation has been observed in other experiments on temperate species, where temperatures were suggested to be too high to induce ephyra production (Willcox et al., 2007). This effect is compounded when examining temperature and duration combined.

Differences in the response to spring warming between the shorter (2, 4 weeks), and the longer winter incubations (6, 8 weeks) in the current experiment may represent the difference between the response to a short-term cold snap, and a seasonal change. In North Sea regions, such as along the French Normandy coast, polyps needed at least 15 days at colder temperatures when moved from 20 to 15 °C, and 9 days when moved from 18 to 10 °C to initiate strobilation (Kroiher et al., 2000). In Horsea Lake polyps, a longer winter incubation resulted in strobilation occurring more rapidly and in more polyps producing more ephyrae following the shift to spring temperatures. To initiate significant strobilation, polyps need to be incubated at an average or cooler-than-average temperature for this region for about 6 weeks.

Most studies examining temperature effects on scyphozoan jellyfish have proposed that moderately warmer temperatures benefit temperate jellyfish populations, by enhancing ephyral growth and reproduction in polyps and medusae (e.g. Purcell, 2005; Widmer, 2005). These studies have focussed on the warmer (summer) temperature threshold. Warmer winter temperatures in temperate regions such as the North Sea, however, are likely to inhibit spring jellyfish blooms, as proposed by Lynam et al. (2004). The current study indicates that winters exceeding 6 weeks and < 7 °C are likely to result in

larger temperate *Aurelia* populations, whereas years that experience a warmer and shorter-than-average winter may experience reduced or delayed strobilation. However, it is still unclear whether induction of strobilation occurs due to reaching a critical temperature threshold (e.g. winter minimum) or a relative change in temperature, and it would be beneficial to understand how consistent these results are between different populations.

This study has important implications in the current climate of global warming, where some regions are experiencing rapid warming and increasing winter temperatures (Belkin, 2009). For example, enclosed and semi-enclosed European seas such as the Baltic and North Seas have experienced rapid warming from 1982 to 2006, with the Baltic Sea warming at a rate of 1 °C per decade (Belkin, 2009). Holst (2012) posited that increasing sea temperatures might benefit *A. aurita* polyps from the North Sea. This study shows that polyps from Horsea Lake, UK, are unlikely to strobilate after experiencing warmer-than-average winter temperatures. In future scenarios of climate warming, temperate polyps are likely to experience shorter, warmer winter periods that may not always reach the long-term average winter minimum. Whilst there are many confounding factors that drive jellyfish population cycles and the appearance of blooms (Brodeur et al., 2008; Lynam et al., 2011), if polyps no longer experience the cues to initiate strobilation, then they are unlikely to produce ephyrae, preventing future bloom formation (Fuchs et al., 2014; Treible & Condon, 2019). Despite evidence that some local populations may be able to adapt to changing environmental conditions (Lu et al., In press), recent warming may be too fast for these species to respond to (IPCC, 2018). Future investigations should focus on this crucial preconditioning period by studying each life stage in isolation and in combination with others, to predict how changing conditions will affect jellyfish populations in the future.

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

Compliance with ethical standards

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.

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