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Effects of temperature and salinity on four species of northeastern Atlantic scyphistomae (Cnidaria: Scyphozoa)

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ABSTRACT: Laboratory incubation experiments were conducted to examine the effects of different temperatures (4, 9, 14, 19, 23°C) and salinities (21, 27, 34) on survival and asexual reproduction of scyphistomae of *Cyanea capillata*, *C. lamarckii*, *Chrysaora hysoscella*, and *Aurelia aurita* in order to better understand how climate variability may affect the timing and magnitude of jellyfish blooms. Significant mortality was observed only for *C. capillata* and *Ch. hysoscella* at the highest and lowest temperatures, respectively, but temperature and salinity significantly affected the asexual reproductive output for all species. As temperature increased, production rates of podocysts increased and, if produced, progeny scyphistomae by side budding also increased. However, strobilation rates, and therefore the mean number of ephyrae produced, decreased when scyphistomae were exposed to elevated temperatures. These results provide a mechanistic explanation for why ephyrae of these species tend to be produced during colder periods of the year whilst summer and early autumn are probably important periods for increasing the numbers of scyphistomae in natural populations.

KEY WORDS: Jellyfish · Scyphistoma · Strobila · Ephyra · Temperature · Salinity · Life cycle

INTRODUCTION

In some locations, jellyfish blooms appear to be occurring more often (Mills 2001, Purcell et al. 2007, Richardson et al. 2009, Dong et al. 2010, Brotz et al. 2012), while in others, decreases have been reported (Dawson et al. 2001, Mills 2001). However, because of a global lack of long-term monitoring (Purcell et al. 2007, Nickell et al. 2010), the question of whether blooms are truly increasing in frequency and intensity has been controversial, although it is frequently stated that increasing global temperatures are likely to favor jellyfish blooms.

Analysis of available time-series suggests that the abundance of jellyfish medusae is often linked with long-term climate cycles (Lynam et al. 2004, 2005, Condon et al. 2013), and environmental conditions are undoubtedly important influences upon jellyfish populations. For example, increases in numbers of *Chrysaora* spp. and *Aurelia* sp. in the Gulf of Mexico have been linked with warm winters, cool dry springs, and warmer than average summers (Robinson & Graham 2013). In the North Sea, the abundance of scyphozoan medusae has been linked with the North Atlantic Oscillation (NAO), although with differing patterns in the northern and southern sub-regions (Lynam et al. 2004, 2005, 2010). Several of the regions, and in particular to the west of Denmark, showed significant negative correlations between medusa abundance of *A. aurita* and *Cyanea lamarckii* and the NAO index of the previous winter. This result seems surprising because positive NAO years

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are associated with warmer winters. The finding of reduced medusae abundances during the following summers is thus the opposite of the suggestion that warming will favor jellyfish.

The life cycles of most non-oceanic jellyfish include an asexually reproductive benthic stage—the scyphistoma. Because planktonic medusae originate from the benthic scyphistomae through the process of strobilation, factors affecting polyp growth and reproduction are likely key controls on the abundance of medusae (Lucas et al. 2012). Benthic asexual reproduction modes in scyphozoan scyphistomae have been grouped into 9 categories (Adler & Jarms 2009). These modes are comprised of production of lateral buds (2 types); stolon buds, regeneration from stolon fragments; production of podocysts; free-swimming buds; gastric cavity regeneration; longitudinal fission and strobilation. Scyphistomae also release juvenile medusae, known as ephyrae, through the process of strobilation, and these ephyrae eventually grow into the sexually reproductive pelagic medusae (Arai 1997, Adler & Jarms 2009, Lucas et al. 2012). Further studies into the effects of environmental conditions on the asexual reproductive modes of the scyphistomae are required (Mills 2001, Boero et al. 2008, Lucas et al. 2012) since their success ultimately determines whether or not medusae blooms will form (Lucas et al. 2012).

Apart from the widely occurring *A. aurita*, the habitat preferences of the scyphistomae of other scyphozoan species are largely unknown, and information on the location and timing of strobilation remains based upon observations of the ephyrae in near-shore plankton samples (Verwey 1942, Hernroth & Gröndahl 1985, Gröndahl 1988, Lucas & Williams 1994). Until scyphistoma populations are found and studied *in situ*, laboratory experiments will be required to learn more about how scyphozoan benthic life history stages may respond to altered physical conditions.

Here we report on laboratory incubation experiments to investigate the effects of different temperatures and salinities on the population growth and strobilation rates of scyphistomae of 4 species of northeastern Atlantic Scyphozoa. We sought to investigate the role that changed environmental conditions may have on scyphistomae asexual reproduction, because the numbers of scyphistomae and the rates of strobilation are likely key factors controlling the numbers of medusae released into the plankton. The specific hypotheses tested were that differences in both temperature and salinity would significantly affect (1) mortality, (2) asexual reproduction, (3) timing of strobilation, and (4) numbers of ephyrae released.

MATERIALS AND METHODS

Founding stock cultures

Experiments were conducted with scyphistomae of *Aurelia aurita*, *Cyanea capillata*, *C. lamarckii*, and *Chrysaora hysoscella*. Scyphistomae of *A. aurita* were sourced from the tests of the ascidian *A. mentula* growing at between 10 and 27 m deep in Scapa Flow, Scotland, during summer 2010. The host ascidians were collected by divers and the scyphistomae were carefully removed at the Scottish Oceans Institute (SOI) with fine-tipped forceps. Scyphistomae were placed inside plastic culture plates filled with 5 µm-filtered North Sea water, salinity 34. Ephyrae released from these scyphistomae were raised at SOI into mature medusae to confirm that they were *A. aurita*. Specimens of scyphistomae collected from Scapa Flow were also supplied to S. Piraino and G. Aglieri at the Universitia del Salento, Leece, Italy, for cytochrome *c* oxidase subunit I DNA barcoding, which confirmed them to be *A. aurita.* During summer 2011, *C. capillata* and *C. lamarckii* medusae were collected near Oban and near St. Andrews, Scotland, respectively. Stock cultures of scyphistomae of these 2 species were initiated using planulae collected from 5 female medusae of each species. Planula larvae of *Ch. hysoscella* were harvested from 3 female medusae collected near Dalefort, Wales, in August 2011. The stock cultures of scyphistomae for all 4 species were maintained at salinity 34 at 10°C, in a dark temperature-controlled room in the SOI. They were fed 1 d old *Artemia franciscana* (Kellog) nauplii once per week for at least 6 mo prior to the start of experiments in order to ensure that the scyphistomae had time to fully develop.

Incubation temperatures and salinities

The locations of the benthic stages of most species of scyphozoa are cryptic. However, ones that have been found are often located in water <30 m deep, so the temperatures selected for the experiments (Table 1) were in the range reported for surface stations in the North Sea (Schulz 2009, Beszczynska-Möller & Dye 2013) with the addition of a 23°C treatment, which is at the upper end of temperature predictions for the southern North Sea by the 2080s (Mathis & Pohlman 2014). Offshore salinities in the North Sea are generally above 35, but lower salinities are found closer inshore, particularly in the estuaries, coastal zone and German Bight during late winter and early spring (Beszczynska-Möller & Dye

2013). The temperatures and salinities tested for each species (Table 1) were thus selected to cover a plausible range, which might be experienced by scyphistomae in the northeastern Atlantic.

Equipment and acclimations

Experimental rearing was conducted inside temperature-controlled incubators (Lucky Reptile Herp Nursery II). The incubators were darkened to remove the potentially confounding effects of the light/dark period on asexual reproduction (Liu et al. 2009, Purcell et al. 2009), and temperature in each incubator was continuously monitored using USB data loggers (Lascar EL-USB-1). The salinity of North Sea water collected from the flow through seawater system at SOI was adjusted by mixing with distilled water and monitored using a calibrated hand-held Bellingham and Stanley refractometer. One scyphistoma from the stock cultures described above was placed in each well of 6-well polycarbonate culture plates filled with 12 ml of the 5 µm-filtered North Sea water, and then gradually acclimated to the target salinity at 10°C in a stepwise manner over 7 d. The scyphistomae were then gradually acclimated to their target temperatures over an additional 7 d. All scyphistomae had attached to the bottoms of their replicate wells by the ends of the acclimation periods. During the experiments, scyphistomae were fed 1 d old *A. franciscana* nauplii to repletion once per week. Uneaten food was removed and water changed the following day using a pipette, with the wells being refilled with 5 µm-filtered seawater of appropriate salinity and temperature.

Data recording

Scyphistomae were examined weekly under a dissecting stereomicroscope for the formation of new podocysts or progeny scyphistomae, to check for strobilation, and to record any mortality. Examinations were conducted as quickly as possible (~15 min per observation) at room temperature (~15°C) to prevent large temperature fluctuations. Progeny scyphistomae were removed from the wells as soon as they had separated from parent scyphistomae in order to eliminate the effects of crowding on asexual reproduction. If, at the end of the 8 wk experiment, a scyphistoma was observed to still be undergoing strobilation, incubations were continued until the last ephyrae was released. At the end of incubation scyphistomae were removed from their experimental wells with fine tipped forceps, and the number of podocysts were counted.

Table 1. Summary of temperatures and salinities tested for each jellyfish species; n refers to the total number of scyphistomae incubated per temperature and salinity combination

Species	Temp. (±1°C)	Salinity	n
Cyanea capillata	4, 9, 14, 19, 23	21, 27, 34	18
Cyanea lamarckii	4, 9, 14, 19	27, 34	18
Chrysaora hysoscella	4, 9, 14, 19, 23	27, 34	18
Aurelia aurita	4, 9, 14, 19, 23	21, 27, 34	15

Data analysis

The response variables were: number of progeny scyphistomae and podocysts produced, whether or not mortality or strobilation had occurred; time until strobilation began; duration of strobilation events; and numbers of ephyrae produced per individual in each treatment group. Since the response variables were either counts (e.g. number of podocysts produced), or were binomial in nature (e.g. strobilated or did not), generalized linear models (GLMs) were used to model the effects of temperature, salinity and their interaction. Best fitting models were selected based on Akaike Information Criteria, followed by analysis of deviance likelihood ratio tests. Model validation followed recommendations in Ver Hoef & Boveng (2007) and Zuur et al. (2013). Relationships between temperature, salinity and response variables were evaluated by calculation of Spearman's correlation coefficient (r_S). All analyses were conducted using R v.2.15.1.

In order to visualize the predicted number of ephyrae under different temperature conditions, the best fitting models were used to predict 30 fitted values within the temperature ranges reported to commonly occur during each month of the year during positive and negative NAO years at stations in the North Sea (www.cefas.defra.gov.uk).

RESULTS

During the present study, scyphistomae to scyphistomae asexual reproduction of *Cyanea capillata* and *Chrysaora hysoscella* was observed to be exclusively by the production of podocysts, while *Cyanea lamarckii* produced both podocysts and typical lateral side buds. *Aurelia aurita* scyphistomae produced podo-

cyst-, lateral side bud- and stolon budded-progeny. However, scyphistomae of all 4 species strobilated during the experiments. A summary of the best fitting GLMs for the effects of temperature, salinity and their interaction on asexual reproductive output and survivorship of the studied scyphistomae is given in Table 2. Descriptive statistics are given in Tables S1 to S4 in the Supplement at www.int-res.com/articles/suppl/m559p073_supp.pdf, and a summary of the results of the Spearman correlation tests is provided in Table 3.

Surviving scyphistomae

Temperature significantly affected the survival of *C. capillata* and *Ch. hysoscella* scyphistomae, but did not significantly affect survival of *C. lamarckii* or *A. aurita*. At higher temperatures survival of *C. capillata* scyphistomae was diminished and all *C. capillata* scyphistomae perished within 3 wk at 23°C (Fig. 1A). In contrast, scyphistomae of *Ch. hysoscella* survived at 23°C but died at 4°C by the end of the 7th wk (Fig. 1C). Salinity did not have significant effects on survival for any of the 4 species.

Production of progeny scyphistomae

C. capillata and *Ch. hysoscella* did not produce progeny scyphistomae during the any of the incubations, and asexual reproduction for these species was limited to the production of podocysts and ephyrae through strobilation. *C. lamarckii* and *A. aurita* produced progeny scyphistomae by means of typical side budding in all treatments, but not in high numbers (Fig. 2A). There were also no significant relationships between the number of progeny produced by *C. lamarckii* and temperature or salinity. *A. aurita* also produced progeny scyphistomae (Fig. 2B), and there were significant relationships with temperature, but not salinity. The interaction was however significant; therefore, salinity was retained in the model.

Table 2. Summary of best fitting generalized linear models for the results of experiments testing the effects of temperature (T) and salinity (S) on jellyfish asexual reproductive output, strobilation and mortality of scyphistomae. The full model was: Response variable ~ T + S + T × S + ε. na: not applicable

Species	Response variable	Significant predictor variables	Family	Link	Explained deviance (%)
Cyanea capillata	Surviving scyphistomae	~ T	Binomial	Logit	44.8
	Progeny scyphistomae	None produced			
	Podocysts produced	~ T	Poisson	Log	43.1
	Strobilating scyphistomae	~ T	Binomial	Logit	49.2
	Onset of strobilation	~ T	Poisson	Log	27.7
	Strobilation duration	~ T + S	Poisson	Log	35.6
	Ephyrae produced	~ T + S	Poisson	Log	53.5
Cyanea lamarcki	Surviving scyphistomae	None	Binomial	Logit	na
	Progeny scyphistomae	None	Poisson	Log	na
	Podocysts produced	~ T	Poisson	Log	31.0
	Strobilating scyphistomae	~ T	Binomial	Logit	23.0
	Onset of strobilation	~ T + S	Poisson	Log	53.0
	Strobilation duration	~ T	Poisson	Log	48.0
	Ephyrae produced	~ T + S + T × S	Poisson	Log	29.0
Chrysaora hysoscella	Surviving scyphistomae	~ T	Binomial	Logit	42.0
	Progeny scyphistomae	None produced			
	Podocysts produced	~ T + S + T × S	Poisson	Log	60.2
	Strobilating scyphistomae	~ T	Binomial	Logit	18.8
	Onset of strobilation	None	Poisson	Log	na
	Strobilation duration	~ T	Poisson	Log	50.9
	Ephyrae produced	~ T + S + T × S	Poisson	Log	23.1
Aurelia aurita	Surviving scyphistomae	None	Binomial	Logit	na
	Progeny scyphistomae	~ T + S + T × S	Poisson	Log	12.0
	Podocysts produced	~ T + S + T × S	Poisson	Log	24.0
	Strobilating scyphistomae	~ T + S	Binomial	Logit	80.0
	Onset of strobilation	None	Poisson	Log	na
	Strobilation duration	None	Poisson	Log	na
	Ephyrae produced	~ T + S	Poisson	Log	86.0

Table 3. Summary of Spearman correlation results (r_S) for experiments testing the effects of temperature (T) and salinity (S) on jellyfish asexual reproductive output, strobilation and mortality of scyphistomae; n = 18 for *Cyanea capillata*, *Chrysaora hysoscella* and *Aurelia lamarckii*, and n = 15 for *A. aurita*. Significant correlations are highlighted in **bold** ($\alpha = 0.05$). na: not applicable

Species	Response variable	Predictor variable	r_S	p
Cyanea capillata	Surviving scyphistomae	T	**−0.633**	**<0.001**
		S	−0.056	0.357
	Podocysts produced	T	**0.354**	**<0.001**
		S	−0.029	0.702
	Strobilating scyphistomae	T	**−0.68**	**<0.001**
		S	0.009	0.876
	Onset of strobilation	T	**−0.494**	**<0.001**
		S	0.132	0.203
	Strobilation duration	T	**−0.498**	**<0.001**
		S	−0.218	**0.033**
	Ephyrae produced	T	**−0.667**	**<0.001**
		S	−0.021	0.728
Cyanea lamarckii	Surviving scyphistomae	T	−0.108	0.195
		S	−0.061	0.470
	Podocysts produced	T	**0.428**	**<0.001**
		S	−0.013	0.874
	Progeny scyphistomae	T	−0.064	0.44
		S	0.071	0.394
	Strobilating scyphistomae	T	**−0.419**	**<0.001**
		S	0.0	1.0
	Onset of strobilation	T	**−0.604**	**0.001**
		S	**−0.586**	**0.001**
	Strobilation duration	T	**−0.699**	**<0.001**
		S	−0.103	0.615
	Ephyrae produced	T	**−0.409**	**<0.001**
		S	0.015	0.851
Chrysaora hysoscella	Surviving scyphistomae	T	**0.707**	**< 0.001**
		S	0.0	1.0
	Podocysts produced	T	**0.659**	**< 0.001**
		S	**0.204**	**0.013**
	Strobilating scyphistomae	T	0.018	0.806
		S	0.013	0.862
	Onset of strobilation	T	−0.187	0.229
		S	−0.099	0.526
	Strobilation duration	T	**−0.668**	**< 0.001**
		S	0.116	0.456
	Ephyrae produced	T	0.035	0.631
		S	0.019	0.794
Aurelia aurita	Surviving scyphistomae	T	−0.027	0.682
		S	−0.094	0.155
	Podocysts produced	T	0.052	0.433
		S	0.022	0.736
	Progeny scyphistomae	T	0.107	0.108
		S	−0.036	0.590
	Strobilating scyphistomae	T	**−0.6172**	**< 0.001**
		S	−0.074	0.267
	Onset of strobilation	T	na	na
		S	−0.222	0.206
	Strobilation duration	T	na	na
		S	**−0.542**	**0.001**
	Ephyrae produced	T	**−0.604**	**< 0.001**
		S	−0.058	0.386

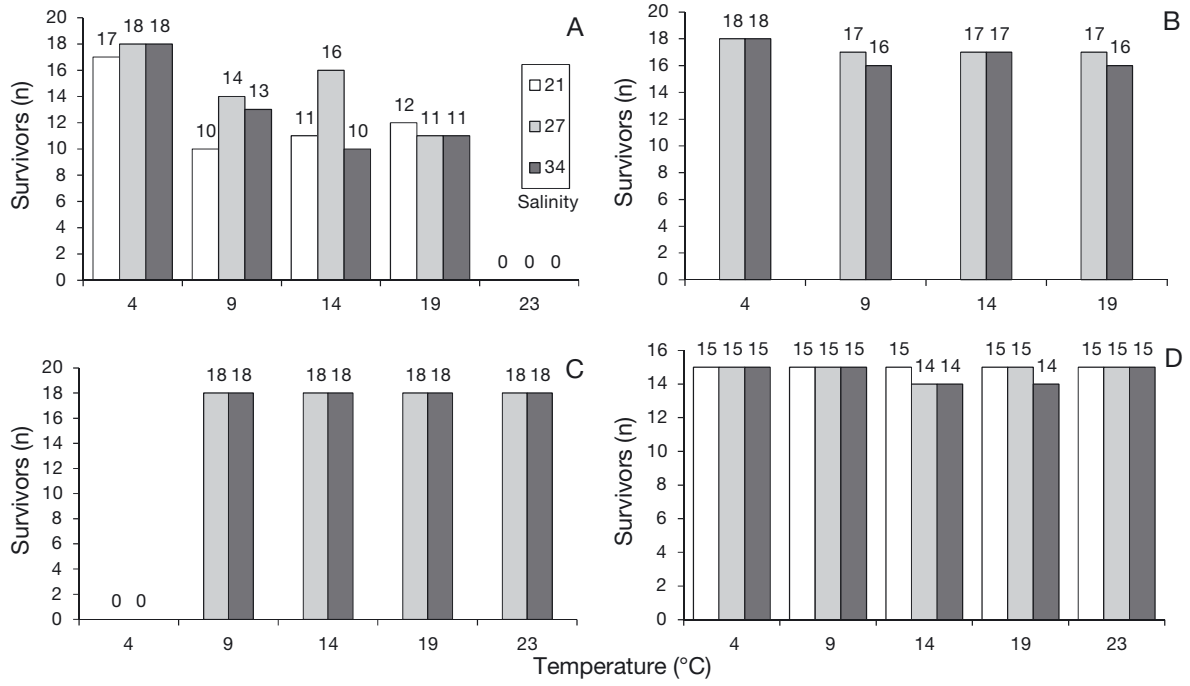

Fig. 1. Total number of surviving scyphistomae at the terminus of the experiments. (A) *Cyanea capillata*. (B) *C. lamarckii*. (C) *Chrysaora hysoscella*. (D) *Aurelia aurita*. At the start of the experiment, n = 15 for *A. aurita* and n = 18 for all other spp.

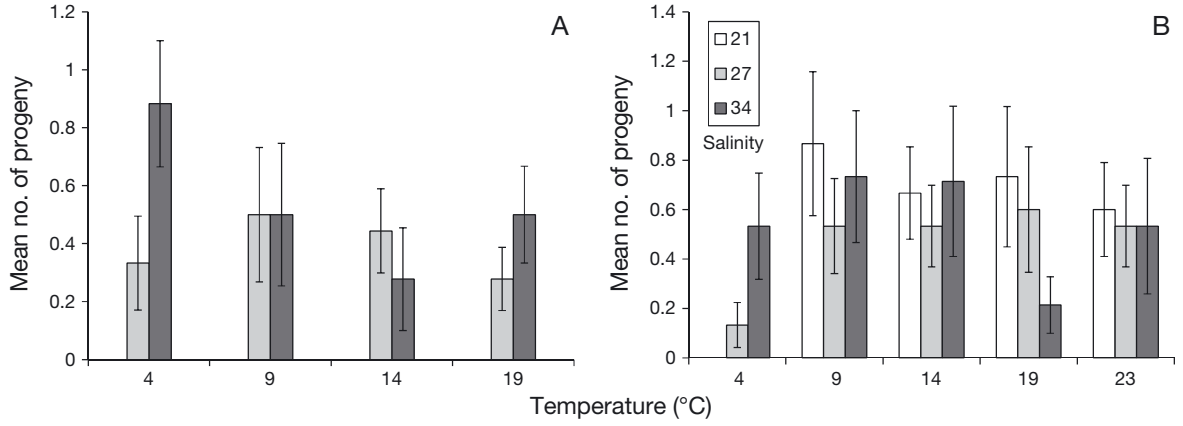

Fig. 2. Mean numbers of progeny produced per scyphistoma. (A) *Cyanea lamarckii*. (B) *Aurelia aurita*. Error bars = SEM

Production of podocysts

Podocysts were produced by scyphistomae of all 4 species during the study with the general trend that the number of podocysts increased with temperature (Fig. 3). Podocyst production was significantly and positively correlated with temperature for *C. capillata* (r_S = 0.354, $p < 0.001$), *C. lamarckii* (r_S = 0.428, $p < 0.001$) and *Ch. hysoscella* (r_S = 0.659, $p < 0.001$), but temperature was not significantly correlated with podocyst production in *A. aurita* (Table 3). The mean number of podocysts produced by scyphistomae of *C. capillata* and *C. lamarckii* was significantly linked with temperature in the GLMs. The greatest number

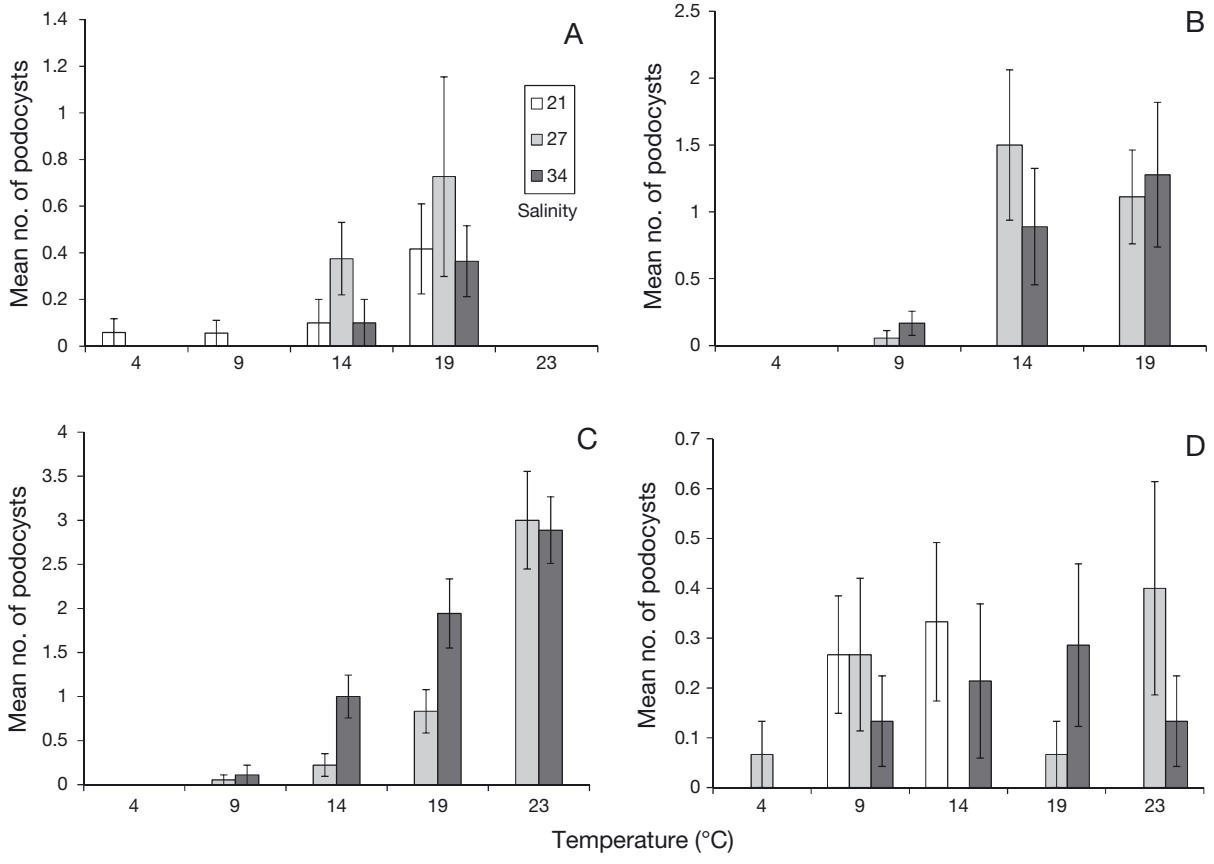

Fig. 3. Mean number of podocysts produced per scyphistoma. (A) *Cyanea capillata*. (B) *C. lamarckii*. (C) *Chrysaora hysoscella*. (D) *Aurelia aurita*. Error bars = SEM

of podocysts, average 3.0 per scyphistoma, was produced at 23°C and salinity 27 by *Ch. hysoscella*. The rates of *Ch. hysoscella* and *A. aurita* podocyst production were significantly and positively correlated with salinity (r_S = 0.204, p = 0.013), and significantly linked in the GLM to temperature and salinity, and the interaction of these 2 factors was also significant (Fig. 3C).

Strobilation

Scyphistomae of all 4 species strobilated during the study (Fig. 4). Strobilation was significantly and negatively correlated with temperature for *C. capillata* (r_S = −0.68, p < 0.001), *C. lamarckii* (r_S = −0.41, p < 0.001) and *A. aurita* (r_S = −0.61, p < 0.001), but temperature was not significantly correlated with strobilation in *Ch. hysoscella* (Table 3). Salinity was not significantly correlated with strobilation for any of the species tested (Table 3.) No scyphistomae strobilated more than once during the 8 wk study. Strobilation of scyphistomae of *C. capillata*, *C. lamarckii* and *Ch. hysoscella* was significantly linked with temperature alone in GLMs, and strobilation of *A. aurita* was significantly linked with temperature and salinity, but not their interaction. None of the scyphistomae perished after strobilating and appeared to be in good condition, which was apparent by the regeneration of mouths and feeding tentacles following liberation of the final ephyra.

Onset of strobilation

Scyphistomae of *C. capillata* and *C. lamarckii* maintained at warmer temperatures strobilated sooner than scyphistomae incubated at cooler temperatures (Fig. 5A,B). However, the number of scyphistomae that strobilated within 2 wk was far fewer than those scyphistomae that strobilated after >2 wk (Figs. 4 & 5). For *C. capillata*, there was a significant negative relationship between the days taken to begin strobilation and temperature, but not with salinity or the interaction of temperature and salinity. For *C. lamarckii*, the mean time to strobilation onset was significantly linked with temperature and salinity, but not their interaction. Nei-

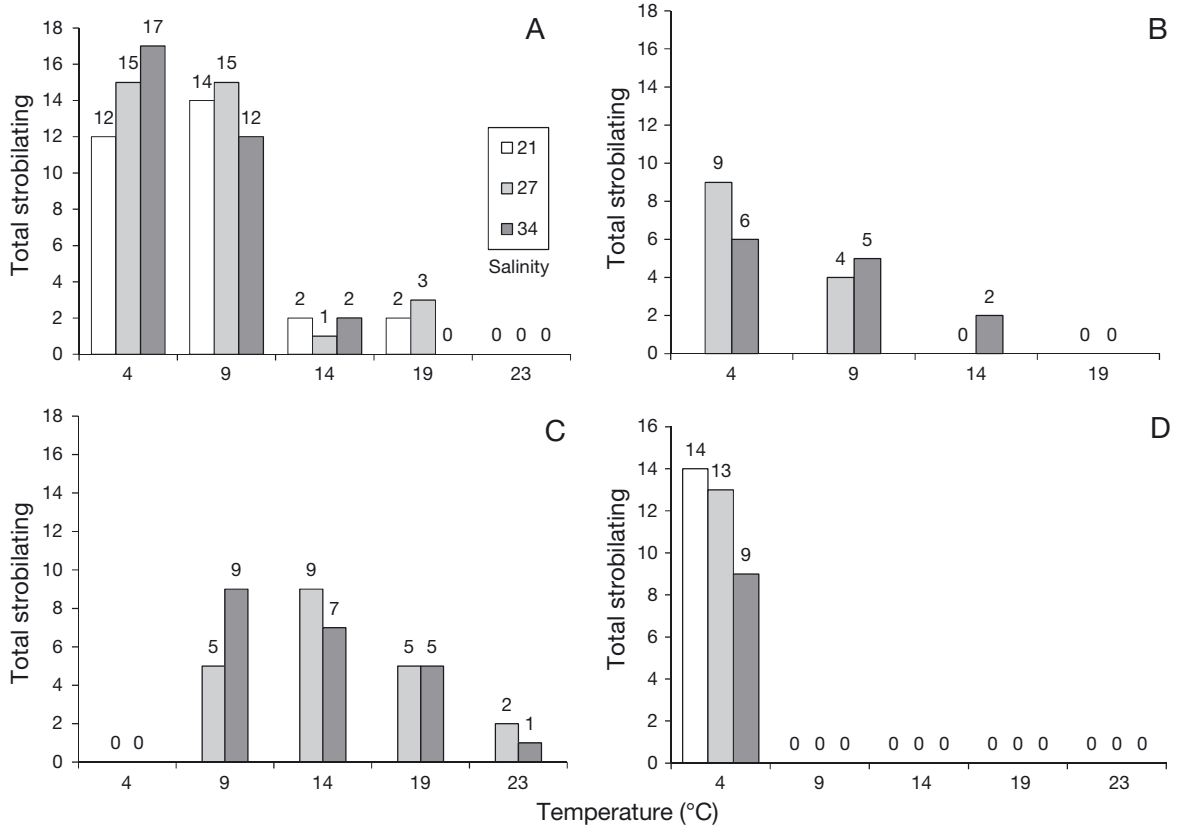

Fig. 4. Total number of scyphistomae that strobilated during the experiments. (A) *Cyanea capillata*. (B) *C. lamarckii*. (C) *Chrysaora hysoscella*. (D) *Aurelia aurita*

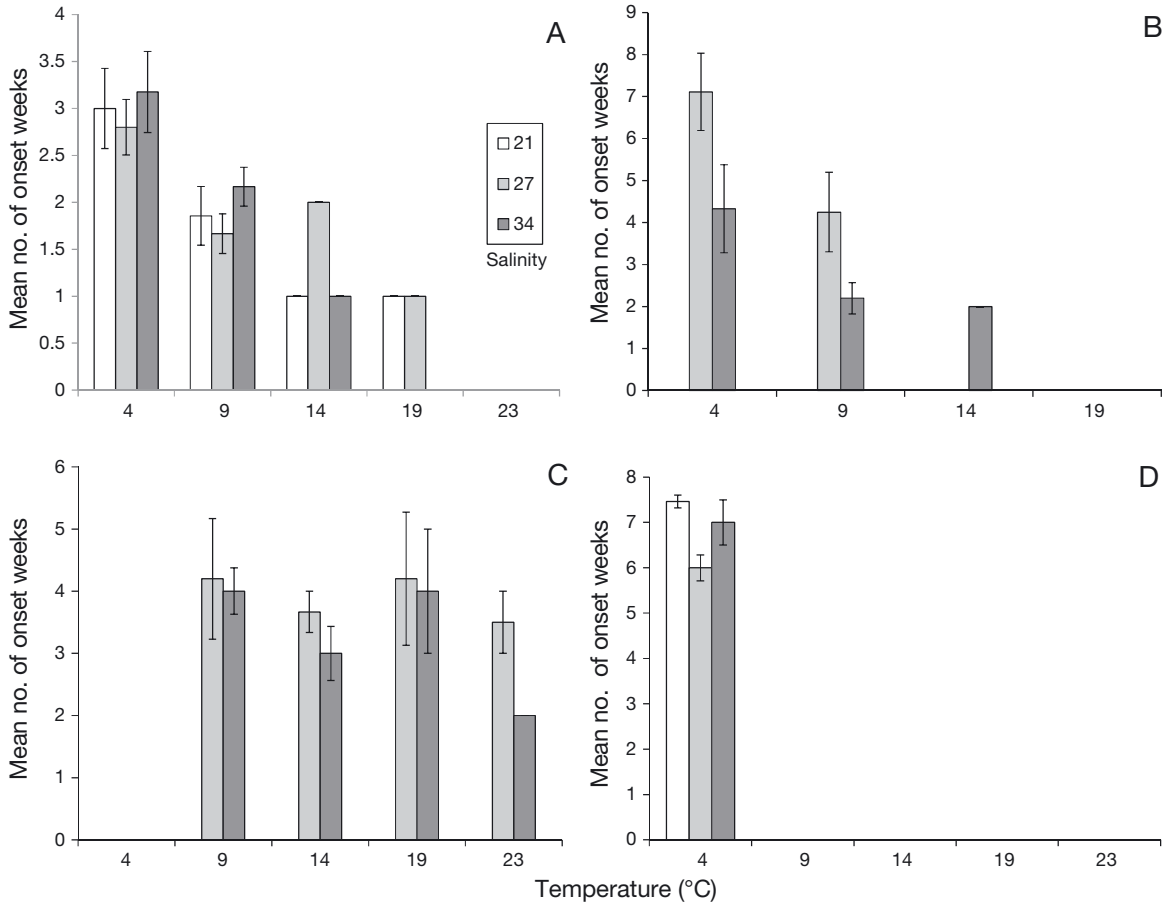

Fig. 5. Mean number of weeks before the onset of strobilation. (A) *Cyanea capillata*. (B) *C. lamarckii*. (C) *Chrysaora hysoscella*. (D) *Aurelia aurita*. Error bars = SEM

ther temperature nor salinity was significantly linked with onset of strobilation in *A. aurita* or *Ch. hysoscella* over the ranges tested.

Duration of strobilation

Temperature was significantly linked with the duration of strobilation in all species except *A. aurita*, with the general trend being that duration decreased as temperature increased (Fig. 6). Salinity was only significantly linked with the duration of strobilation for *C. capillata* (Fig. 6A). Strobilation duration was significantly and negatively correlated with temperature for *C. capillata* (r_S = –0.49, $p < 0.001$), *C. lamarckii* (r_S = –0.69, $p < 0.001$) and *Ch. hysoscella* (r_S = –0.66, $p < 0.001$), but temperature was not significantly correlated with strobilation duration in *A. aurita* since strobilation only occurred at 4°C (Table 3). Salinity was significantly correlated with strobilation duration for *C. capillata* (r_S = –0.21, $p = 0.03$), and *A. aurita* (r_S = –0.54, $p = 0.001$).

Production of ephyrae

Temperature and salinity were significantly linked with ephyra production, with the general trend that mean ephyra production decreased as temperature increased for all species tested (Fig. 7, Table 2). The interaction of temperature and salinity was also significant for *C. lamarckii* and *Ch. hysoscella* in the GLMs. The greatest mean number of ephyrae, 19.3 per scyphistoma, were produced by *A. aurita* at 4°C and salinity 27 (Fig. 7). The number of ephyrae produced was significantly and negatively correlated with temperature for *C. capillata* (r_S = –0.66, $p < 0.001$), *C. lamarckii* (r_S = –0.41, $p < 0.001$) and *A. aurita* (r_S = –0.6, $p < 0.001$), but temperature was not significantly correlated with the number of ephyrae produced for *Ch. hysoscella* (Table 3), and salinity was not significantly correlated with the number of ephyrae produced for any of the 4 species examined. For *C. capillata* and *Ch. hysoscella*, the mean number of ephyrae produced increased to an optimum temperature but then decreased as temperatures increased further.

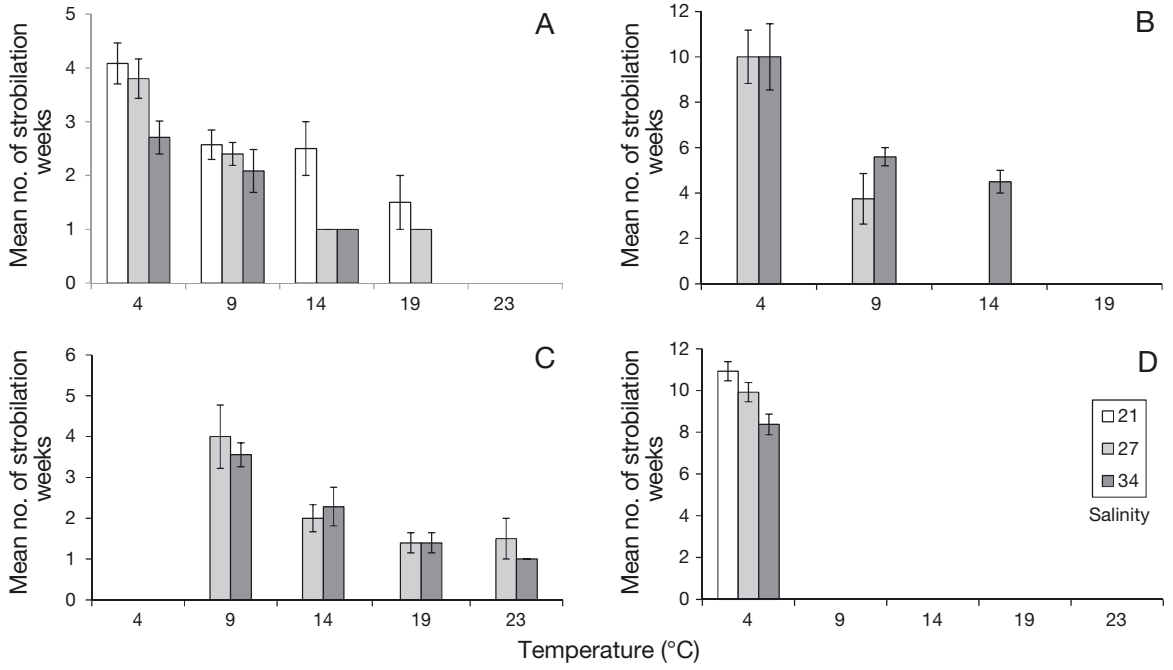

Fig. 6. Mean number of weeks to complete the process of strobilation. (A) *Cyanea capillata*. (B) *C. lamarckii*. (C) *Chrysaora hysoscella*. (D) *Aurelia aurita*. Error bars = SEM

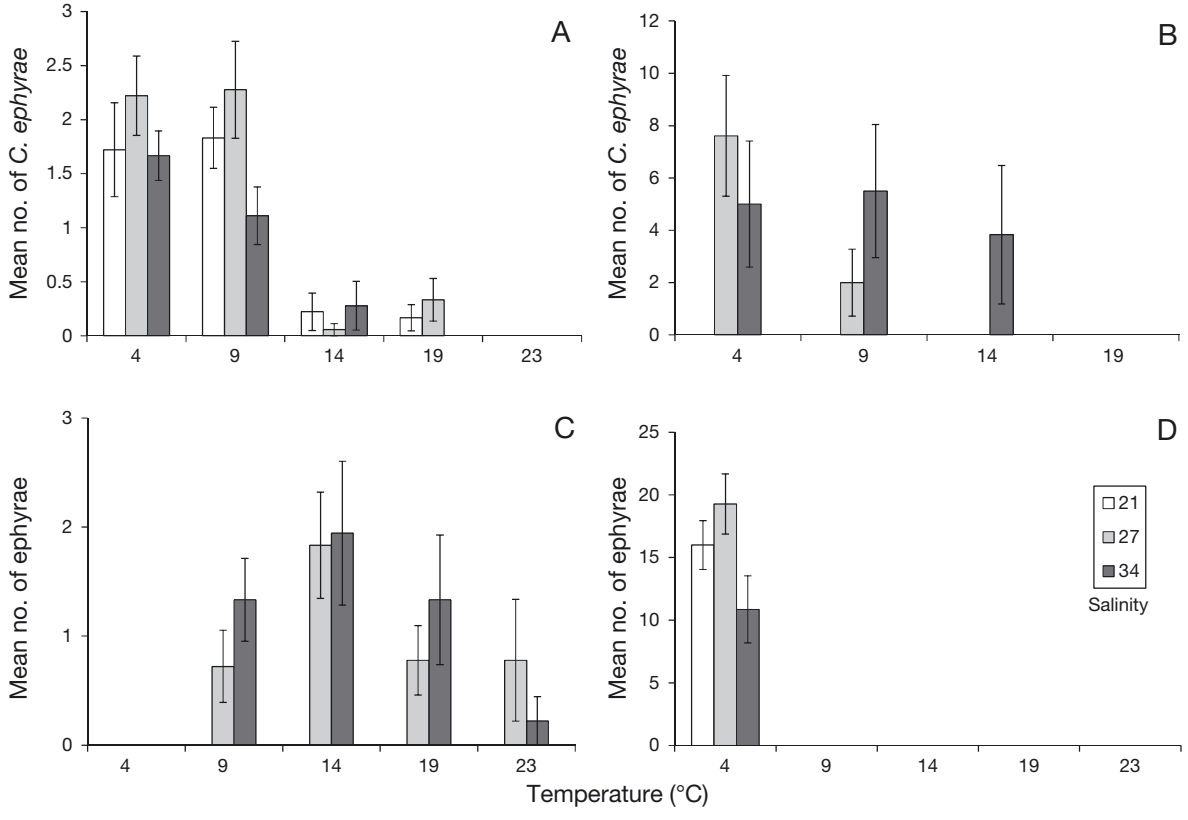

Fig. 7. Mean number of ephyrae produced per scyphistoma. (A) *Cyanea capillata*. (B) *C. lamarckii*. (C) *Chrysaora hysoscella*. (D) *Aurelia aurita*. Error bars = SEM

The temperature at which the maximum number of ephyrae was produced was also slightly higher in *Ch. hysoscella* compared with the other species. For *C. lamarckii*, higher temperatures led to fewer ephyrae being released per scyphistoma whilst strobilation did not occur at all in *A. aurita* when the scyphistomae were held at temperatures above 4°C.

Potential effect of high and low NAO scenarios on the production of ephyrae

Our results suggest that when the NAO is in a positive phase, warmer winter sea temperatures may decrease the number of *A. aurita* and *C. lamarckii* scyphistomae that strobilate, with the effect being that fewer ephyrae are added to the system (Fig. 8). Conversely, when the NAO is in a negative phase, cooler sea temperatures during winter may increase the number of scyphistomae that strobilate, resulting in more ephyrae. By summer/autumn, correlations of sea temperature with previous NAO have largely disappeared (Lynam et al. 2005), so that we would not expect much predictive power for the effect of NAO on the other asexual reproductive modes, e.g. via podocyst production.

DISCUSSION

Results from the present study showed that asexual reproductive outputs of scyphistomae of 4 species of northeastern Atlantic jellyfish are significantly affected by temperature and salinity. These findings

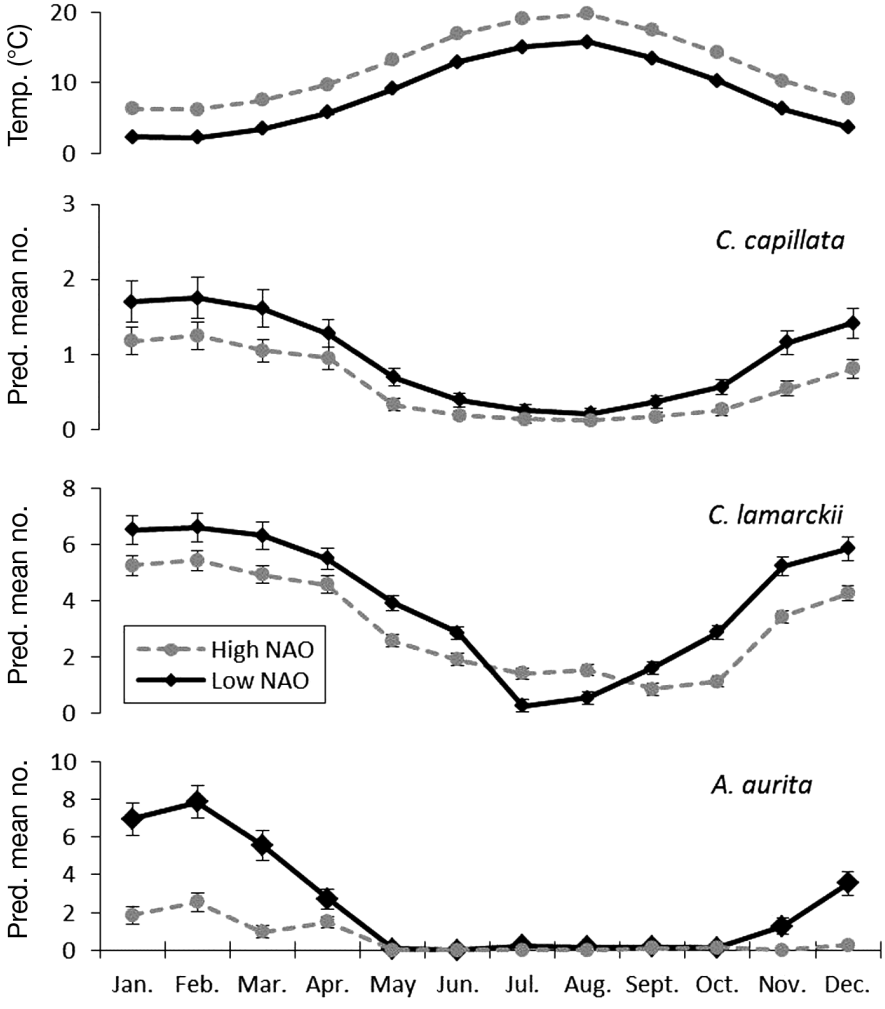

Fig. 8. Hypothetical model of the mean number of ephyrae produced per scyphistoma of *Cyanea capillata*, *C. lamarckii* and *Aurelia aurita* under high and low North Atlantic Oscillation (NAO) sea surface temperature conditions. Generalized linear model (GLM) predictions were derived from present experimental results made at salinity = 34, confidence limits = ±SE

provide a possible mechanistic explanation for previously reported correlative interannual climate-related variability in jellyfish medusae abundance in the North Sea (Lynam et al. 2005, 2004), as well as indicating that a future warmer northeastern Atlantic may not be so jellyfish-dominated as some have suggested, unless the reason is due to a strong increase in the abundance of more Lusitanian species.

Around the UK, *Cyanea capillata* medusae have been recorded more frequently along the northwestern coastline, giving it a more northerly distribution. In contrast, *Chrysaora hysoscella* tends to be found in more southerly waters, although the medusae have occasionally been observed along the northern Scottish coast (Russell 1970, Doyle et al. 2007, Holst 2012, NBN 2016). Medusae of *Cyanea lamarckii* have been recorded all around the UK, including in the southern North Sea and English Channel (NBN 2016), whilst *Aurelia aurita* is similarly distributed. These broad geographical patterns in medusae distribution seem to be broadly supported by the relationships between scyphistomae survival and temperature seen in the experiments. *C. capillata* failed to survive at 23°C whilst *Ch. hysoscella* scyphistomae suffered 100% mortality at the lowest temperature tested. Temperature did not significantly affect survival of *C. lamarckii* or *A. aurita* scyphistomae.

Across all the species studied, scyphistomae responded to warmer temperatures by increasing benthic asexual reproductive output through the production of podocysts and/or progeny scyphistomae. The greatest number of podocysts in this study were produced by scyphistomae of *Ch. hysoscella* at a rate of about 0.37 podocysts per week at 23°C at salinity 27, which was slower than the rates reported for *Ch. fuscescens* (1.65 podocysts wk^{-1}) from the northeast Pacific Ocean (Widmer 2008a) and *Ch. quinquecirrha* (4.3 podocysts wk^{-1}) in the Chesapeake Bay (Cargo & Schultz 1967). In natural populations, podocyst production is probably maximal during the summer to early autumn, which would be in agreement with findings for other *Cyanea* (Gröndahl, 1988, Brewer & Feingold 1991, Thein et al. 2013) and *Chrysaora* spp. (Cargo & Schultz 1967, Cargo & Rabenold 1980, Thein et al. 2013). Excystment of podocysts was not observed in the present study, but if patterns are similar to some other species (Cargo & Schultz 1967, Cargo & Rabenold 1980, Gröndahl 1988, Brewer & Feingold 1991, Thein et al. 2013), then podocysts may excyst when sea temperatures drop during autumn. This behaviour could act as a mechanism for timing the development of the emergent scyphistomae in time to strobilate during winter or early spring.

During this study, progeny scyphistomae were only produced by *C. lamarckii* and *A. aurita*, and neither species produced them in great abundance. The results for *A. aurita* were unexpected in light of other studies, which have reported elevated scyphistoma production at higher temperatures (Han & Uye 2010, Schiariti et al. 2014). In our study the Orkney population of *A. aurita* produced very few progeny scyphistomae at 4°C and progeny scyphistomae were produced at temperatures beyond that with the general trend of fewer progeny scyphistomae being produced with increasing temperature above 4°C, which was similar to results for scyphistomae of *A. labiata* (Purcell 2007). Several studies have suggested that in general *Aurelia* spp. may be locally adapted (Edwards 1965, Connelly et al. 2001. Schroth et al. 2002, Lucas et al. 2012, Pascual et al. 2014).

In the present experiments, scyphistomae exposed to cooler temperatures tended to decrease their production of podocysts and progeny scyphistomae, and instead began strobilating. The lowest numbers of ephyrae also tended to be produced at the highest temperatures but there were some differences in the temperature at which the maximal number of strobilating scyphistomae occurred. For *Ch. hysoscella*, the maximal strobilation temperature was slightly higher (9 and 14°C) compared with the other species. In the Gullmar Fjord, Sweden, *C. capillata* has been recorded as strobilating during the coldest months of the year (Gröndahl 1988), and the same was observed for *C. capillata* from the Niantic River estuary, Connecticut, USA (Brewer & Feingold 1991). In the southern North Sea, *A. aurita* ephyrae have been observed from the end of January through to the middle of March (Lucas & Williams 1994, Lucas 2001). Observations on the timing of ephyrae release in natural populations of *Ch. hysoscella* are lacking, but our experimental results suggest strobilation in this species is possible in slightly higher temperatures, compared with the other species. Again, these findings seem consistent with the broad temperature preferences of the 4 species studied.

Numerous studies have sought to uncover the internal mechanisms responsible for strobilation in scyphistomae (Arai 1997, Lucas et al. 2012 and references therein). Several early jellyfish researchers hypothesised that a minimum temperature threshold may be required for scyphistomae to strobilate (Russell 1970 and references therein). Recent work has shown that the precursor hormone (CL390), controlling strobilation in *A. aurita*, is encoded in response to seasonal temperature change (Fuchs et al. 2014). Strobilation has thus been associated with colder

temperatures across a range of Scyphozoa in temperate waters and is presumably a mechanism for maximising the temporal match between the ephyrae and the later-developing spring zooplankton bloom. This hypothesis is supported by evidence of the remarkably long point-of-no return under starvation demonstrated by *A. aurita* ephyrae (Fu et al. 2014). The findings here support the hypothesis that the 4 species of scyphozoan studied must experience low sea temperatures for appropriate durations in order for the majority of scyphistomae to strobilate, but there were inter-specific differences; thus, the precise minimum temperatures required are species, and possibly population, specific.

In the experiments reported here, increasing temperature decreased strobilation durations. This finding is in accordance with those reported elsewhere for a number of temperate (Purcell et al. 1999, Purcell 2007, Holst 2012) and tropical (Sugiura 1965, Lotan & Fine 1994) jellyfish species. In order to determine whether natural populations of scyphistomae are able to strobilate more than once during an annual cycle, the amount of time required for scyphistomae to initiate the process of strobilation (onset when temperatures are below the critical threshold), the strobilation duration, and the amount of time required for scyphistomae to recover and be ready to strobilate again, must be known. The complete sequence of initiation, strobilation and recovery constitute a strobilation requirement timeline (SRT). The recovery periods for scyphistomae were not the focus of the present study, so those periods must be estimated, based on laboratory culturing experience, and probably have durations of at least 4 wk in well-fed individuals (C. Widmer pers. obs.). For example, the SRT for *A. aurita* scyphistomae in this study at 4°C and salinity 34 would be about 19.4 wk (data from Table S4 in the Supplement at www.int-res.com/articles/suppl/m559p073_supp.pdf) comprised of: Onset (7 wk) + Duration (8.4 wk) + Estimated recovery (4 wk) = 19.4 wk.

Using this method, the 'strobilation window,' or length of time when annual sea surface temperatures (SST) are likely to fall below the critical minimum temperature thresholds can be determined. In Scapa Flow, *A. aurita* scyphistomae normally experience annual SSTs ranging from ca. 4 to 14°C (www.divesitedirectory.co.uk/uk_scotland_scapa.html) with salinities near 35 all year round (Turrell et al. 1996). Since the SRT for *A. aurita* was 19.4 wk, one can estimate that populations of this species probably do not strobilate more than once during an annual season.

Once initiated, the process of strobilation can be inhibited by further changes in temperature (Chen & Ding 1983, Widmer 2008b, You et al. 2008, Holst 2012). Affected ephyrae continue to develop and are released as normal, but no further ephyrae are produced (Widmer 2008b). Once sea temperatures begin to increase during spring, the minimum strobilation temperature thresholds cease to be met, thus closing the strobilation window and ending the process for the season. Asexual reproduction then shifts to the production of podocysts and progeny scyphistomae.

Our findings for the numbers of ephyrae produced by strobilating *A. aurita* scyphistomae are similar to findings from the northwest Mediterranean Sea (Purcell et al. 2012), and from Taiwan (Liu et al. 2009). Our results both concur and contradict with findings from previous similar studies on the effects of temperature (Holst 2012) and salinity (Holst & Jarms 2010) on strobilation and ephyra production of the same 4 species of scyphistomae. When scyphistomae from the German Bight were maintained in simulated conditions reflective of warmer winter temperatures (10°C versus 5°C), ephyra production was enhanced for *A. aurita*, *Ch. hysoscella,* and *C. lamarckii* (Holst 2012), and more ephyra were produced per strobila in *C. capillata* and *C. lamarckii* (Holst 2012). In the present study, scyphistomae of *Aurelia* originating from Scapa Flow, Orkney, only produced ephyrae at 4°C and the greatest numbers of ephyrae were produced by *A. aurita*, *C. capillata* and *C. lamarckii* in the coldest temperatures tested (4 to 9°C). However, our findings for strobilation and ephyra production of *Ch. hysoscella* generally concur with the results of Holst (2012).

Maximal numbers of *A. aurita*, *C. capillata* and *C. lamarckii* ephyrae from the German Bight were produced at salinity 28 (Holst & Jarms 2010). Our findings concur; in the present study most ephyrae were produced at salinity 27. We found that there was a significant interaction between temperature and salinity for the number of ephyrae produced by scyphistomae of *C. capillata* and *C. lamarckii*, meaning that for these species the synergistic effects of temperature and salinity on ephyra production may be more prominent than either factor acting alone. Assuming that scyphistomae are affected by sea surface conditions, our findings suggest that more ephyrae of these species are likely to be produced during years with abundant rainfall and low sea temperatures than in years with little rainfall and warm sea temperatures.

Scyphistomae in the present study were cultivated singly in replicate wells and progeny were removed as soon as they were produced in order to avoid the

potentially confounding effects of replicate mates. For example, scyphistomae of *A. aurita* from the Gulf of Mexico release a water transportable substance, neck-inducing factor, that stimulates nearby scyphistomae to strobilate (Loeb 1974, Loeb & Blanquet 1974). Additionally, scyphistomae abundance has been shown to be density dependent, with intraspecific competition decreasing asexual reproduction rates until equilibrium is reached (Willcox et al. 2007, Melica et al. 2014). Scyphistomae from the German Bight were cultivated for extended periods with many scyphistomae in each replicate (Holst & Jarms 2010, Holst, 2012), which may have been affected by water transportable substances or by scyphistoma density, potentially affecting asexual reproduction rates. However, cosmopolitan species such as *A. aurita* may also actually comprise a species complex as revealed by recent molecular studies (Dawson & Jacobs 2001). Contrasting results may be the result of local adaptations, suggesting that regionally focused studies will be required in order to predict population responses under climate change (Edwards 1965, Connelly et al. 2001, Purcell 2007, Lucas et al. 2012, Lee et al. 2013, Pascual et al. 2014).

Our acclimation periods to the experimental conditions were relatively rapid, but we did not observe any mortality or obvious deleterious effects during our acclimation protocol. Furthermore, many jellyfish medusae are able to quickly acclimate to new environmental conditions. For example, pulsation rates of field-collected medusae of *Chyrsaora quinquecirrha* reached equilibrium in 3 h when transferred from 29 to 15°C (Gatz et al. 1973). A number of hydromedusae species from the Puget Sound osmoconform to salinities ranging from 23 to 38 within a few hours, altering their densities and regaining equilibrium buoyancy (Mills 1984). Even though we used a rapid acclimation scheme relative to the natural environment, our findings are in line with the idea of minimum temperature thresholds needing to be met in order for strobilation to occur (Russell 1970 and references therein) and the timings of ephyrae release (Verwey 1942, Russell 1970, Hernroth & Gröndahl 1985, Lucas & Williams 1994). Future work should determine how the rate of temperature and salinity changes affects asexual reproductive output.

Our data support the hypothesis that temperature and salinity influence asexual reproductive modes and rates of scyphistomae in northeastern Atlantic waters. Links between the NAO and sea temperatures in the North Sea are strongest during the winter and early spring, so potentially affect the period when scyphistomae are strobilating (Lynam et al. 2004). A hypothetical model derived from GLM predictions from our results shows the overall effect of fewer ephyrae added to the system in positive phase NAO years (Fig. 8). Conversely, when the NAO is in a negative phase, cooler sea temperatures during winter may increase the number of scyphistomae that strobilate, resulting in more ephyrae. Climate variability is, however, likely linked with many other changes that may affect scyphistoma reproduction; an obvious factor being changes in planktonic food (Ottersen et al. 2001). Better-nourished strobilae produce more ephyrae than poorly nourished ones (Spangenberg 1967, Purcell et al. 1999, Ishii & Watanabe 2003, Wiesenthal 2012). Furthermore, enhanced survival of ephyrae and young medusae could easily lead to changes observed in population abundances later in the year, regardless of the numbers of ephyrae released.

CONCLUSIONS

Plasticity in asexual reproductive modes of scyphistomae plays an important role in the long-term maintenance of jellyfish populations (Boero et al. 2008, Arai 2009, Lucas et al. 2012). In this study, the general trend was that as temperature increased, benthic asexual output increased. Benthic asexual reproduction probably occurs throughout much of the year, with the majority occurring during summer when prey availability is high. For the species studied, the present results suggest that the majority of strobilation probably takes place during the colder months, which is in agreement with the presence of ephyrae in the northeastern Atlantic plankton samples (Verwey 1942, Russell 1970, Hernroth & Gröndahl 1985, Lucas & Williams 1994), and other experimental data (Holst 2012). During years when open strobilation window durations are short (such as high NAO phases), one can predict that fewer ephyrae will be produced by the scyphistomae, and instead they will maximise benthic asexual reproduction. During years with long open strobilation windows (such as low NAO phases), benthic reproduction should be slowed, but more ephyrae are likely to be produced. The combination of SRTs and species-specific minimum temperature strobilation thresholds could explain the negative correlation between the NAO and medusa abundance in parts of the North Sea (Lynam et al. 2004, 2005). However, these patterns are complicated by differences at sub-regional scales, which Lynam et al. (2005) suggested were linked to complexities in the local oceanography.

Furthermore, medusae of some species, such as *Cyanea capillata* may be able to overwinter (Hay et al. 1990), thus potentially masking the effects of inter-annual temperature variability on their abundance (Lynam et al. 2004). Although the scyphistomae of *C. capillata* appear able to continue strobilation over a wider range of temperatures than *C. lamarckii* or *Aurelia aurita*, differences in the minimum temperature strobilation thresholds suggest that *C. capillata* in particular, may become less common in areas such as the North Sea under warming scenarios, whilst the range of *Chrysaora hysoscella* may increase (Mathis & Pohlman 2014). Strobilation of *A. aurita* appeared to be particularly sensitive to increased temperatures in our experiments but *Aurelia* spp. are very widely distributed and successful in coastal waters from the tropics to the sub-Arctic. One explanation of the different results in the present study and Holst (2012) is that we are dealing with locally adapted sub-populations. If this hypothesis is true then replacement of locally cold adapted subpopulations by visibly similar *Aurelia* clades adapted to warmer waters may occur (Dawson & Martin 2001). Further experiments comparing the temperature responses of *Aurelia* spp. scyphistomae collected from different locations, ideally with accompanying genetic taxonomy, are needed to test this idea.

In summary, scyphistomae responded to high temperatures by decreasing or ceasing strobilation altogether, and by increasing rates of benthic asexual reproduction. The precise minimum temperatures required to open strobilation windows are species and probably population specific and seem to explain the broad temperature preferences observed at the medusa stages.

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LITERATURE CITED

Adler L, Jarms G (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. Mar Biol 156:1411–1420

Arai MN (1997) A functional biology of Scyphozoa. Chapman & Hall, London

Arai MN (2009) The potential importance of podocysts to the formation of scyphozoan blooms: a review. Hydrobiologia 616:241–246

Beszczynska-Möller A, Dye SR (eds) (2013) ICES report on ocean climate 2012. ICES cooperative research report No. 321. International Council for the Exploration of the Sea, Copenhagen. http://www.ices.dk/sites/pub/Publication%20Reports/Cooperative%20Research%20Report%20(CRR)/crr321/IROC%202012.pdf

Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T, Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299–310

Brewer RH, Feingold JS (1991) The effect of temperature on the benthic stages of *Cyanea* (Cnidaria, Scyphozoa), and their seasonal distribution in the Niantic River estuary, Connecticut. J Exp Mar Biol Ecol 152:49–60

Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in large marine ecosystems. Hydrobiologia 690:3–20

Cargo DG, Rabenold GE (1980) Observations on the asexual reproductive activities of the sessile stages of the sea nettle *Chrysaora quinquecirrha* (scyphozoan). Estuaries 3:20–27

Cargo DG, Schultz LP (1967) Further observations on the biology of the sea nettle and jellyfishes in Chesapeake Bay. Chesapeake Sci 8:209–220

Chen JK, Ding GW (1983) Effect of temperature on the strobilation of jellyfish (*Rhopilema esculenta Kishinouye*—scyphozoa, rhizostomeae). Acta Zool Sin 29:195–206

Condon RH, Duarte CM, Pitt KA, Robinson KL and others (2013) Recurrent jellyfish blooms are a consequence of global oscillations. Proc Natl Acad Sci USA 110: 1000–1005

Connolly SR, Menge BA, Roughgarden J (2001) A latitudinal gradient in recruitment of intertidal invertebrates in the Northeast Pacific Ocean. Ecology 82:1799–1813

Dawson MN, Jacobs DK (2001) Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). Biol Bull 200:92–96

Dawson MN, Martin LE (2001) Geographic variation and ecological adaptation in *Aurelia* (Scyphozoa, Semaeostomeae): some implications from molecular phylogenetics. Hydrobiologia 451:259–273

Dawson,MN, Martin LE, Penland LK (2001) Jellyfish swarms, tourists, and the Christ-child. Hydrobiologia 451:131–144

Dong Z, Liu D, Keesing JK (2010) Jellyfish blooms in China: dominant species, causes and consequences. Mar Pollut Bull 60:954–963

Doyle TK, Houghton JDR, Buckley SM, Hays GC, Davenport J (2007) The broad-scale distribution of five jellyfish species across a temperate coastal environment. Hydrobiologia 579:29–39

Edwards C (1965) The hydroid and the medusa *Neoturris pileata.* J Mar Biol Assoc UK 45:443–468

Fu Z, Shibata M, Makabe R, Ikeda H, Uye S (2014) Body size reduction under starvation, and the point of no return, in ephyrae of the moon jellyfish *Aurelia aurita.* Mar Ecol Prog Ser 510:255–263

Fuchs B, Wang W, Graspeuntner S, Li Y and others (2014) Regulation of polyp-to-jellyfish transition in *Aurelia aurita.* Curr Biol 24:263–273

Gatz AJ, Kennedy VS, Mihursky JA (1973) Effects of tempera-

ture on activity and mortality of the scyphozoan medusa, *Chrysaora quinquecirrha.* Chesapeake Sci 14:171–180

Gröndahl F (1988) A comparative ecological study on the scyphozoans *Aurelia aurita, Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. Mar Biol 97:541–550

Han CH, Uye SI (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 Benthos Res 5:98–105

Hay SJ, Hislop JRG, Shanks AM (1990) North Sea Scyphomedusae; summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth J Sea Res 25:113–130

Hernroth L, Gröndahl F (1985) On the biology of *Aurelia aurita* (L.): 2. Major factors regulating the occurrence of ephyrae and young medusae in the Gullmar Fjord, western Sweden. Bull Mar Sci 37:567–576

Holst S (2012) Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. Hydrobiologia 690:127–140

Holst S, Jarms G (2010) Effects of low salinity on settlement and strobilation of scyphozoa (Cnidaria): Is the lion's mane *Cyanea capillata* (L.) able to reproduce in the brackish Baltic Sea? Hydrobiologia 645:53–68

Ishii H, Watanabe T (2003) Experimental study of growth and asexual reproduction in *Aurelia aurita* polyps. Sess Org 20:69–73

Lee PLM, Dawson MN, Neill SP, Robins PE, Houghton JDR, Doyle TK, Hays GC (2013) Identification of genetically and oceanographically distinct blooms of jellyfish. J R Soc Interface 10:20120920

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

Loeb MJ (1974) Strobilation in the Chesapeake Bay sea nettle *Chrysaora quinquecirrha*—II. Partial characterization of the neck-inducing factor from strobilating polyps. Comp Biochem Physiol A 47:291–301

Loeb MJ, Blanquet RS (1974) Strobilation in the Chesapeake Bay sea nettle *Chrysaora quinquecirrha*—III. Dissociation of the neck-inducing factor from strobilating polyps. Comp Biochem Physiol A 49:423–432

Lotan A, Fine M, (1994) Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. Mar Ecol Prog Ser 109:59–65

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

Lucas CH, Williams JA (1994) Population dynamics of the scyphomedusa *Aurelia aurita* in Southampton Water. J Plankton Res 16:879–895

Lucas CH, Graham WM, Widmer CL (2012) Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Adv Mar Biol 63:133–196

Lynam CP, Hay SJ, Brierley AS (2004) Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol Oceanogr 49:637–643

Lynam CP, Hay SJ, Brierley AS (2005) Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. J Mar Biol Assoc UK 85: 435–450

Lynam CP, Attrill MJ, Skogen MD (2010) Climatic and oceanic influences on the abundance of gelatinous zooplankton in the North Sea. J Mar Biol Assoc UK 90: 1153–1159

Mathis M, Pohlman T (2014) Projection of physical conditions in the North Sea for the 21st century. Clim Res 61:1–17

Melica V, Invernizzi S, Caristi G (2014) Logistic density-dependent growth of an *Aurelia aurita* polyps population. Ecol Modell 291:1–5

Mills CE (1984) Density is altered in hydromedusae and ctenophores in response to changes in salinity. Biol Bull 166:206–215

Mills CE (2001) Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451:55–68

NBN (National Biodiversity Network) (2016) National Biodiversity Network database. http://data.nbn.org.uk (accessed 14 February 2016)

Nickell T, Davidson K, Fox C, Miller P, Hays G (2010) Developing the capacity to monitor the spatial and temporal distribution of jellyfish in western Scottish waters. The Crown Estate, London

Ottersen G, Planque B, Belgrano A, Post E, Reid P, Stenseth N (2001) Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14

Pascual M, Fuentes V, Canepa A, Atienza D, Gili JM, Purcell JE (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. Mar Ecol 36:994–1002

Purcell JE (2007) Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata.* Mar Ecol Prog Ser 348:183–196

Purcell JE, White JR, Nemazie DA, Wright DA (1999) Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha.* Mar Ecol Prog Ser 180:187–196

Purcell JE, Uye S, Lo W (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar Ecol Prog Ser 350:153–174

Purcell JE, Hoover RA, Schwarck NT (2009) Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions *in situ*. Mar Ecol Prog Ser 375:139–149

Purcell JE, Atienza D, Fuentes V, Olariaga A, Tilves U, Colahan C, Gili JM (2012) Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. Hydrobiologia 690:169–180

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol Evol 24:312–322

Robinson KL, Graham WM (2013) Long-term change in the abundances of northern Gulf of Mexico scyphomedusae *Chrysaora* sp. and *Aurelia* spp. with links to climate variability. Limnol Oceanogr 58:235–253

Russell FS (1970) The Medusae of the British Isles. II. Pelagic scyphozoa with a supplement to the first volume on Hydromedusae. Cambridge University Press, Cambridge

Schiariti A, Morandini A, Jarms G, von Glehn Paes R, Franke S, Mianzan H (2014) Asexual reproduction strategies and blooming potential in Scyphozoa. Mar Ecol Prog Ser 510:241–253

Schroth W, Jarms G, Streit B, Schierwater B (2002) Speciation and phylogeography in the cosmopolitan marine

moon jelly, *Aurelia* sp. BMC Evol Biol 10:1–10

Schulz A (2009) North Sea atlas. Temperature, salinity, density and heat content—monthly means for the period 1902 to 1954. Bundesamt für Seeschifffahrt und Hydrographie, Hamburg

Spangenberg DB (1967) Iodine induction of metamorphosis in *Aurelia*. J Exp Zool 165:441–449

Sugiura Y (1965) On the effects of temperature on the strobilation of *Mastigias papua*. Biol Bull 128:493–496

Thein H, Ikeda H, Uye SI (2013) Ecophysiological characteristics of podocysts in *Chrysaora pacifica* (Goette) and *Cyanea nozakii* Kishinouye (Cnidaria: Scyphozoa: Semaeostomeae): effects of environmental factors on their production, dormancy and excystment. J Exp Mar Biol Ecol 446:151–158

Turrell WR, Slesser G, Payne R, Adams RD, Gillibrand PA (1996) Hydrography of the East Shetland Basin in relation to decadal North Sea variability. ICES J Mar Sci 53: 899–916

Ver Hoef JM, Boveng PL (2007) Quasi-Poisson vs. negative binomial regression: How should we model overdispersed count data? Ecology 88:2766–2772

Verwey J (1942) Die Periodizität im Auftreten und die aktiven und passiven Bewegungen der Quallen. Arch Neerl Zool 6:363–468

Widmer CL (2008a) Life cycle of *Chrysaora fuscescens* (Cnidaria: Scyphozoa) and a key to sympatric ephyrae. Pac Sci 62:71–82

Widmer CL (2008b) How to keep jellyfish in aquariums: an introductory guide for maintaining healthy jellies. Wheatmark, Tucson, AZ

Wiesenthal AA (2012) The effect of temperature and food availability on the asexual reproduction of *Aurelia aurita* and *Cyanea capillata*. University of St. Andrews

Willcox S, Moltschaniwskyj NA, Crawford C (2007) Asexual reproduction in scyphistomae of *Aurelia* sp.: effects of temperature and salinity in an experimental study. J Exp Mar Biol Ecol 353:107–114

You K, Ma C, Gao H, Li F, Zhang M, Wang B, Wei R (2008) The effects of temperature decrease on the scyphistomae strobilation of jellyfish, *Rhopilema esculentum* Kishinouye. J World Aquac Soc 39:706–711

Zuur AF, Hilbe JM, Ieno EN (2013) A beginner's guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists, 1st edn. Highland Statistics, Newburgh

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