

# Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish

Sabine Holst

Published online: 9 March 2012  
© Springer Science+Business Media B.V. 2012

**Abstract** Recent studies have correlated fluctuations in jellyfish abundances with climatic changes, leading to speculation that the warming trend in the North Sea will affect the strobilation activity of Scyphozoa. The present study provides long-term data (10–22 months) on temperature effects on the species *Aurelia aurita*, *Cyanea capillata*, *Cyanea lamarckii* and *Chrysaora hysoscella*. Strobilation at current winter temperature (5°C) in the German Bight was compared to strobilation at warmer winter temperatures. Simulated winter temperature of 10°C had several positive effects on strobilation, as compared to 5°C: 1. A longer strobilation period or higher ephyra production per polyp in *A. aurita*, *C. lamarckii* and *Ch. hysoscella*; 2. Higher percentages of polyps strobilating in *A. aurita* and *Ch. hysoscella*; 3. More ephyrae per strobila in *C. capillata* and *C. lamarckii*; 4. A shorter strobilation duration in *C. capillata* and *C. lamarckii*. Cold winter temperatures of 5°C promoted strobilation in *C. capillata*, but inhibited strobilation in *A. aurita* and reduced ephyra production in *C. lamarckii* and *Ch. hysoscella*. These results

suggest that climate warming will benefit *A. aurita*, but not cold-water *C. capillata*. The distributions of *C. lamarckii* and *Ch. hysoscella* probably could expand to the north.

**Keywords** *Aurelia* · *Cyanea* · *Chrysaora* · Polyp · Temperature · Reproduction

## Introduction

Reports of mass occurrences of large jellyfish (Scyphozoa) in many marine ecosystems worldwide have increased in recent decades (Purcell et al., 2007; Richardson et al., 2009). Negative impacts of such medusa blooms on ecosystems, fisheries, industries and tourism are obvious: medusae are food competitors of fish and feed on fish larvae and small fish (Barz & Hirche, 2007; Sabatés et al., 2010), the gelatinous bodies clog fishing nets and cooling systems of coastal industries, and jellyfish stinging swimmers have negative effects on the tourism industry (CIESM, 2001; Purcell et al., 2007). It is possible that consequences of anthropogenic activities, including overfishing, eutrophication, species invasions and especially climate change, have contributed to increased jellyfish abundances (Purcell et al., 2007; Richardson et al., 2009; Purcell, 2011).

Recent analyses of temperature data show a clear warming trend in global average air and ocean temperature (IPCC, 2007). A pronounced winter

---

Guest editors: J. E. Purcell, H. Mianzan & J. R. Frost / Jellyfish Blooms: Interactions with Humans and Fisheries

---

S. Holst (✉)  
Senckenberg am Meer, German Center for Marine Biodiversity Research, c/o Biozentrum Grindel und Zoologisches Museum, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany  
e-mail: sabine.holst@senckenberg.de

warming trend has been observed in the North and Baltic seas, which is predicted to continue in the future (HELCOM, 2007; Belkin, 2009). Recent rapid climate change has changed the abundances, population structures and biographical ranges of benthic and planktonic North Sea species (Mieszkowska et al., 2006; Wiltshire et al., 2010). Climate regime shifts also affect jellyfish populations. Changes in temperature, salinity, currents, predator–prey interactions and competition have measurable effects on jellyfish abundance and distribution (Purcell, 2005, 2009; Molinero et al., 2008; Lynam et al., 2010). These environmental changes will affect both the pelagic and the benthic stages of metagenetic medusae; however, the role of the polyps has been neglected in most analyses and models because of the lack of data on polyp ecology (Lynam et al., 2010).

The medusae of four semaeostome scyphozoans, *Aurelia aurita* (Linnaeus, 1758), *Cyanea capillata* (Linnaeus, 1758), *Cyanea lamarckii* Péron and Lesueur, 1809 and *Chrysaora hysoscella* (Linnaeus, 1766), occur in the German Bight during the summer months, and mass occurrences have been documented in some years (Russell, 1970; Möller, 1980a; Hay et al., 1990; Barz & Hirche, 2007). Like most scyphozoans, the life cycle of these species includes planktonic medusa and benthic polyp generations. After settlement and metamorphosis of the planula larvae, the polyp populations increase by asexual reproduction. Each polyp seasonally produces one to several young medusae (ephyrae) in a process of transversal fission called strobilation. This process contributes to the development of jellyfish blooms because polydisc strobilation allows single polyps to produce many ephyrae (Boero et al., 2008).

Information on the environmental factors and stressors that determine the induction, timing and magnitude of the strobilation process is limited to a few species (e.g. *Aurelia* spp., reviewed in Purcell et al., 2012). Moreover, the benthic stage is completely undiscovered or undescribed for most scyphozoans (Tronolone et al., 2002; Jarms, 2010). Although many laboratory investigations on scyphopolyps have shown that temperature significantly affects the asexual polyp reproduction and strobilation (e.g. Holst et al., 2007; Purcell, 2007; Willcox et al., 2007; You et al., 2008; Liu et al., 2009), most of these studies were restricted to short periods of a few weeks and polyps were often exposed to extreme, abrupt changes, whereas changes

in situ would be less severe (Purcell, 2005). Long-time investigations on the effects of natural seasonal temperature cycles on polyp ecology are unavailable for most species (but see Gröndahl, 1988; Brewer & Feingold, 1991; Miyake et al., 2002; Purcell et al., 2009; Di Camillo et al., 2010; Ishii & Katsukoshi, 2010). In the present study, I compare the long-term (10–22 months) effects of different temperature conditions on strobilation and ephyra production of four semaeostome jellyfish species from the North Sea to show the possible effects of increasing winter temperatures on the strobilation activity of Scyphozoa in the North Sea. Strobilation at temperature conditions similar to the current temperatures in the German Bight was compared to that at warmer winter temperatures. Additional experiments without a temperature change were conducted to determine the importance of temperature changes as inducers of strobilation in scyphozoan polyps. I tested the null hypotheses to ascertain whether the percentages of polyps strobilating and the numbers of ephyrae produced per strobila were independent of temperature; second, whether the percentages of strobilating polyps and the number of ephyrae produced per strobila were independent of polyp age; and third, whether the duration of strobilation was independent of the number of ephyrae per strobila and of temperature.

## Materials and methods

Polyps of the species *A. aurita*, *C. capillata*, *C. lamarckii* and *Ch. hysoscella* were reared from planulae collected from female medusae in the summer periods of 2003 and 2004 around the island of Helgoland (details in Holst & Jarms, 2007, 2010). Watch glasses or polyethylene plates (for *C. lamarckii*) colonized by polyps in the laboratories of the Biologische Anstalt Helgoland were transported to the Zoological Institute of the University of Hamburg (Biocenter Grindel) 1–2 weeks after planula settlement. The substrates were transferred into 150-ml glass bowls filled with filtered North Sea water (salinity  $35 \pm 2$ ). The bowls were kept in incubators at 15°C in darkness before the experiments. Only well-developed polyps with extended tentacles were used for the experiments, whereas small or contracted polyps were carefully removed from the substrates with a needle. Polyps were fed nauplii of *Artemia salina* for 1–2 h every

7–10 days, after which the seawater in the bowls was replaced with fresh filtered seawater of the same temperature. During strobilation, only half of the water was changed carefully, and uneaten food was removed from the bowls with a pipette to avoid disturbing the strobilation process. Polyps of each species were cultured in three different temperature groups (Table 1). In the 15°C group, the temperature was constant 15°C throughout the year. In the groups 15–10–15°C and 15–05–15°C, the temperature was 15°C until mid-October and lowered to 10°C in autumn and 5°C in winter, respectively. The temperatures were decreased in steps of 2.5°C per month (Fig. 1), and all cultures were kept in incubators in darkness. Polyps were monitored for 12 months (*A. aurita* from 15 September, and *C. capillata* from 15 October) or 10 months (*C. lamarckii* and *Ch. hysoscella* from 15 October) in the first year after settlement. Additional 10-month-long experiments (from 15 October) were conducted in the second year after settlement with *A. aurita* and *C. capillata* polyps. The polyps were counted monthly in all replicates, and all cultures were checked weekly to detect beginning strobilations. When strobilation appeared in the cultures, each strobila was monitored individually. The developing ephyrae in each strobila and the released ephyrae in the cultures were counted at least twice per week.

#### Calculations and statistics

The numbers of ephyrae produced monthly in each temperature group were summed and divided by the number of polyps to calculate ephyra production for

each month. To account for production and mortality of polyps, the mean numbers of polyps (counted monthly) were calculated over the duration of the experiment (Table 1) and used in calculations and statistics. The total numbers of ephyrae produced per mean polyp numbers were calculated for each temperature group. The percentages of strobilating polyps in the first year were calculated for each replicate from the total numbers of strobilae divided by the mean numbers of polyps in each replicate. Percentages were arcsine square root transformed before statistical analysis to test the first null hypothesis,  $H_{01}$ : the percentages of polyps strobilating were independent of the temperature treatments. In *C. lamarckii*, all polyps strobilated once in all temperature groups, therefore the percentages of polyps that strobilated twice were compared to test  $H_{01}$ . Individually monitored strobilations in the first year were used to calculate the mean numbers of ephyrae per strobila to test  $H_{02}$ : the numbers of ephyrae produced per strobila were independent of the temperature treatments. Strobilations from replicates 1–3 were used for analysis in all species and temperature groups; additional strobilations were included from replicates 4–6 in *A. aurita* 15°C, *C. capillata* 15–10–15°C, *C. capillata* 15–05–15°C and *Ch. hysoscella* 15–05–15°C. For  $H_{01}$  and  $H_{02}$ , data with normal distributions were tested by one-way analysis of variance (ANOVA) followed by a Fisher's least significance difference (LSD) post-hoc test. Data not normally distributed were tested by a Kruskal–Wallis ANOVA on ranks and a Student–Newman–Keuls post-hoc test. Two experimental groups were compared with a Mann–Whitney Rank Sum Test.

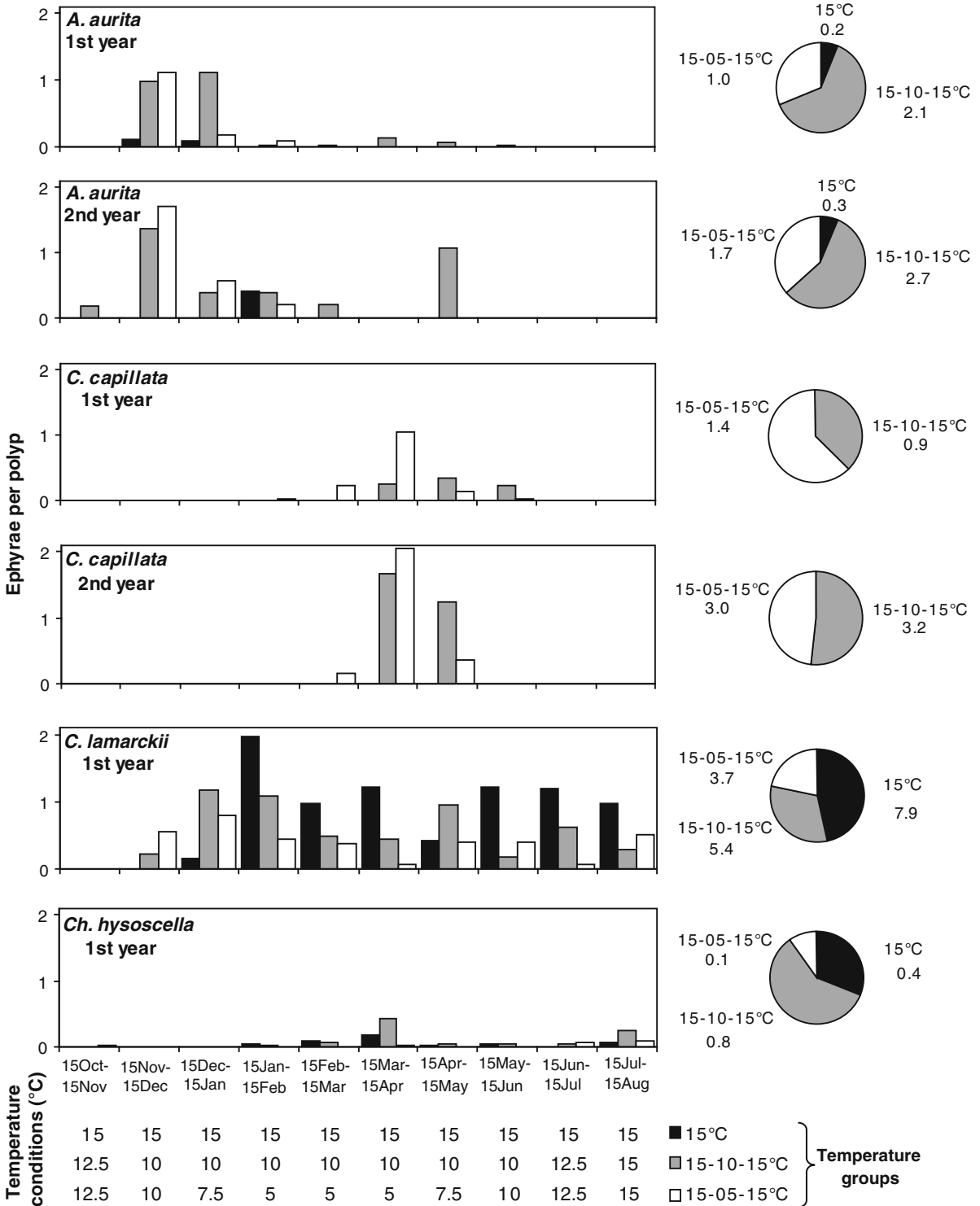
**Table 1** Replicates (*n*) in temperature groups used for analyses of strobilation in first year (1y) and second year (2y) after planula settlement in four species of scyphozoans

Species	Year	<i>n</i>	15°C		15–10–15°C		15–05–15°C	
			Start	Mean	Start	Mean	Start	Mean
<i>A. aurita</i>	1y	6	79	87.3 ± 4.9	78	102.6 ± 19.9	81	114.7 ± 32.5
	1y	3	29	37.1 ± 4.8	32	46.3 ± 11.9	36	54.0 ± 16.3
	2y	3	33	46.3 ± 15.2	32	47.2 ± 21.8	35	49.7 ± 22.0
<i>C. capillata</i>	1y	6	71	73.7 ± 4.0	75	86.3 ± 11.2	81	96.6 ± 17.3
	1y	3	25	26.0 ± 2.9	25	26.0 ± 2.9	26	28.0 ± 6.4
	2y	3	11	18.2 ± 8.3	20	28.9 ± 10.1	24	39.1 ± 13.2
<i>C. lamarckii</i>	1y	6	86	76.3 ± 7.4	86	64.5 ± 14.1	85	60.5 ± 17.0
<i>Ch. hysoscella</i>	1y	7	108	85.0 ± 22.3	108	92.9 ± 15.7	113	81.9 ± 28.8

The total polyp numbers at the beginning of the experiments (Start) and numbers of polyps in monthly counts (mean ± standard deviation) in different temperature groups (see Fig. 1) are listed

**Ephyrae per polyp monthly**

**Ephyrae per polyp in 10 months**



◀ **Fig. 1** Numbers of ephyrae per polyp produced monthly (*left side*) and total numbers of ephyrae produced per mean numbers of polyps counted monthly during 10 months of observation (15 Oct–15 Aug, *right side*) in different temperature groups of *A. aurita*, *C. capillata*, *C. lamarckii* and *Ch. hysoscella* polyps. The culture temperature was constant 15°C from 15th July to 15th October in all temperature groups (not shown in the figure). Polyp numbers in different temperature groups are shown in Table 1

For comparisons among strobilations 1 and 2 years after settlement, the same three replicates of each temperature group of *A. aurita* and *C. capillata* polyps were used in both years (Table 1). The same 10-month period (15 October–15 August) were analysed in both years. The percentages of strobilating polyps and the numbers of ephyrae produced per strobila were calculated for both years, as described above, and compared by a Mann–Whitney Rank Sum Test. Two null hypotheses were tested,  $H_{03}$ : The percentages of strobilating polyps were independent of polyp age and  $H_{04}$ : The number of ephyrae produced per strobila was independent of the polyp age.

The durations of strobilations (days) were determined from the number of days between the start of the strobilation, when first constrictions of the polyp body appeared, until the end the strobilation, when the last ephyra detached from the strobila. Only strobilations that began and ended at the same temperature were used in the analysis. Strobilae in the first year after polyp settlement were analysed in *C. lamarckii* and *Ch. hysoscella*, and in the first and second years combined in *A. aurita* and *C. capillata*. Strobilations were analysed at 15, 10 and 5°C culture temperatures. Two null hypotheses were tested by analysis of covariance (ANCOVA),  $H_{05}$ : The duration of strobilation was independent of the number of ephyrae per strobila and  $H_{06}$ : The duration of strobilation was independent of the temperature treatments. ANCOVA-tests were conducted separately for each species. In all tests, duration was the dependent variable; the number of ephyrae per strobila and the culture temperature were covariates.

## Results

### Ephyra production and strobilation rates

#### *A. aurita*

The first *A. aurita* strobilations occurred in autumn in all temperature groups in the first and second years

after polyp settlement. Ephyra were produced until next May in both years in the 15–10–15°C group, whereas ephyra production stopped after a temperature decrease to 5°C in January in the 15–05–15°C groups (Fig. 1, left side). Few ephyrae per polyp were produced in the temperature group with constant 15°C and the most ephyrae per polyp were produced in the 15–10–15°C group in the first and in the second year after settlement (Fig. 1, right side). Significantly higher percentages of *A. aurita* polyps strobilated after a temperature decrease in autumn than at constant 15°C, and  $H_{01}$  was rejected for both years (Figs. 2, 3; Table 2). The numbers of ephyrae produced per strobila did not differ significantly among the temperature groups in the first year or in the second year and  $H_{02}$  was not rejected (Fig. 2; Table 2). The percentages of strobilating polyps were higher in the second than in the first year, but the differences were not significant, and  $H_{03}$  was not rejected (Fig. 3; Table 3). Although the maximum numbers of ephyrae per strobila were higher in the second year than in the first, the means differed only slightly among groups, and  $H_{04}$  was not rejected (Fig. 3; Table 3).

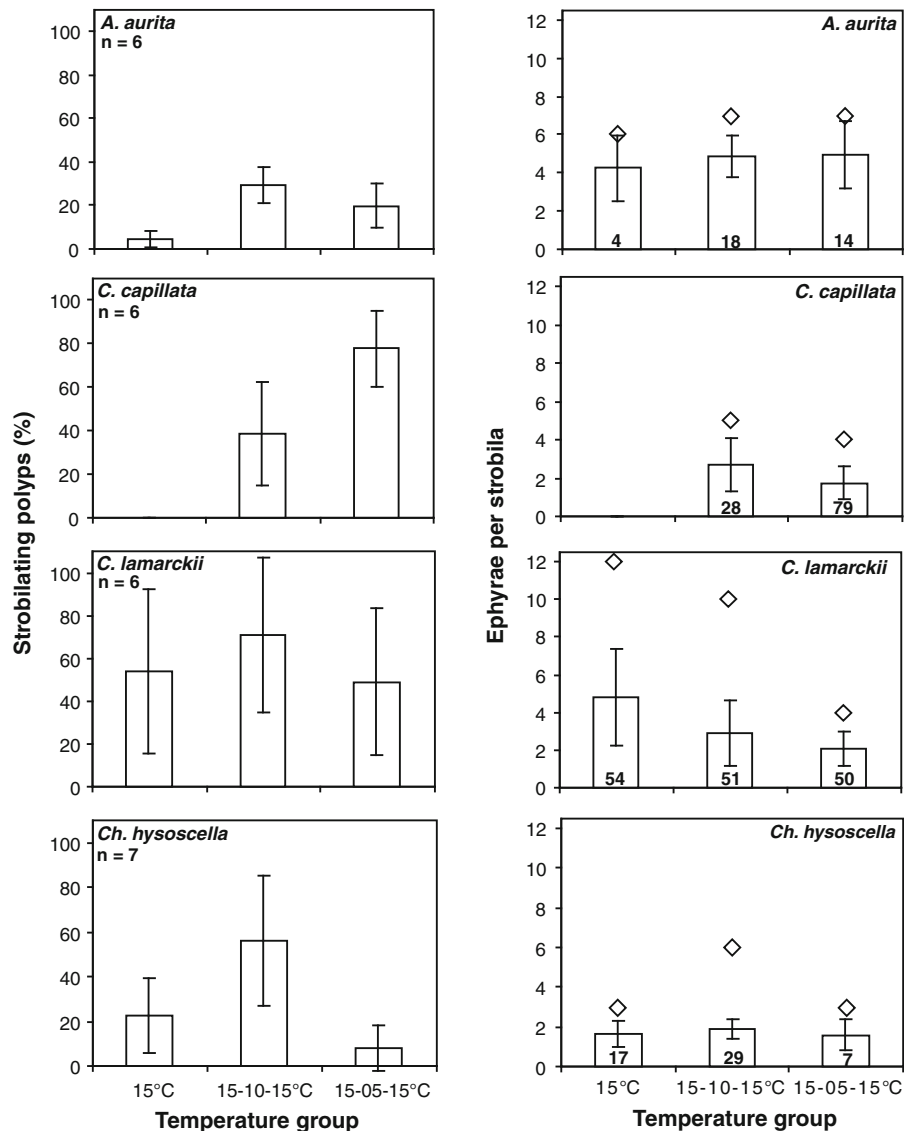
#### *C. capillata*

*C. capillata* polyps never strobilated in constant 15°C during 22 months of observation. The first ephyra appeared in February–March at the cold winter temperature (5°C) in both years, whereas the first ephyra appeared at least 1 month later at the 10°C winter temperature (Fig. 1, left side). Ephyra production continued until the beginning (second year) or end of May (first year). In the first year, production of ephyrae per polyp was higher in 5°C winter temperature, whereas it was slightly higher in 10°C winter temperature in the second year (Fig. 1, right side). In the first year, the percentages of polyps strobilating were significantly higher in the 15–05–15°C group than in the 15–10–15°C and 15°C groups and  $H_{01}$  was rejected (Fig. 2; Table 2). Although the percentages of polyps strobilating differed only slightly for the 15–10–15°C and the 15–05–15°C groups, no strobilation occurred at 15°C and  $H_{01}$  was rejected in the second year as well (Fig. 3; Table 2). The numbers of ephyrae per strobila were lower in groups with 5°C than in those with 10°C winter temperature, but differences were only significant in the first year ( $H_{02}$

rejected, Fig. 2; Table 2). The percentages of strobilating polyps did not differ significantly in polyps of different ages and  $H_{03}$  was not rejected (Fig. 3; Table 3); however, the mean numbers of ephyrae per strobila were significantly higher in the second year in the 15–10–15°C group and the 15–05–15°C group ( $H_{04}$  rejected, Fig. 3; Table 3).

### *C. lamarckii*

In *C. lamarckii* cultures, the first ephyra appeared after a temperature decrease to 10°C in groups 15–10–15°C and 15–05–15°C; however, the most ephyrae per polyp were produced in the constant 15°C group, whereas the fewest were in the coldest winter temperature (5°C;



**Fig. 2** Strobilating polyps (mean % ± SD) (left side) and ephyrae produced per strobila (mean number ± SD) (right side) in the first year after polyp settlement in different temperature groups of *A. aurita*, *C. capillata*, *C. lamarckii* and *Ch. hysocella* polyps; *n* number of replicates (numbers of polyps as shown in Table 1). The numbers of analysed strobilae appear

inside the bars. Diamond maximal number of ephyrae produced by one strobila. The observation time was 12 months for *A. aurita* (15 Sep–15 Sep) and *C. capillata* (15 Oct–15 Oct) and 10 months for *C. lamarckii* and *Ch. hysocella* (15 Oct–15 Aug). Test statistics are shown in Table 2

Fig. 1). All *C. lamarckii* polyps strobilated at least once in all temperature groups (>100%). The percentages of polyps strobilating twice were the highest in the 15–10–15°C groups, but the differences were not significant, and  $H_{01}$  was not rejected (Fig. 2; Table 2). The number of ephyrae produced per strobila, however, was significantly higher at constant 15°C than in treatments with temperature decreases, and  $H_{02}$  was rejected (Fig. 2; Table 2).

### *Ch. hysoscella*

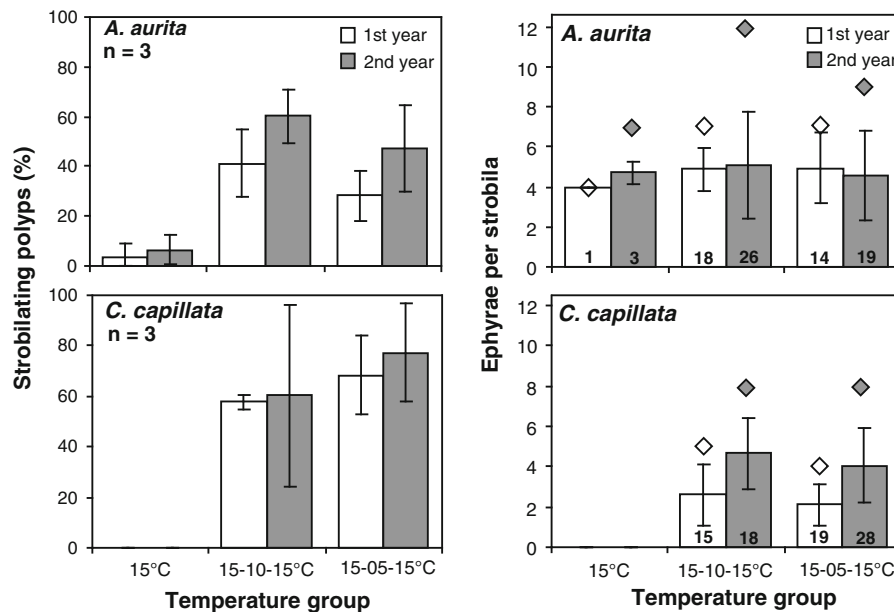
The monthly ephyra production per polyp was relatively low in *Ch. hysoscella* (Fig. 1, left side). The most ephyrae per polyp were in the 15–10–15°C group, and the fewest ephyrae per polyp were produced in the 15–05–15°C group (Fig. 1, right side). The percentages of strobilating polyps were significantly higher in the 15–10–15°C group than in the other groups, and  $H_{01}$  was rejected (Fig. 2; Table 2). In the 15°C and 15–05–15°C groups, maxima of three ephyrae were produced per strobila, whereas as many as six ephyrae per strobila were produced in the 15–10–15°C group (Fig. 2); however, the production of more than three ephyrae occurred

only in 7% of analysed strobilae. Consequently, differences in ephyra production per strobila were not significant among temperature groups and  $H_{02}$  was not rejected (Fig. 2; Table 2).

### Temperature change as a strobilation inducer or inhibitor

Small percentages of polyps strobilated at constant 15°C in *A. aurita*, demonstrating that temperature decrease was an important strobilation inducer; however, ephyra production stopped after temperature decreased further to 5°C in winter. This result demonstrated that a low winter temperature of 5°C inhibited strobilation activity from February on whereas a higher winter temperature of 10°C lead to a longer strobilation period until spring (Fig. 1). Temperature increases from 5 to 10°C in spring and then to 15°C in summer did not induce strobilation in *A. aurita* (Fig. 1).

Strobilation never occurred at constant 15°C in *C. capillata* and ephyra production was lower when temperature rose in spring and summer following strobilation at 5 or 10°C winter temperatures (Fig. 1). No ephyra was produced at temperatures exceeding



**Fig. 3** Strobilating polyps (mean %  $\pm$  SD) (left side) and ephyrae produced per strobila (mean number  $\pm$  SD) (right side) in the first year and in the second year after polyp settlement in different temperature groups of *A. aurita*, *C. capillata*, *C. lamarckii* and *Ch. hysoscella* polyps,  $n$  number of replicates

(numbers of polyps are shown in Table 1). The numbers of analysed strobilae appear inside the bars. Diamond maximal number of ephyrae produced by one strobila. In both analyses, the observation time was 10 months (15 Oct–15 Aug) in both years. Test statistics are shown in Table 3

10°C in summer, suggesting strobilation inhibition at warmer temperatures in *C. capillata*. In *C. lamarckii*, ephyra production started earlier after a temperature decrease to 10°C than at constant 15°C (Fig. 1), showing a positive effect of temperature decrease on strobilation induction, although the total ephyra production was the highest at constant 15°C. In *Ch. hysoscella*, strobilation activity was low in all temperature treatments without clear responses to temperature changes (Fig. 1).

#### Temperature effects on strobilation duration and ephyrae per strobila

A significant effect of the number of ephyrae per strobila on the strobilation duration was shown by

ANCOVA for all tested species (Fig. 4), and  $H_{05}$  was rejected. Correlations among temperature treatments and strobilation duration were not possible for *A. aurita* because strobilation occurred mostly at 10°C; thus, data at other temperatures were insufficient. In all other tested species, the ANCOVA confirmed a significant effect of temperature treatment on the strobilation duration (Fig. 4), and  $H_{06}$  was rejected.

#### Discussion

Scyphopolyps are difficult to find and investigate in the field because of their small sizes and their preferences of colonizing the undersides of substrates and concealed habitats (Pierce, 2009; Di Camillo

**Table 2** Test statistics on the effects of temperature treatments on the percentages of strobilating polyps ( $H_{01}$ ) and ephyrae produced per strobila ( $H_{02}$ ) in four species of scyphozoans

Species	Null hypothesis	Polyp age	Test statistic	<i>P</i>
<i>A. aurita</i>	$H_{01}$	1y	$F_{2,15} = 16.936$	0.001
		2y	$F_{2,6} = 14.779$	0.005
	$H_{02}$	1y	$H_2 = 0.573$	0.751
		2y	$H_2 = 0.315$	0.854
<i>C. capillata</i>	$H_{01}$	1y	$H_2 = 13.940$	<0.001
		2y	$H_2 = 6.161$	0.025
	$H_{02}$	1y	$T_{28,79} = 1936.000$	0.003
		2y	$T_{18,28} = 482.000$	0.182
<i>C. lamarckii</i>	$H_{01}$	1y	$F_{2,15} = 1.224$	0.322
	$H_{02}$	1y	$H_2 = 40.367$	<0.001
<i>Ch. hysoscella</i>	$H_{01}$	1y	$F_{2,18} = 9.486$	0.002
	$H_{02}$	1y	$H_2 = 0.477$	0.788

The temperature groups, numbers of replicates, mean values and observation times are shown in Figs. 2 and 3. Strobilations in the first year after polyp settlement (1y) were analysed in all species. Strobilations in the second year (2y) were analysed in *A. aurita* and *C. capillata*

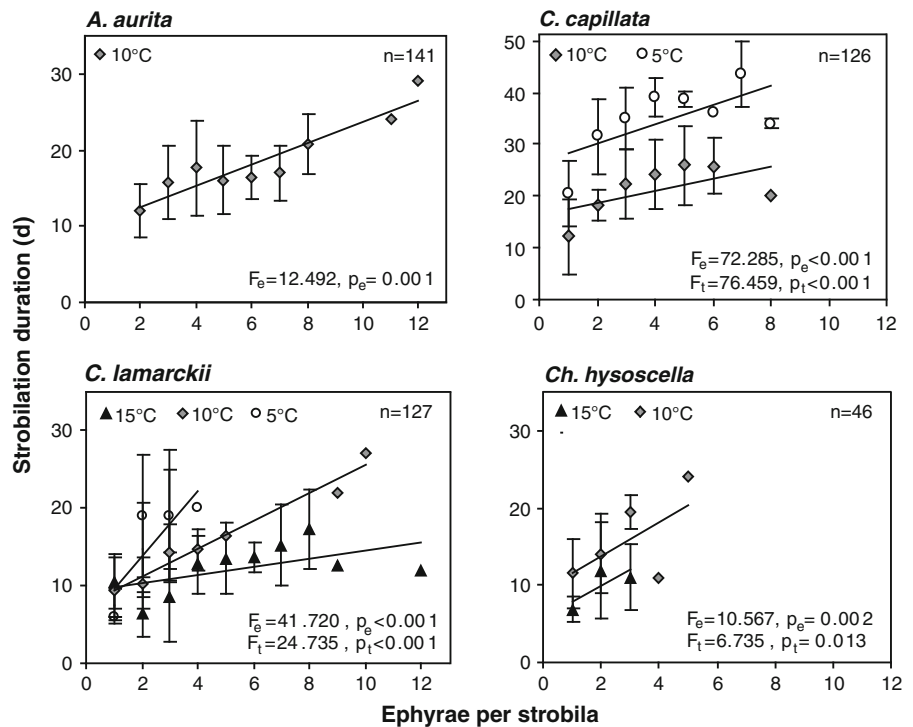
**Table 3** Test statistics of comparisons on strobilations in the first and second year after polyp settlement in two scyphozoan species

Species	Null hypothesis	15°C		15-10-15°C		15-5-15°C	
		Test statistics	<i>P</i>	Test statistics	<i>P</i>	Test statistics	<i>P</i>
<i>A. aurita</i>	$H_{03}$	$T_{3,3} = 9.0$	0.700	$T_{3,3} = 7.0$	0.200	$T_{3,3} = 7.0$	0.200
	$H_{04}$	No test, $n < 3$		$T_{18,26} = 424.5$	0.645	$T_{14,19} = 259.5$	0.439
<i>C. capillata</i>	$H_{03}$	No strobilae		$T_{3,3} = 8.0$	0.400	$T_{3,3} = 8.5$	0.400
	$H_{04}$	No strobilae		$T_{15,18} = 169.0$	0.002	$T_{19,28} = 292.5$	<0.001

Percentages of strobilating polyps ( $H_{03}$ ) and ephyrae produced per strobila ( $H_{04}$ ) in different temperature treatments were analysed. Replicates, mean values and observation times are shown in Fig. 3



**Fig. 4** Strobilation durations (mean days  $\pm$  SD) in individually-monitored strobilae at different constant temperatures in relation to ephyrae numbers produced in the strobilae of *A. aurita*, *C. capillata*, *C. lamarckii* and *Ch. hysoscella*. The effect of ephyra numbers produced per strobila (e) on the strobilation duration and the effect of the temperature treatment (t) on the strobilation duration were tested by ANCOVA. *n* number of analysed strobilae. *df* = 1 for all performed tests. *F* and *P* values are shown in the figures



et al., 2010). Laboratory investigations allow quantification of polyp survival and reproduction and are therefore an important source of data (e.g. Purcell, 2007; Willcox et al., 2007; Liu et al., 2009; Sötje & Jarms, 2009; Holst & Jarms, 2010). Although the results from field observations may differ from laboratory experiments (Purcell et al., 2009), the results of this study demonstrated that simulation of natural temperature cycles in the laboratory can be used to test the effects of seasonal temperature changes on strobilation. The strobilation activity documented in two consecutive years in two species (*A. aurita* and *C. capillata*) showed that repeated temperature cycles in the laboratory experiments caused very similar responses of the polyps. The temperature cycles in the present experiments with 15°C maximum summer temperature and 5°C minimum winter temperature differed from the natural annual temperature cycles because of 2.5°C temperature changes per month. Nevertheless, the laboratory temperature conditions were similar to temperatures found recently in the German Bight (Wiltshire & Manly, 2004; [www.bsh.de/en/Marine\\_data](http://www.bsh.de/en/Marine_data)). The parallel experiments with warmer winter temperatures (10°C) indicated how warmer winter temperatures, as

observed and predicted to progress in the North Sea (Belkin, 2009), could affect the strobilation activity of scyphopolyps in situ. In these experiments, warmer winter temperature (10°C in comparison to 5°C) positively affected strobilation in several ways: 1. A longer strobilation period or higher ephyra production per polyp (in *A. aurita*, *C. lamarckii* and *Ch. hysoscella*; Fig. 1); 2. Higher percentages of polyp strobilation (in *A. aurita* and *Ch. hysoscella*; Fig. 2); 3. More ephyrae per strobila (in *C. capillata*, *C. lamarckii*, see Fig. 2); 4. A shorter strobilation duration (in *C. capillata* and *C. lamarckii*, see Fig. 4). Many of the changes in species abundances, population structure and biogeographical ranges occur as a result of increased reproductive output and juvenile survival in response to increased warming (Mieszowska et al., 2006). The results of this study suggest that this could also be true for the North Sea scyphozoans investigated.

In *A. aurita*, the experiments showed significantly higher percentages of strobilations after a temperature decrease in autumn compared to constant 15°C demonstrating the importance of a temperature decrease for strobilation induction in this species. Spring strobilation only occurred in experiments with 10°C winter

temperature, but did not occur with rising temperature in spring after a cold winter period of 5°C. Perhaps under natural conditions, autumn strobilation in *A. aurita* polyps can happen only if the temperature decreases slowly and the period of moderate temperature of about 10°C lasts for several weeks, whereas a rapid temperature decrease may lead to inhibition of strobilation in autumn. In agreement with this idea, in situ autumn strobilations of *A. aurita* were observed in areas with moderate winter temperatures, such as in Sylt, German Bight (Thiel, 1938), Osterschelde, Netherlands (Korringa, 1953), and Gullmarfjord, western Sweden (Hernroth & Gröndahl, 1985, Gröndahl, 1988); however, in areas with a rapid temperature decrease in autumn, such as in several Baltic Sea areas, a later start of the strobilation activity in *A. aurita* was documented, and strobilation occurred mainly in winter and spring (Palmén, 1954; Kändler, 1961; Thiel, 1962; Rasmussen, 1973; Möller, 1980b). The ephyrae may survive the cold winter periods in deep water layers without further development, which could explain the main time of ephyra abundance in the plankton in autumn and spring (Rasmussen, 1973; Hernroth & Gröndahl, 1985; Gröndahl, 1988). In Southampton Water and Horsea Lake in southern England, ephyra production begins in December and lasts 7 months (Lucas, 1996; Lucas et al., 1997), confirming the results of this study of an extended strobilation phase in *A. aurita* at warmer winter temperatures (Fig. 1). Recent molecular genetic study detected that *A. aurita* is not a single species, but includes members of several molecular species (Dawson, 2003). *A. aurita* populations occurring in the North Atlantic and adjacent seas are probably adapted to the temperature regime in these areas (Dawson, 2003), and therefore, our results reflect the strobilation behaviour of polyps from this temperature regime only.

The tests of this study showed shorter strobilation duration and higher ephyra production per strobila of *C. capillata* polyps at warmer temperatures. On the other hand, cold winter temperatures had positive effects on strobilation in *C. capillata* polyps; strobilation started earlier at colder temperatures, and unlike *A. aurita*, ephyra production was not inhibited by the cold winter temperature (5°C). In these experiments, *C. capillata* was the only species without any strobilation during 22 months at the warm temperature of 15°C. Strobilation induction of *C. capillata* may strictly depend on a temperature decrease, which

may explain why the distribution of the species is limited to northern boreal areas (Russell, 1970), whereas *Cyanea* medusae from the warmer U.S. Atlantic, the Gulf of Mexico and Australian waters may represent other species of *Cyanea* (Bayha, 2005; Dawson, 2005). In the North Sea, *C. capillata* medusae are rare in the southern part and do not appear in the English Channel. In the Irish Sea, their occurrence also is limited to the northern part (Russell, 1970; Hay et al., 1990; Doyle et al., 2007). The simulated annual seasons in present experiments induced ephyra production from February until June, which matched field observations on *C. capillata* strobilation and occurrence of the ephyrae in areas with a similar temperature regime (Hartlaub, 1894; Verwey, 1942; Gröndahl, 1988). Although the polyps are obviously adapted to cold temperature conditions, they have not been reported from the southern or eastern Baltic Sea, where the *C. capillata* medusae appear each summer (Möller, 1980a; Barz et al. 2006). Recent studies demonstrated that *C. capillata* polyps are able to strobilate at a low salinity of 12 and may be more widespread in the Baltic Sea than previously thought (Holst & Jarms, 2010). In accordance with previous studies (Gröndahl, 1988), the results of this study confirm that *C. capillata* polyps are tolerant of cold temperatures, indicating that the low Baltic Sea winter temperatures probably do not limit their distribution. I therefore believe that the only reason why the polyps have not been found in this area to date is that there were too few efforts undertaken to find them.

The medusae of *C. lamarckii* have a more southern distribution in the North and Irish seas than do *C. capillata* medusae (Russell, 1970; Hay et al., 1990; Doyle et al., 2007). In the Baltic Sea, *C. lamarckii* medusae appear rarely in Danish waters (Rasmussen, 1973), whereas they occur periodically from March until June off the Swedish west coast (Gröndahl, 1988). *C. lamarckii* ephyrae were not found in 4 years of plankton sampling on the Swedish west coast and no strobilation was observed on settling plates in the field, leading to the conclusion that *C. lamarckii* polyps do not strobilate there (Gröndahl, 1988). *C. lamarckii* polyps have not yet been described in their natural habitat, but present laboratory studies indicate positive effects of warm temperature on strobilation: higher production of ephyrae per strobila and shorter strobilation duration. This may enable their distribution to

expand to the northern North Sea with rising winter temperatures due to climate changes. From there, the polyps may also extend into the Baltic Sea because of their high tolerance of low salinity (Holst & Jarms, 2010). The present experiments demonstrated a long strobilation phase of *C. lamarckii* polyps from winter until the next summer in agreement with observations of abundant *C. lamarckii* medusae of various sizes and different developmental stages from spring until late summer in the German Bight and off the Dutch coast (Verwey, 1942; Künne, 1952).

*Ch. hysoscella* medusae also are distributed mainly in the southern North and Irish seas (Russell, 1970; Hay et al., 1990; Doyle et al., 2007). Verwey (1942), suggested strobilation of *Ch. hysoscella* with increasing temperature in spring and summer, but the polyps have not yet been found in their natural habitat in the North Sea. A mild winter in 1988 in the German Bight was followed by early appearance and high abundance of *Ch. hysoscella* medusae in the summer, leading to the conclusion that polyp's survival during the winter was higher at warm temperatures (Merck, 1990). These observations agree with experimental results of this study showing very low ephyra production at cold winter temperatures and shorter strobilation duration at warmer temperatures. *Ch. hysoscella* planulae are able to settle at salinities at least as low as 20 (Holst & Jarms, 2010), and thus *Ch. hysoscella* medusae and polyps may be able to spread from the North Sea into the Baltic Sea with continued climate warming.

The number of ephyrae produced by each strobila is affected by temperature, other abiotic factors, food supply and polyp size (Russell, 1970; Purcell et al., 1999). The results of this study agree with those of previous laboratory experiments on polyp cultures demonstrating that warm temperatures increase the strobilation rates of polyps and ephyra production, except at very high temperatures (Purcell et al., 1999, 2012; Purcell, 2007; Liu et al., 2009). The number of ephyrae in the strobila increases with polyp's size (Russell, 1970). This may explain why the *C. capillata* polyps in the present experiments were able to produce more ephyrae by the second year when they grew to a larger size. Salinity also is known to affect strobilation rates of North Sea Scyphozoa (Holst & Jarms, 2010) and other species (reviewed in Purcell et al., 2009). Purcell et al. (2009) concluded that the combined effects of temperature, salinity, light and food determined the amount and time of strobilation in situ.

Only a few recent studies have monitored polyps in situ (see Purcell et al., 2009; Di Camillo et al., 2010; Ishii & Katsukoshi, 2010). Climatic changes in the North Sea related to the North Atlantic Oscillation (NAO) affect jellyfish abundances and may also affect the strobilation of the benthic polyps in this area (Lynam et al., 2010); however, the effects of the NAO depends on the depth that macrozoobenthos animals occur, and therefore, the estimation of the NAO's effect on strobilation is not possible without knowing the locations and depths of polyp habitats (Lynam et al., 2005). The effect of the NAO on North Sea polyps is likely to be high because strobilation occurs mainly in winter and spring when the NAO's influence is the greatest in the North Sea (Lynam et al., 2010). The results of the present study support the idea that variable winter temperatures affect the strobilation activity of North Sea Scyphozoa.

Increasing winter temperature probably will affect the abundances and distributions of scyphozoan jellyfish species in the North Sea. The more southerly species, *C. lamarckii* and *Ch. hysoscella* could expand to the northern parts of the North Sea and possibly into the Baltic Sea. The adaptable species *A. aurita* presumably will benefit from warmer temperatures, having longer strobilation periods (present study), faster growth due to higher feeding rates (Hansson, 1997; Widmer, 2005) and higher reproduction rates of medusae (Ishii & Takagi, 2003). The cold water *C. capillata* might be the only North Sea scyphozoan that could suffer from warmer temperatures; however, *C. capillata* ephyra production also occurred at the warm winter temperature of 10°C (Fig. 1). In general, I assume that the abundances of scyphozoan jellyfish in the North and Baltic seas will increase in future years if the water temperatures continue to increase as predicted (Belkin, 2009). This assessment agrees with the opinion of other authors suggesting an increase of gelatinous predators (scyphomedusae, hydromedusae, siphonophores and ctenophores) in the North Sea due to climate changes, including increasing temperatures, the reduction of the ocean pH and probably, the increasing Atlantic inflow into the North Sea (Attrill et al., 2007; Boersma et al., 2007; Doyle et al., 2008; Lilley et al., 2009; Licandro et al., 2010). The results of this study and previous studies clearly show the linkage between physical environmental factors and ephyra production and thus forecasts of the abundance and distribution of scyphomedusae might be possible

by circulation models in future (Johnson et al., 2001, 2005; Barz et al., 2006). More knowledge on the locations of polyp habitats and on the reproduction cycles of the benthic polyp stage in the field is necessary for successful monitoring and understanding the population dynamics in scyphozoan jellyfish.

**Acknowledgments** I thank PD Dr. Gerhard Jarms for his support, for imparting his knowledge on polyp culturing and for providing the research facilities. I am grateful to the Biologische Anstalt Helgoland (Alfred Wegener Institute) for providing the guest laboratory and I am thankful for the assistance of students and technicians of the Biocenter Grindel. I thank Drs. Ilka Sötje, Jennifer Purcell, and the reviewers for their helpful comments on the manuscript, and Dr. Caroline Stolter for her help in the statistics. This study is part of a Ph. D. thesis conducted at the Biocenter Grindel and Zoological Museum in Hamburg supported by EUROGEL (EUROpean GELatinous Zoo-plankton, European Commission Contract no. EVK-CT-2002-00074).

## References

- Attrill, M. J., J. Wright & M. Edwards, 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography* 52: 480–485.
- Barz, K. & H.-J. Hirche, 2007. Abundance, distribution and prey composition of scyphomedusae in the southern North Sea. *Marine Biology* 151: 1021–1033.
- Barz, K., H.-H. Hinrichsen & H.-J. Hirche, 2006. Scyphozoa in the Bornholm Basin (central Baltic Sea) – the role of advection. *Journal of Marine Systems* 60: 167–176.
- Bayha, K. M., 2005. The molecular systematics and population genetics of four coastal ctenophores and scyphozoan jellyfish of the United States Atlantic and Gulf of Mexico. Dissertation, University of Delaware: 283 pp.
- Belkin, I. M., 2009. Rapid warming of large marine ecosystems. *Progress in Oceanography* 81: 207–213.
- Boero, F., J. Boullion, C. Gravilli, M. P. Miglietta, T. Parsons & S. Piraino, 2008. Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series* 356: 299–310.
- Boersma, M., A. M. Malzahn, W. Greve & J. Javidpour, 2007. The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. *Helgoland Marine Research* 61: 153–155.
- Brewer, R. H. & J. S. Feingold, 1991. The effect of temperature on the benthic stages of *Cyanea* (Cnidaria: Scyphozoa), and their seasonal distribution in the Niantic River estuary, Connecticut. *Journal of Experimental Marine Biology and Ecology* 152: 49–60.
- CIESM, 2001. Gelatinous zooplankton outbreaks: theory and practice. CIESM Workshop Series 14: 112 pp.
- Dawson, M. N., 2003. Macro-morphological variation among cryptic species of the moon jellyfish, *Aurelia* (Cnidaria: Scyphozoa). *Marine Biology* 143: 369–379.
- Dawson, M. N., 2005. *Cyanea capillata* is not a cosmopolitan jellyfish: morphological and molecular evidence for *C. annaskala* and *C. rosea* (Scyphozoa: Semaestomeae: Cyaneidae) in south-eastern Australia. *Invertebrate Systematics* 19: 361–370.
- Di Camillo, C. G., F. Betti, M. Bo, M. Martinelli, S. Puce & G. Bavestrello, 2010. Contribution to the understanding of seasonal cycle of *Aurelia aurita* (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom* 90: 1105–1110.
- Doyle, T. K., J. D. R. Houghton, S. M. Buckley, G. C. Hays & J. Davenport, 2007. The broad-scale distribution of five jellyfish species across a temperate coastal environment. *Hydrobiologia* 579: 29–39.
- Doyle, T. K., H. De Haas, D. Cotton, B. Dorschel, V. Cummins, J. D. R. Houghton, J. Davenport & G. C. Hays, 2008. Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *Journal of Plankton Research* 30: 963–968.
- Gröndahl, F., 1988. A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *Cyanea lamarckii* in the Gullmar Fjord, western Sweden. *Marine Biology* 97: 541–550.
- Hansson, L. J., 1997. Effect of temperature on growth rate of *Aurelia aurita* (Cnidaria, Scyphozoa) from Gullmarsfjorden, Sweden. *Marine Ecology Progress Series* 161: 145–153.
- Hartlaub, C., 1894. Die Coelenteraten Helgolands. *Wissenschaftliche Meeresuntersuchungen Helgoland Neue Folge* 1: 161–206.
- Hay, S. J., J. R. G. Hislop & A. M. Shanks, 1990. North Sea scyphomedusae; summer distribution, estimated biomass and significance particularly for 0-Group gadoid fish. *Netherlands Journal of Sea Research* 25: 113–130.
- HELCOM, 2007. Climate change in the Baltic Sea Area – HELCOM thematic assessment in 2007. *Baltic Sea Environment Proceedings* 111: 1–49.
- Hemroth, L. & F. Gröndahl, 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. *Bulletin of Marine Science* 37: 567–576.
- Holst, S. & G. Jarms, 2007. Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea. *Marine Biology* 151: 863–871.
- Holst, S. & G. Jarms, 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.
- Holst, S., I. Sötje, H. Tieman & G. Jarms, 2007. Life cycle of the rhizostome jellyfish *Rhizostoma octopus* (L.) (Scyphozoa, Rhizostomeae), with studies on cnidocysts and statoliths. *Marine Biology* 151: 1695–1710.
- IPCC, 2007. Summary for policymakers. In Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller (eds), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

- Ishii, H. & K. Katsukoshi, 2010. Seasonal and vertical distribution of *Aurelia aurita* polyps on a pylon in the innermost part of Tokyo Bay. *Journal of Oceanography* 66: 329–336.
- Ishii, H. & A. Takagi, 2003. Development time of planula larvae on the oral arms of the scyphomedusa *Aurelia aurita*. *Journal of Plankton Research* 25: 1447–1450.
- Jarms, G., 2010. The early life history of Scyphozoa with emphasis on Coronatae a review with a list of described life cycles. *Verhandlungen des Naturwissenschaftlichen Vereins Hamburg* 45: 17–31.
- Johnson, D. R., H. M. Perry & W. D. Burke, 2001. Developing jellyfish strategy hypotheses using circulation models. *Hydrobiologia* 451: 213–221.
- Johnson, D. R., H. M. Perry & W. M. Graham, 2005. Using nowcast model currents to explore transport of non-indigenous jellyfish into the Gulf of Mexico. *Marine Ecology Progress Series* 305: 139–146.
- Kändler, R., 1961. Über das Vorkommen von Fischbrut, Decapodenlarven und Medusen in der Kieler Förde. *Kieler Meeresforschung* 17: 48–65.
- Korringa, P., 1953. The shell of *Ostrea edulis* as a habitat. *Archives Neerlandaises de Zoologie* 10: 32–59.
- Künne, C., 1952. Untersuchungen über das Großplankton in der Deutschen Bucht und im Nordsyler Wattenmeer. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 4: 1–54.
- Licandro, P., D. V. P. Conway, M. N. Daly Yahia, M. L. Fernandez De Puelles, S. Gasparini, J. H. Hecq, P. Tranter & R. R. Kirby, 2010. A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters* 6: 688–691.
- Lilley, M. K. S., J. D. R. Houghton & G. C. Hays, 2009. Distribution, extent of inter-annual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. *Journal of the Marine Biological Association of the United Kingdom* 89: 39–48.
- 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.
- Lucas, C. H., 1996. Population dynamics of *Aurelia aurita* (Scyphozoa) from an isolated brackish lake, with particular reference to sexual reproduction. *Journal of Plankton Research* 18: 987–1007.
- Lucas, C. H., A. G. Hirst & J. A. Williams, 1997. Plankton dynamics and *Aurelia aurita* production in two contrasting ecosystems: comparison and consequences. *Estuarine, Coastal and Shelf Science* 45: 209–219.
- Lynam, C. P., S. J. Hay & A. S. Brierley, 2005. Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. *Journal of the Marine Biological Association of the United Kingdom* 85: 435–450.
- Lynam, C. P., M. J. Attrill & M. D. Skogen, 2010. Climatic and oceanic influences on the abundance of gelatinous zooplankton in the North Sea. *Journal of the Marine Biological Association of the United Kingdom* 90: 1153–1159.
- Merck, T., 1990. Untersuchungen zur ökologischen Nische von *Chrysaora hysoscella*. *Jahresbericht der Biologischen Anstalt Helgoland* 1989: 53–54.
- Mieszkowska, N., R. Leaper, P. Moore, M. A. Kendall, M. T. Burrows, D. Lear, E. Poloczanska, K. Hiscock, P. S. Moschella, R. C. Thompson, R. J. Herbert, D. Lafolley, J. Baxter, A. J. Southward & S. J. Hawkins, 2006. Marine biodiversity and climate change. Assessing and predicting the influence of climate change using intertidal rocky shore biota. Final report for United Kingdom funders. *Marine Biological Association Occasional Publications* 20: 1–53.
- Miyake, H., M. Terazaki & Y. Kakinuma, 2002. On the polyps of the common jellyfish *Aurelia aurita* in Kagoshima Bay. *Journal of Oceanography* 58: 451–459.
- Molinero, J. C., M. Casini & E. Buecher, 2008. The influence of the Atlantic and regional climate variability on the long-term changes in gelatinous carnivore populations in the northwestern Mediterranean. *Limnology and Oceanography* 53: 1456–1467.
- Möller, H., 1980a. A summer survey of large zooplankton, particularly scyphomedusae, in North Sea and Baltic. *Meeresforschung* 28: 61–68.
- Möller, H., 1980b. Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG). *Marine Biology* 60: 123–128.
- Palmén, E., 1954. Seasonal occurrence of ephyrae and subsequent instars of *Aurelia aurita* (L.) in the shallow waters of Tvärminne, S. Finland. *Archivum Societatis Zoologicae Botanicae Fennicae Vanamo* 8: 122–138.
- Pierce, J., 2009. Prediction, location, collection and transport of jellyfish (Cnidaria) and their polyps. *Zoo Biology* 28: 163–176.
- Purcell, J. E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom* 85: 461–476.
- Purcell, J. E., 2007. Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata*. *Marine Ecology Progress Series* 348: 183–196.
- Purcell, J. E., 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia* 616: 23–50.
- Purcell, J. E., 2011. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annual Review of Marine Science*. doi:10.1146/annurev-marine-120709-142751.
- Purcell, J. E., J. R. White, D. A. Nemazie & D. A. Wright, 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Marine Ecology Progress Series* 180: 486–487.
- Purcell, J. E., S.-I. Uye & W.-T. Lo, 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series* 350: 153–174.
- Purcell, J. E., R. A. Hoover & N. T. Schwarck, 2009. Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions in situ. *Marine Ecology Progress Series* 375: 139–149.
- 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 polyps from the northwestern Mediterranean Sea. *Hydrobiologia*, this issue. doi:10.1007/s10750-012-1047-7.
- Rasmussen, E., 1973. Systematic and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11: 1–507.

- Richardson, A. J., A. Bakun, G. C. Hays & M. J. Gibbons, 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution* 24: 312–322.
- Russell, F. S., 1970. The medusae of the British Isles II. Pelagic Scyphozoa with a supplement to the first volume on hydromedusae. Cambridge University Press, Cambridge.
- Sabatés, A., F. Pagès, D. Atienza, V. Fuentes, J. E. Purcell & J.-M. Gili, 2010. Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. *Hydrobiologia* 645: 153–165.
- Sötje, I. & G. Jarms, 2009. Derivation of the reduced life cycle of *Thecoscyphus zibrowii* Werner, 1984 (Cnidaria, Scyphozoa). *Marine Biology* 156: 2331–2341.
- Thiel, M. E., 1938. Scyphomedusae. In Bronn, H. G. (ed.), Dr. H. G. Bronn's Klassen und Ordnungen des Tierreichs. Akademische Verlagsgesellschaft, Leipzig.
- Thiel, H., 1962. Untersuchungen über die Strobilisation von *Aurelia aurita* LAM. an einer Population der Kieler Förde. *Kieler Meeresforschungen* 18: 198–230.
- Tronolone, V. B., A. C. Morandini & A. E. Bigotto, 2002. On the occurrence of scyphozoan ephyrae (Cnidaria, Scyphozoa, Semaestomeae and Rhizostomeae) in the southeastern Brazilian coast. *Biota Neotropica* 2: 1–18.
- Verwey, J., 1942. Die Periodizität im Auftreten und die aktiven und passiven Bewegungen der Quallen. *Archives Néerlandaises de Zoologie* 6: 363–468.
- Widmer, C. L., 2005. Effects of temperature on growth of north-east Pacific moon jellyfish ephyrae, *Aurelia labiata* (Cnidaria: Scyphozoa). *Journal of the Marine Biological Association of the United Kingdom* 85: 569–573.
- Willcox, S., N. Moltchanowskyj & 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.
- Wiltshire, K. H. & B. F. J. Manly, 2004. The warming trend at Helgoland Roads, North Sea: Phytoplankton response. *Helgoland Marine Research* 58: 269–273.
- Wiltshire, K. H., A. Kraberg, I. Bartsch, M. Boersma, H.-D. Franke, J. Freud, C. Gebühr, G. Gerdts, K. Stockmann & A. Wichels, 2010. Helgoland Roads, North Sea: 45 years of change. *Estuaries and Coasts* 33: 295–310.
- You, K., C. Ma, H. Gao, G. Li, M. Zhang, B. Wang & R. Wei, 2008. The effects of temperature decrease on the scyphistomae strobilation of Jellyfish, *Rhopilema esculentum* Kishinouye. *Journal of the World Aquaculture Society* 39: 706–711.