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Morphological plasticity in *Aurelia* polyps, with subsequent effects on asexual fecundity and morphology of young medusae

Luciano M. Chiaverano*, William M. Graham

Division of Marine Science, University of Southern Mississippi, 1020 Balch Blvd., Stennis Space Center, MS 39529, USA

ABSTRACT: A key step toward better knowledge of the causes and mechanisms of mass occurrences (blooms) in scyphozoan jellyfish is to assess the extent of environmentally induced effects on the phenotype of different phases in their complex life cycle. Laboratory experiments were carried out to quantify the extent of environmentally induced changes in *Aurelia* sp.9 polyp morphology, and subsequent effects on asexual propagation and ephyra morphology, in response to temperature and food quantity. Size and shape of polyps was highly plastic to environmental variation, and environmentally induced morphology had a significant effect on asexual fecundity and propagation strategy. Polyp size positively correlated with the number of buds, new polyps, and ephyrae produced per polyp, but negatively correlated with investment per bud. Environmentally induced polyp morphology had a significant effect on the morphology of ephyra at release. These findings suggest that asexual fecundity in *Aurelia* sp.9 polyps is likely ultimately limited by body size, which can be environmentally mediated. This work also shows, for the first time, that polyp and ephyra traits are linked. Environmentally induced variation in polyp morphology can be carried into the next life-cycle phase and affect the morphology of ephyrae at release. We conclude that environmentally induced effects on polyp morphology can potentially control the number of new polyps produced, as well as the number of medusae released into the water column. Hence, in scyphozoan jellyfish, metamorphosis is not necessarily a new beginning, and environmental conditions experienced by the polyp can have a significant effect on traits of subsequent phases.

KEY WORDS: Jellyfish · Blooms · Phenotypic plasticity · Budding · Strobilation · Environmental variation · Life history · Complex life cycle

INTRODUCTION

The life cycle of most blooming scyphozoan jellyfish consists of 2 distinct phases: a pelagic medusa and a benthic polyp (Dawson & Hamner 2009). Scyphomedusae are typically dioecious and reproduce sexually, while polyps propagate exclusively by several modes of asexual reproduction (Schiariti et al. 2014). Under certain environmental conditions, polyps undergo strobilation, resulting in the release of free-swimming ephyrae that will develop into medusae (Fautin 2002). Several scyphozoan species have the ability to release ephyrae into the water column in great numbers, which often results in medusa blooms (Dawson & Hamner 2009). When abundant, medusae can have negative effects not only on food web dynamics by reducing the amount of energy transferred to upper trophic levels (Ruzicka et al. 2012, Robinson et al. 2014), but also on human enterprise such as fishing (Dong et al. 2010), aquaculture (Doyle et al. 2008), power generation and desalination (Daryanabard & Dawson 2008), and tourism (Fenner et al. 1996).

Since most scyphozoan medusae are produced and released from benthic polyps, it is reasonable to presume a direct relationship between polyp abundance and medusa population size (Lucas et al. 2012, Schiariti et al. 2014). In fact, it has been pro-

*Corresponding author: luciano.chiaverano@usm.edu

posed that processes affecting the polyp stage can be considerably more important at determining the size of medusa populations than processes in the plankton (Lucas 2001), and some of these processes remain relatively unknown despite recent advances in understanding polyp ecology (Lucas et al. 2012). For instance, environmentally induced effects on the morphology of jellyfish polyps remains almost unexplored (but see Keen & Gong 1989, Schroth et al. 2002), and very little is known about the relationship between polyp morphology and asexual fecundity. Few previous studies have shown that larger polyps produce more buds (Keen & Gong 1989) and more ephyrae (Kroiher et al. 2000, Ishii & Watanabe 2003) than smaller counterparts, suggesting that environmentally induced effects on polyp morphology (i.e. size and/or shape) can have potential effects not only on asexual propagation capacity, but also on abundance of medusae (Lucas 2001, Willcox et al. 2008, Hoover & Purcell 2009). Due to the tight coupling between benthic and pelagic stages in species with complex life cycles (Boero et al. 2008), environmentally induced traits in one may have latent effects on subsequent phases (Pechenik et al. 1990, 1998, Giménez 2006, Pechenik 2006). This topic has been studied in several marine invertebrates with complex life cycles, including ascidians (Marshall et al. 2003), bryozoans (Woollacott et al. 1989), and crabs (Giménez et al. 2004), but it remains relatively unexplored in scyphozoans. Ishii & Watanabe (2003) showed that larger polyps released larger ephyrae than smaller individuals, while Kroiher et al. (2000) found no correlation between polyp and ephyra size. Thus, it is still uncertain whether environmentally induced polyp traits can have an effect on ephyra traits.

In this study, we experimentally investigated environmental effects on the phenotype of moon jellyfish polyps (*Aurelia* sp.9; Dawson et al. 2005) from the Gulf of Mexico in order to answer the following main questions: (1) Do *Aurelia* sp.9 polyps exhibit morphological plasticity in response to environmental variation? (2) Can environmentally induced polyp morphology affect polyp asexual propagation and the morphology of ephyra at release?

MATERIALS AND METHODS

Experimental procedure

Aurelia sp.9 medusae (see Chiaverano et al. 2016) were collected during fall (September 2006) in the central northern Gulf of Mexico, 10 km south of Dauphin Island, Alabama, USA (30° 09′ 28″ N, 88° 08′ 22″ W; Fig. 1). In this system, *Aurelia* polyps most likely strobilate in spring (May), medusae reach maturity and sexually reproduce in late summer (August), and planulae are released throughout the fall (authors' pers. obs.). Ten mature female individuals (>25 cm bell diameter) were dip netted from the surface and transported to the Dauphin Island Sea Lab. Four randomly chosen individuals (mean ± SD bell diameter = 29.5 ± 2.3 cm) were placed exumbrella facing down in separate glass pans (H × W × D: 10 × 45 × 35 cm) filled with filtered seawater (30 µm, 25°C, 30 psu). Planula larvae were collected from the oral arms of each female medusa using a Pasteur pipette and placed in a 500 ml container filled with filtered seawater (25°C, 30 psu; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m582p079_supp.pdf). Larval density varied from 20 to 31 planulae ml^{-1} across all 4 containers. Since female *Aurelia* medusae are brooders (Arai 1997), all planula larvae from a

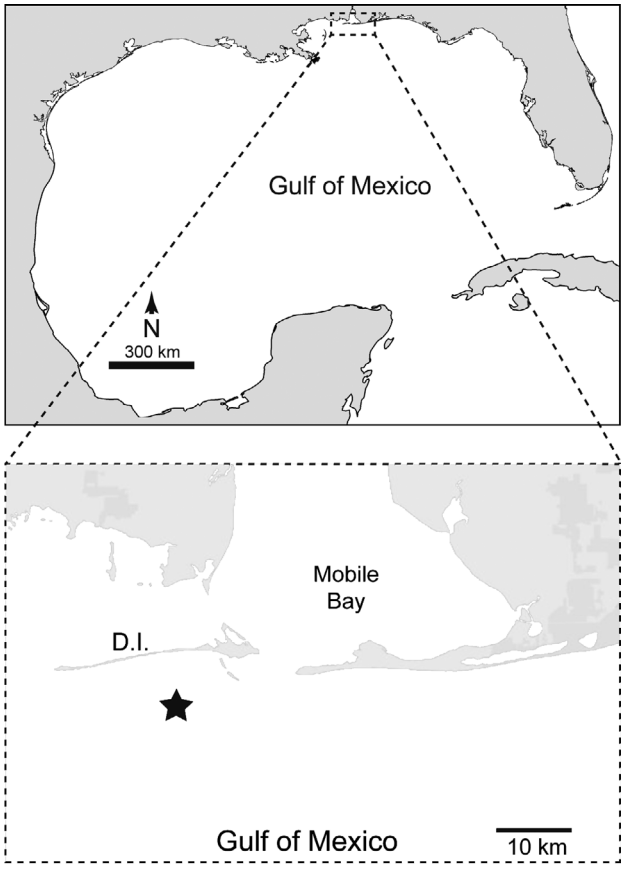

Fig. 1. Study area in the northern Gulf of Mexico showing the collection site (star) for *Aurelia* sp.9 medusae, 10 km south of Dauphin Island (D.I.)

single female individual share the same mother; however, inferences on paternity cannot be made because the possibility of 1 female medusa being fertilized by more than 1 male cannot be ruled out. Therefore, all planulae collected from the same female medusae were considered to be at least half-siblings (i.e. a half-sibling family) and are hereafter referred to as 'family' (Fam; Fig. S1). Planulae from each Fam were split into 20 plastic vessels (250 ml), which were filled with filtered seawater (25°C, 30 psu) and contained a dark gray, 5 × 5 cm PVC plate that served as a substrate for planula settlement. Each vessel represented an experimental unit. Between 200 and 310 planulae (10 ml aliquot from each Fam vessel) were placed in each experimental unit. A total of 80 vessels (i.e. experimental units), 20 Fam^{-1}, were used in this experiment (Fig. S1). Experimental units corresponding to each Fam were randomly split evenly into 2 groups, which were randomly assigned to 2 temperature treatments. The first group was placed in a temperature-controlled water bath set at 20°C, while the second group was placed in a water bath set at 28°C (Fig. S2). Each unit had a water-proof lid that prevented water from the bath from entering the vessel. Temperature levels represent temperature differences between the central northern Gulf of Mexico (e.g. Dauphin Island, Alabama) and southeastern Gulf of Mexico (e.g. Long Key, Florida) during fall (Baranova et al. 2014), when most *Aurelia* sp.9 planula larvae are released into the water column and metamorphose into polyps (authors' pers. obs.). The laboratory experiment was designed to quantify morphological and reproductive responses to environmental attributes while controlling for potential genetic or maternal effects. For this study, we employed a completely randomized design, with 4 Fams split into 4 different environmental conditions given by the factorial combination of 2 levels of water temperature with 2 levels of food quantity, with each experimental treatment replicated 5 times (Fig. S2).

Once in the temperature treatments, most larvae took 48 h to settle on the PVC plates and metamorphosed into polyps. Water was then changed (80% of total volume) in all units, and unsettled planulae were siphoned out and discarded. Twelve polyps were randomly chosen and kept per experimental unit. Within each temperature treatment, all units of each Fam were then equally and randomly divided into 2 groups: one was fed twice wk^{-1} (on Days 2 and 5 of the week), while the other group was fed 4 times wk^{-1} (on Days 2, 4, 5, and 6 of the week; Fig. S2). Polyps were fed *Artemia* sp. nauplii ad libitum for 3 h, and then the remaining prey items were siphoned out, containers were cleaned using swabs, and water was changed in all units to standardize both disturbance and water quality across treatments. Food levels were chosen to represent habitats of the Gulf of Mexico where both primary and secondary production is relatively high (low), thus food is likely to be abundant (scarce) and readily available (limited) for polyps (Salmerón-García et al. 2011). Salinity was kept at 30 psu, and a 12:12 h dark:light cycle was implemented throughout the experiment, which started during the third week of September (2006) and lasted 24 wk.

Measurements

All experimental units were inspected under a dissecting microscope (32–40×) at 2 d intervals for 24 wk. Lateral budding (Schiariti et al. 2014) was the only mode of asexual propagation (besides strobilation) observed in *Aurelia* sp.9 polyps. Thus, during each inspection, the number of original alive polyps and the number of buds per polyp (BPP, i.e. young polyps still attached to parent polyps) were counted. Once detached from parent polyps, bud total height (BTH) and bud disc diameter (BDD) were recorded from each bud (Fig. 2A). Detached buds were then removed from all experimental units and recorded as newly produced polyps (NPP). The objective of removing new polyps from all experimental units was to minimize the effects of polyp density across treatments (Schiariti et al. 2015) and to standardize polyp age throughout the duration of the experiment. BPP, BTH, BDD, and NPP were recorded for 16 wk. Mean trait values were obtained per experimental unit and used in subsequent statistical analysis.

At the end of Week 16, we recorded 8 morphological features from all polyps in each experimental unit using a micrometer attached to a binocular microscope. Since minor movements of the experimental units cause polyps to slightly change body shape or retract tentacles, all measurements were performed on fully relaxed polyps. Individuals usually took no longer than 1 min to fully relax after a minor perturbation. Morphological features included: total polyp height (TPH), mouth disc diameter (MDD), calyx width at mid-height (CAW), calyx height (CAH), stalk height (STH), stalk width at mid-height (STW), tentacle length (TEL), and tentacle width at mid-length (TEW; Fig. 2A). Measurements of TEL and TEW were performed on fully extended tentacles, evidenced in *Aurelia* sp.9 polyps by the presence of defined nematocyst clusters (clusters are not visible if tentacles are

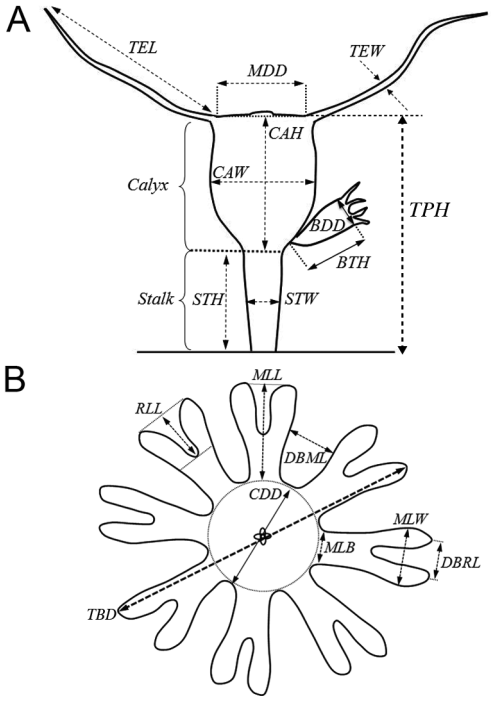

Fig. 2. Schematics of (A) a polyp (side view) and (B) an ephyra (oral view) of *Aurelia* sp.9, showing all morphological features measured for this study. Polyp features: TPH: total polyp height; MDD: mouth disc diameter; CAH: calyx height; CAW: calyx width; STH: stalk height; STW: stalk width; TEL: tentacle length; TEW: tentacle width; BTH: bud total height; BDD: bud disc diameter. Ephyra features: TBD: total body diameter; CDD: central disc diameter; MLL: marginal lappet length; MLW: marginal lappet width; MLB: marginal lappet base; RLL: rhopalial lappet length; DBRL: distance between rhopalial lappets; DBML: distance between marginal lappets. All units were recorded in mm

not fully extended; authors' pers. obs.). To reliably record TPH, CAW, and CAH, as well as STW and STH, the settling plate was placed perpendicular to the bottom, allowing those measurements to be taken from above. All morphological features were measured at least 2 wk before the onset of strobilation. Mean trait values were obtained for each experimental unit and used in subsequent statistical analyses.

The strobilation process started in Weeks 18 and 22 of the experiment in polyps raised at 28 and 20°C, respectively (see 'Results'). This process was carefully monitored, and the number of ephyrae per strobila (EPS) was recorded immediately after the uppermost ephyra was released. Ephyrae released in each experimental unit were collected using a Pasteur pipette and placed in separate 300 ml containers (corresponding to experimental units) filled with filtered seawater (30 µm) and a solution of $MgCl_2$ (7% w/v) to relax them for subsequently recording of morphological features (Spangenberg 1965). Between 15 and 30 ephyrae were randomly selected from each unit and digitally photographed under the microscope (32–40×). Eight morphological features were recorded on each ephyra based on Gambill & Jarms (2014) using the software ImagePro Plus©: total body diameter (TBD), central disc diameter (CDD), marginal lappet length (MLL), marginal lappet width (MLW) at mid-length of the rhopalial lappet, marginal lappet width at its base (MLB), rhopalial lappet length (RLL), distance between marginal lappets at mid-length (DBML), and distance between rhopalial lappets (DBRL) (Fig. 2B). No ephyra traits were recorded after Week 24 of the experiment. Mean trait values were obtained for each experimental unit and used in subsequent statistical analyses.

Size correction

To account for differences in shape, morphology must be characterized independently of size. Because both polyps and ephyrae did not share the same allometry among treatments, each morphological feature was size-corrected using the method of Lleonart et al. (2000), which scales all individuals to the same size and also adjusts their shape accounting for differences in allometry using the following formula:

$$Y_i^* = Yo_i\,(Xm / Xo_i)^b \quad (1)$$

where Y_i^* is the size-corrected morphological character for individual i. Yo is the measured character on individual i, and Xo represents size of individual i. In this case, TPH and TBD were used as a proxy of size for polyps and ephyrae, respectively, because these features correlated strongly and positively with the rest of the morphological features ($r > 0.7$, $p < 0.001$; Tables S1 & S2). Xm is the mean overall TPH or TBD of all measured individuals from all treatments, and 'b' is the within-treatment (each Temp × Food combination) slope of the regression between log-transformed body size (Xo_i) and a log-transformed given measured character (Yo_i). All size-independent morphological features of polyps and ephyrae were included in 2 separate principal component analyses (PCAs, correlation matrix) to obtain independent components of shape. Principal component scores were obtained per experimental unit and used in subsequent statistical analyses.

The total NPPs per parent polyp was estimated for each experimental unit using the following weighted average formula:

$$\sum_{i=1}^{n=16} = \frac{\mathrm{PP}i}{\mathrm{OSP}i} \quad (2)$$

where OSP and PP represent the number surviving polyps and the number of new polyps produced, respectively, during a given week (i) per experimental unit. Thus, NPP, BPP, and EPS were included in a PCA (correlation matrix). The first component (PC1) explained 93% of the total variance and was used as a proxy of asexual fecundity (see Hughes 1992, Hunter & Hughes 1995, Ayre 1995, Sherman & Ayre 2008), since feature loadings were high and positive on this axis (Table S3).

Estimated parameters

Polyp volume (POV) was estimated by adding the volumes of the upper calyx, the lower calyx, and the stalk (tentacles excluded), which were obtained using the formula for the volume of a truncated cone (twice), and a cylinder, respectively (Fig. S3). Bud volume (BUV) was estimated using the formula for the volume of a cone (Fig. S3). The BUV:POV ratio was used as a proxy for investment per bud (Keen & Gong 1989). BUV was then multiplied by total NPP to obtain total BUV produced per polyp (TBUV). The TBUV:POV ratio was used as a proxy of investment into budding (Keen & Gong 1989). Mean values were obtained per treatment and used in subsequent statistical analysis.

Statistical analysis

The effects of temperature (Temp), food quantity (Food), Fam, and their interactions on polyp morphology (i.e. size and shape), polyp asexual fecundity and investment, as well as on ephyra morphology, were tested by 2 × 2 × 4 full factorial ANOVAs using general linear models (GLMs, balanced design). Both Temp and Food were treated as fixed factors, while Fam was included as a random factor. To account for potential Type I errors, statistical significance was determined after alpha values were Bonferroni-corrected. Multiple comparisons were carried out by Tukey's tests. The significance of relationships between polyp morphology and polyp asexual fecundity and investment, as well as ephyra morphology, was assessed by linear regressions via GLMs. All statistical analyses were performed in Statistica v.6.

RESULTS

Mean polyp survival was high (75–85%; Table S4) throughout the experiment, and polyp density did not vary significantly among treatments (ANOVA, $F_{15,79} = 0.55$, $p = 0.809$).

Environmentally induced effects on polyp morphology

The results of the 2 × 2 × 4 ANOVA indicated no significant effects of Fam on polyp size (Table S5). Therefore, Fam was eliminated from the model and polyp morphology was re-analyzed by using a 2 × 2 ANOVA (via GLMs) with Temp and Food as fixed factors. ANOVA detected a significant Temp × Food interaction effect on polyp size ($F_{1,76} = 49.2$, $p < 0.0001$). All individuals raised at 20°C were significantly larger in size than their counterparts exposed to 28°C independently of food quantity (Tukey's $p < 0.001$; Fig. 3A). Within temperatures, polyps fed twice wk^{-1} were significantly smaller than individuals fed 4 times wk^{-1} (Tukey's $p < 0.001$; Fig. 3A).

Seven principal components were extracted from the PCA using size-corrected morphological features. The first 2 first principal components (PC1 and PC2) explained 70.3 and 19.7% of the total variation in polyp shape, respectively (Table 1). An increase (decrease) in PC1 scores indicated an increase (decrease) in CAH, CAW, and STW, and a decrease (increase) in STH. An increase (decrease) in PC2 scores indicated an increase (decrease) in TEL and a decrease (increase) in TEW (Table 1). The results of the 2 × 2 × 4 ANOVA indicated no significant effects of Fam on either PC1 or PC2 (Table S5). Fam was then eliminated from the model and polyp morphology was re-analyzed by using a 2 × 2 ANOVA (via GLMs) with Temp and Food as fixed factors. ANOVA detected a significant Temp × Food interaction effect on PC1 ($F_{1,76} = 51.2$, $p < 0.0001$) and PC2 ($F_{1,76} = 62.8$, $p < 0.0001$). All individuals raised at 20°C had relatively thinner, shorter calyxes and longer, thinner stalks than their counterparts exposed to 28°C regardless of food quantity (Tukey's $p < 0.001$; Fig. 3B). Within temperatures, polyps fed twice weekly had relatively wider, taller calyxes and shorter, thicker stalks than individuals fed 4 times weekly (Tukey's $p < 0.001$; Fig. 3B). In addition, polyps fed twice developed relatively longer, thinner tentacles than counterparts fed 4 times regardless of Temp (Tukey's $p < 0.001$), while Temp had a significant effect on tentacle shape only on polyps fed twice (Tukey's $p < 0.001$; Fig. 3C).

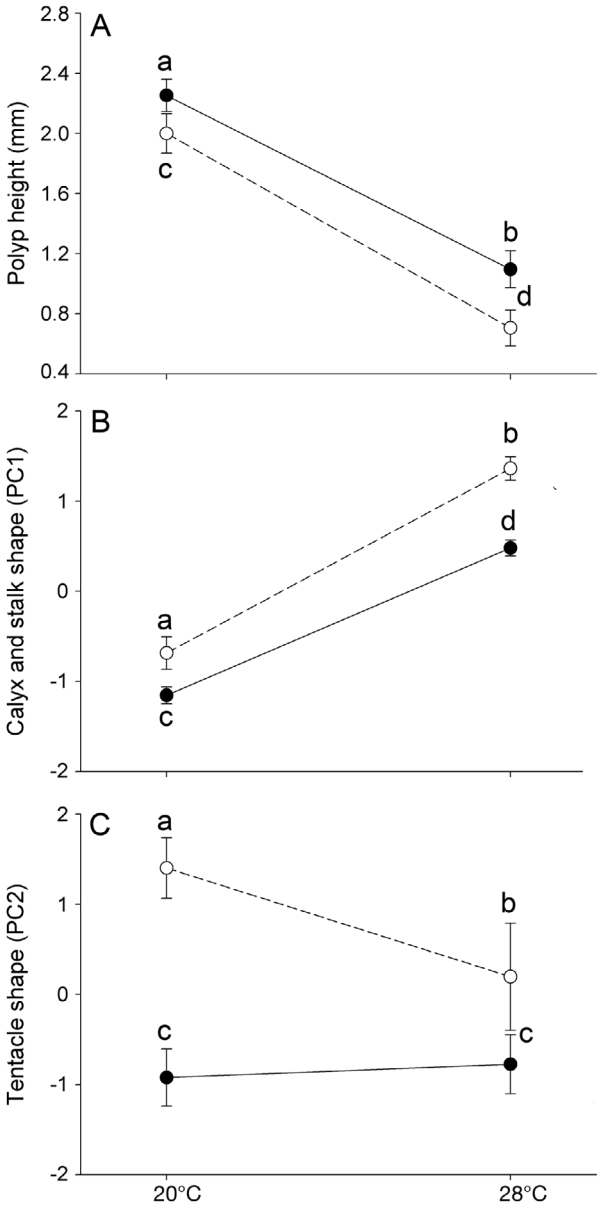

Fig. 3. Morphological plasticity in (A) body size and (B,C) shape of *Aurelia* sp.9 polyps exposed to different environmental conditions. Solid symbols (solid line) indicate polyps fed 4 times wk^{-1}, while open symbols (dashed line) indicate individuals fed twice wk^{-1}. As PC1 scores increase, calyx height, calyx width, and stalk width increase, while stalk height decreases. As PC2 scores increase, tentacle length increases, while tentacle width decreases. Different letters indicate significant differences (post-hoc ANOVA; Tukey's $p < 0.001$) among treatments

Environmentally induced effects on asexual propagation

All asexual propagation traits recorded from each experimental treatment are provided in Table S6.

Table 1. Results of the principal component analysis (PCA) showing the loadings for each size-corrected morphological feature recorded on *Aurelia* sp.9 polyps in this study

Polyp size-independent features	Shape PC1	Shape PC2
Mouth disc diameter (MDD)	0.95	−0.11
Calyx width (CAW)	0.79	−0.44
Calyx height (CAH)	0.92	0.12
Stalk height (STH)	−0.94	0.09
Stalk width (STW)	0.71	0.32
Tentacle length (TEL)	−0.36	0.83
Tentacle width (TEW)	0.33	−0.79
Variance explained (%)	70.30	19.70

Polyps raised at 28°C started budding and strobilating 2 and 4 wk earlier, respectively, than counterparts raised at 20°C independently of food quantity (Fig. S4). Results of the 2 × 2 × 4 ANOVA indicated no significant Fam effects (Table S7) on asexual fecundity (PC1). This random factor was then excluded from the model and PC1 scores were analyzed using a 2 × 2 ANOVA using Temp and Food as fixed factors. ANOVA detected significant main effects of Temp ($F_{1,76} = 1411$, $p < 0.0001$) and Food ($F_{1,76} = 701$, $p < 0.0001$) on asexual fecundity. Individuals raised at 20°C had significantly higher asexual fecundity (produced more buds, more new polyps, and had more EPS) than their counterparts raised at 28°C regardless of food levels (Tukey's $p < 0.001$), and individuals fed 4 times wk^{-1} had significantly higher fecundities than counterparts fed twice wk^{-1} (Tukey's $p < 0.001$; Fig. 4A).

Results of the 2 × 2 × 4 ANOVA indicated a significant Temp × Food × Fam interaction effect on both the investment per bud and the total investment into budding (Table S7). Polyps raised at 28°C displayed a significantly higher investment per bud than counterparts raised at 20°C independently of food level (Tukey's $p < 0.001$; Fig. 4B). Hence, each bud produced by polyps raised at 20°C (large polyps) represented 2.1% (±0.83 [SD]) of the parent POV, while buds released by individuals grown at 28°C (small polyps) represented 4.2% (±0.98) of parent POV. Food quantity had a significant effect on investment per bud only in individuals raised at 20°C. (Tukey's $p < 0.001$; Fig. 4B). Increased temperature had a positive effect on total investment into budding in polyps fed 4 times wk^{-1}, while the opposite response was observed in individuals fed twice wk^{-1} (Tukey's $p < 0.001$; Fig. 4C). Food quantity had a significant effect on total investment into budding only in polyps raised at 28°C (Tukey's $p < 0.001$; Fig. 4C).

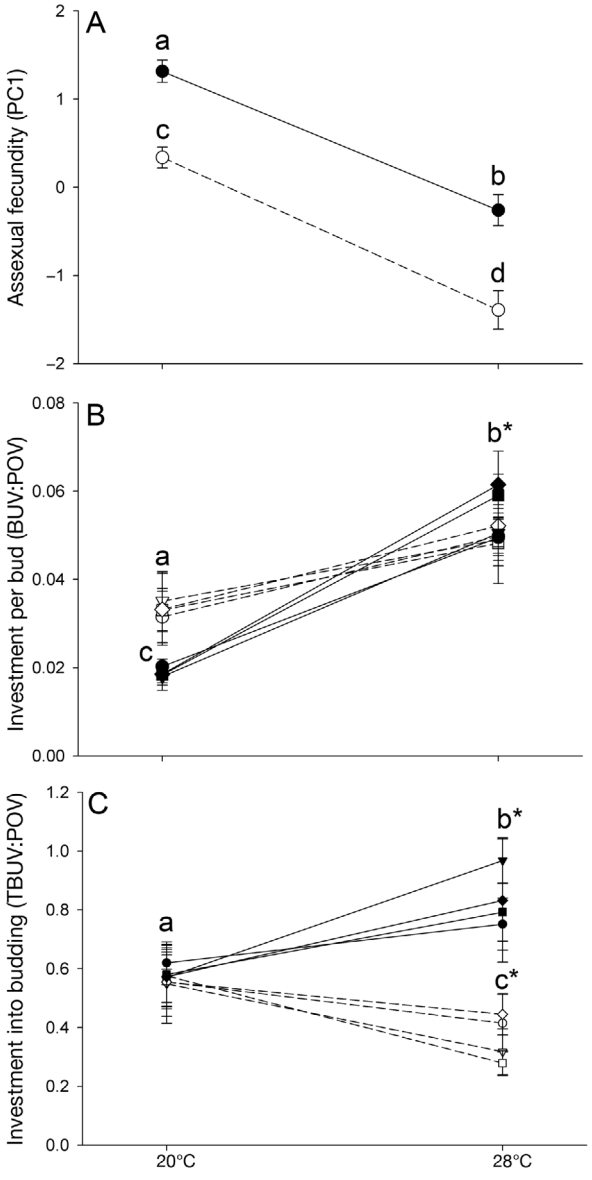

Fig. 4. (A) Asexual fecundity, (B) investment per bud, and (C) total investment into budding in *Aurelia* sp.9 polyps exposed to different environmental conditions. Solid symbols (solid line) indicate polyps fed 4 times wk^{-1}, while open symbols (dashed line) indicate individuals fed twice wk^{-1}. Investment per bud represents the ratio of bud volume to parent polyp volume (BUV:POV), the total investment into budding is the ratio of the total volume of new polyps produced relative to parent polyp volume (TBUV:POV). Different letters indicate significant differences among treatments (Tukey test at $\alpha = 0.01$). Asterisks denote significant effect of family (Fam) within experimental environments. Different symbols indicate different families

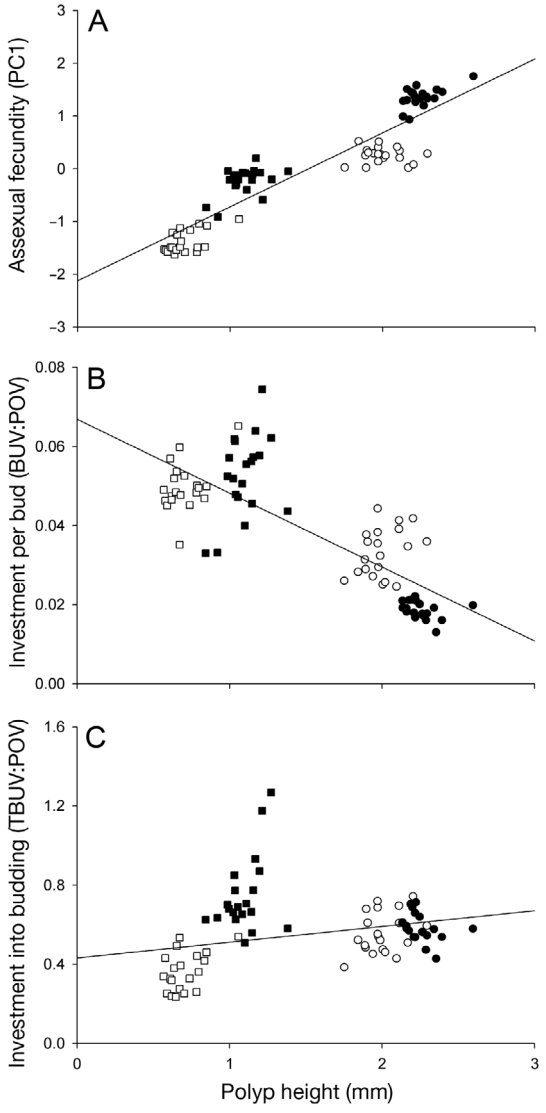

Fig. 5. Relationship between polyp size and (A) asexual fecundity, (B) investment per bud, and (C) total investment into budding. Squares and circles indicate polyps raised at 28 and 20°C, respectively, while solid and open symbols indicate individuals fed 4 and 2 times wk^{-1}, respectively. The line represents the best fit of a linear regression (general linear model). An increase in PC1 indicates an increase in the number of buds $polyp^{-1}$, number of new polyps produced by each polyp, and number of ephyrae stacked per strobila. BUV: mean volume per bud; POV: mean parent polyp volume; TBUV: combined volume of all buds produced per polyp

Polyp morphology vs. asexual propagation

Polyp size was highly positively correlated with asexual fecundity ($F_{1,78} = 295$, r = 0.89, $p < 0.0001$; Fig. 5A). A significantly positive relationship between polyp size and asexual fecundity was also detected within environments (i.e. Temp × Food combinations), except in the 20°C / fed twice wk^{-1} combination (Table S8). On the other hand, polyp size exhibited a significant negative relationship with investment per bud ($F_{1,78}$: 83.4; r = –0.72, $p < 0.0001$; Fig. 5B). Total investment into budding was weakly correlated with

polyp size ($F_{1,78}$ = 8.2, r = 0.31, p < 0.01; Fig. 5C). Further analysis using non-linear regression models (generalized additive model, GAM) revealed a significant curvilinear relationship (inverted 'u-shape') between these 2 variables (GAM: r = 0.76; non-linear p < 0.0001), indicating that total investment into budding was highest in mid-size polyps (Fig. 5C).

Environmentally induced effects on ephyra morphology

The 2 × 2 × 4 ANOVA model did not detect significant main or interaction effects of Fam on the size of ephyrae (Table S9). This factor was then excluded from the model and ephyra size was analyzed using a 2 × 2 ANOVA with Temp and Food as fixed factors. ANOVA detected a significant Temp × Food interaction effect ($F_{1,76}$ = 20.3, p < 0.001) on ephyra size. Ephyrae released from polyps raised at 20°C were significantly larger than their counterparts released from polyps raised at 28°C (Tukey's p < 0.01), regardless of food quantity (Fig. 6A). Within a given temperature, ephyrae from polyps fed 4 times wk^{-1} were significantly larger than those released from polyps fed twice wk^{-1} (Tukey's p < 0.001; Fig. 6A).

Seven PCs were extracted using size-corrected morphological features of ephyrae. The first axis (PC1) explained 95% of the total variation and represented ephyra body shape (Table 2). An increase in PC1 indicated an increase in CDD and inner lappet width (ILW), and a decrease in MLL, DBRL, and DBML. The 2 × 2 × 4 ANOVA model detected a Temp × Food × Fam interaction effect (Table S9) on ephyra shape. Ephyrae released from polyps raised at 28°C had significantly larger CDDs, thicker and shorter marginal lappets, and shorter DBRL and DBML, than individuals released from polyps grown at 20°C, independently of food quantity (Tukey's p < 0.001; Fig. 6B). Within Temp, ephyrae released from polyps fed twice wk^{-1} had significantly higher PC1 scores than their counterparts released from polyps fed 4 times wk^{-1} (Tukey's p < 0.0001; Fig. 6B). In addition, a significant Fam effect (Tukey's p < 0.001) on ephyra shape was detected only in individuals released from polyps raised at 28°C and fed 4 times (Fig. 6B).

Polyp morphology vs. ephyra morphology

Results from the GLM indicated a strong relationship between environmentally induced polyp traits and ephyra traits at release. Polyp size was highly

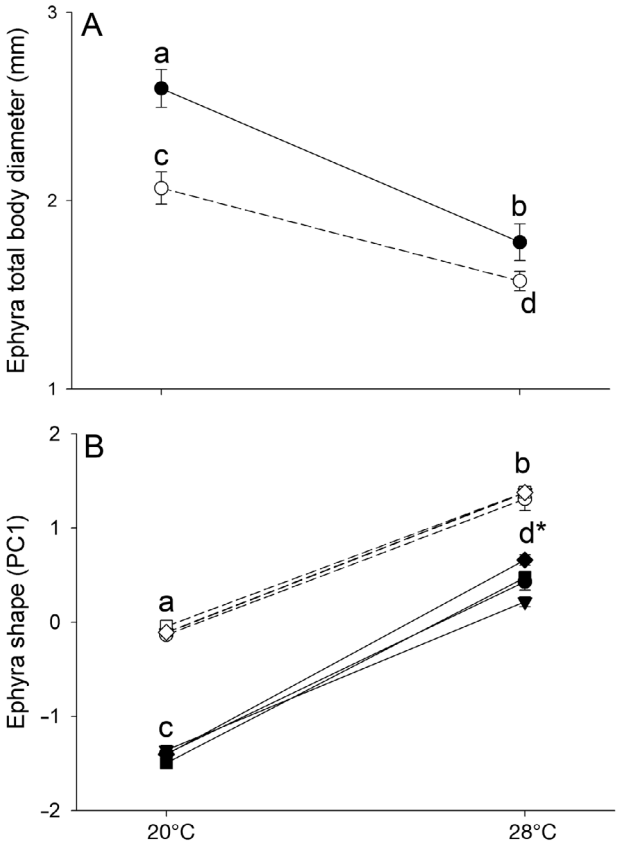

Fig. 6. (A) Size and (B) shape of *Aurelia* sp.9 ephyrae released from polyps raised at different environmental conditions. Solid symbols (solid line) indicate polyps fed 4 times wk^{-1}, while open symbols (dashed line) indicate individuals fed twice wk^{-1}. As PC1 scores increase, marginal lappet length and width, rhopalial lappet length, and distance between rhopalial lappets increase, while central disc diameter, width of the marginal lappet base, and distance between marginal lappets decrease. Different letters indicate significant differences tested by Tukey tests at α = 0.01. Asterisks denote a significant genetic (family) effect within environmental treatments. Different symbols indicate different families

Table 2. Results of the principal component analysis (PCA) showing the loading values for each size-corrected morphological feature recorded on *Aurelia* sp.9 ephyrae released from all polyps raised under different environmental conditions

Ephyra size-corrected features	PC1 (shape)
Central disc diameter (CDD)	−0.93
Marginal lappet length (MLL)	0.89
Marginal lappet base (MLB)	−0.88
Marginal lapper width (MLW)	0.92
Rhopalial lappet length (RLL)	0.97
Distance between marginal lappets (DBML)	−0.88
Distance between rhopalial lappets (DBRL)	0.96
Variance explained (%)	94.90

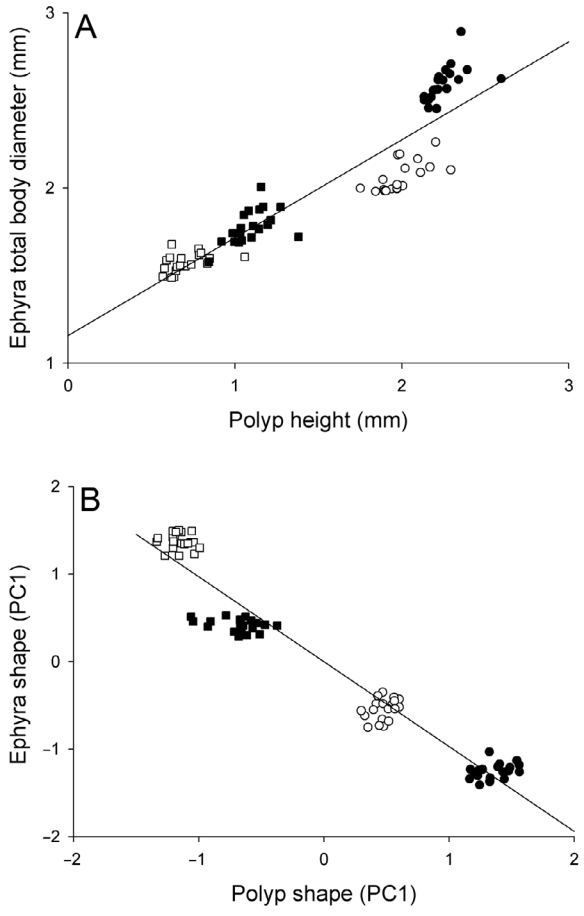

Fig. 7. Relationships between *Aurelia* sp.9 (A) polyp size and ephyra size at release and (B) polyp shape and ephyra shape at release. Squares and circles represent polyps raised at 28 and 20°C, respectively, while solid and open symbols indicate individuals fed 4 and 2 times wk^{-1}, respectively. The line represents the best fit of a linear regression (general linear model). An increase in PC1 scores of ephyra shape indicates in increase in marginal lappet length and width, rhopalial lappet length, and distance between lappet tips, as well as a decrease in relative central disc diameter, marginal lappet width at base, and distance between marginal lappets. As PC1 scores of polyp shape increase, calyx height, calyx width, and stalk width increase, while stalk height decreases

positively correlated to ephyra size (GLM: $r^2 = 0.92$, $p < 0.0001$; Fig. 7A), indicating that larger polyps produced larger ephyrae. Polyp size and ephyra size were also significantly correlated within environments, except in the 28°C / fed twice wk^{-1} combination (Table S10). A strong negative relationship between the shape of polyps and the shape of ephyrae at release was also detected (GLM: $r^2 = -0.94$, $p < 0.0001$; Figs. 7B & 8). No significant relationship was detected between shape of polyps and ephyrae within environments (GLM, $p > 0.05$).

DISCUSSION

Polyp morphology

Aurelia sp.9 polyps displayed ecophenotypic plasticity in body size and shape (calyx, stalk, and tentacles) when exposed to different combinations of temperature and quantities of food. Previous work has shown that jellyfish polyp size is negatively correlated with temperature (Schroth et al. 2002, Willcox et al. 2007, Han & Uye 2010), but positively correlated with an increase in both the frequency and amount of food supplied (Keen & Gong 1989, Ishii & Watanabe 2003, Han & Uye 2010). In this study, the significantly smaller size of polyps raised at high temperatures (28°C) compared to those raised at cool temperatures (20°C), independent of food quantity, suggests that the effect of increased temperature on polyp size was dominant over the effect of increased food supply. The Temperature–Size rule in biology (Ray 1960) states that ectotherms that develop at high temperatures become relatively smaller as adults than individuals that grow at low temperatures (Atkinson 1994, Angilletta & Dunham 2003). Most empirical evidence suggests that increased temperatures increase not only growth rates, metabolism, and oxygen demand (Pauly 1998), but also speed up development, thus shortening development time (i.e. time to reproduction) (Kingsolver & Huey 2008). Therefore, if increasing temperature has a greater effect on development rate than on growth rate, individuals will reach full development at smaller sizes (van der Have & de Jong 1996). Over the course of our experiment, we observed that polyps started budding after reaching the 16-tentacle stage, a trait considered to be indicative of full development (Webster & Lucas 2012).

Budding and strobilation began earlier in polyps raised at high temperature (28°C) than in individuals grown in cool temperature (20°C) independently of food availability, suggesting a faster development rate with increased temperature. Previous studies with polyps of *A. aurita* showed that the 16-tentacle stage is reached earlier in individuals exposed to relatively warm temperatures than in counterparts developing at lower temperatures (Webster & Lucas 2012). In *Aurelia* sp.1, the length of the strobilation preparation period decreased with increased temperature (Wang et al. 2015), while hydrozoan polyps of *Moerisia lyonsi* shortened the time required to produce buds with increased water temperature (Ma & Purcell 2005). Somatic growth in *Aurelia* spp. polyps slows down considerably once asexual reproduction

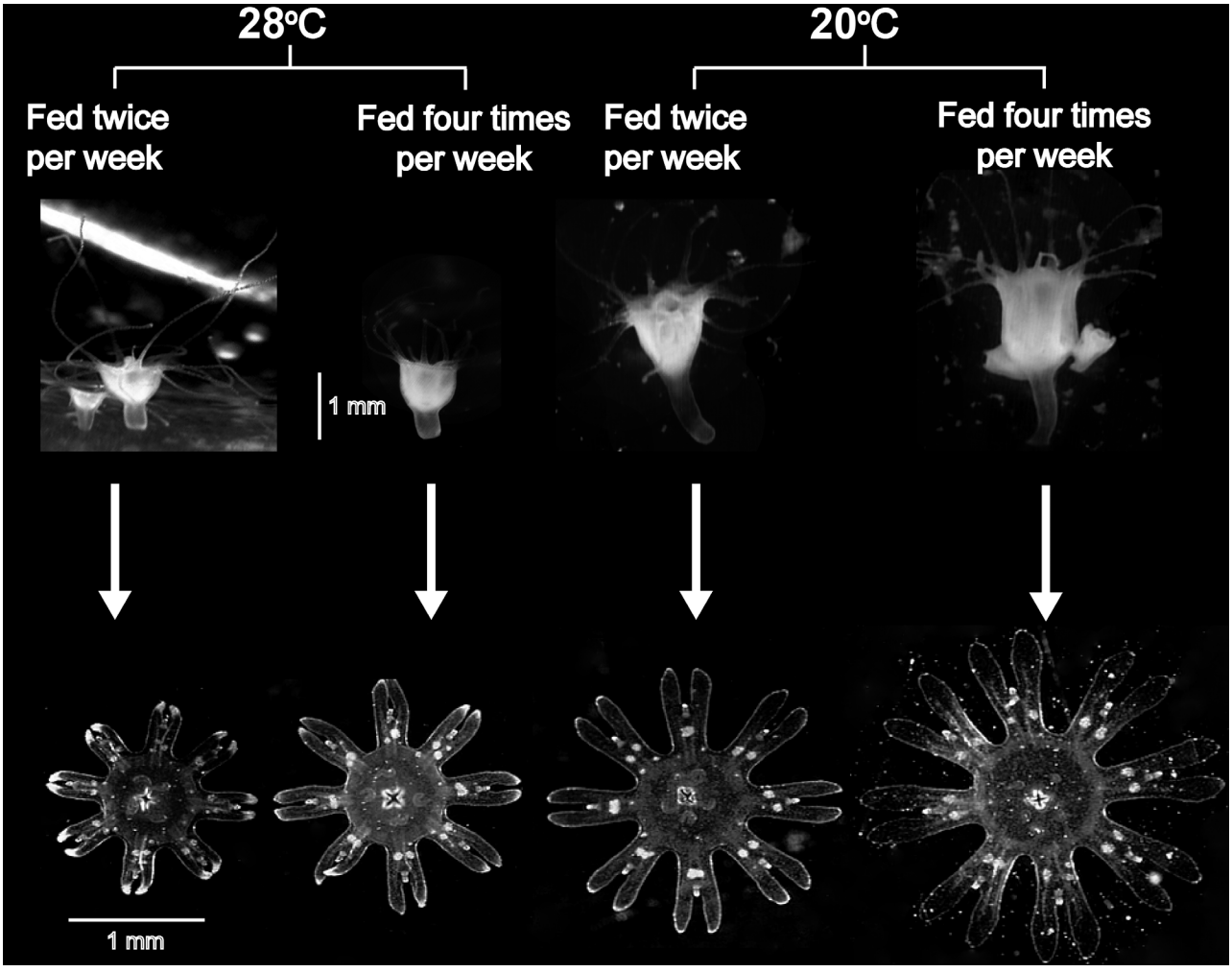

Fig. 8. Summary of environmentally induced morphology in *Aurelia* sp.9 polyps (top row) and the subsequent effects on the morphology of ephyra at release (bottom row)

begins, perhaps due to most energy being allocated into producing new polyps (Willcox et al. 2007, Han & Uye 2010). Thus, it is possible that increased temperature shortens the length of the period during which *Aurelia* sp.9 polyps can allocate most energy into somatic growth, possibly explaining the observed smaller body sizes reached by well-fed polyps exposed to high temperatures, which was also observed by Han & Uye (2010) in polyps of other *Aurelia* species.

Aurelia sp.9 polyps responded to a size constraint imposed by high water temperature and/or low food availability by widening and enlarging their calyxes, which potentially increase feeding surface area. Similar responses were observed in polyps of *A. aurita*: small individuals that were fed infrequently increased their feeding surface area relative to body volume significantly faster than larger counterparts fed more frequently (Keen & Gong 1989). A relatively larger calyx may also facilitate the ingestion of more prey items and/or larger prey, since the calyx can be quite expandable (Schiariti et al. 2008, Webster & Lucas 2012). In addition, experimental studies on other passive suspension feeders, such as anemones, indicate that both the size and the number of prey captured are positively related to the individual feeding surface (Sebens 1981, 1982). Remarkably, in the present study, the size and shape of tentacles exhibited plasticity almost exclusively in response to food independently of body size. In passive suspension feeders, encounters with prey depend on water motion and prey motility (Shimeta & Jumars 1991, Shimeta & Koehl 1997), and rates of prey contact in a given environment greatly depend on the surface area of

the capture apparatus (Sebens 1982). Therefore, it is plausible that by lengthening their tentacles and widening their calyxes, which may in turn increase potential feeding and capture surface, polyps of *Aurelia* sp.9 may be able to maximize rates of encounter with prey in environments with reduced food concentration (Keen & Gong 1989).

Asexual propagation

Asexual propagation in *Aurelia* sp.9 polyps also exhibited ecophenotypic plasticity. Asexual fecundity in this species (i.e. BPP, NPP, and EPS) increased with improved food supply, but declined with increased water temperature. In our experiments, however, the effect of temperature on asexual fecundity appeared to be dominant over the effect of food supply. Polyps raised at 20°C and fed 2 times wk^{-1} still had more buds developing at a time, produced more new polyps, and stacked more EPS than individuals exposed to 28°C and twice the amount of food. There is a consensus from previous studies that budding rates and medusae production increase with increased food supply (Ishii & Watanabe 2003, Ma & Purcell 2005, Han & Uye 2010, Lucas et al. 2012), which is in agreement with the results of the present study as long as the effect of food supply is evaluated taking into consideration the dominant effects of temperature.

The dominant, negative effect of increased temperature on budding rates and number of ephyrae $polyp^{-1}$ observed in this study diverges from the majority of previous laboratory and field studies showing that polyp and ephyrae production increase with increasing water temperatures (reviewed by Purcell et al. 2009, 2012, Lucas et al. 2012). However, Liu et al. (2009) showed that budding rates and ephyra production of *A. aurita* from Taiwan decreased with increased temperature (from 20 to 30°C), and their unexpected results were attributed to high polyp mortality caused by heat stress. In this study, the decreased budding rates and number of ephyrae $polyp^{-1}$ with increasing water temperature could not be attributed to polyp mortality, since survival was high and did not vary significantly among treatments. Therefore, the observed differences in asexual fecundity among treatment in this study were mainly caused by BPP, since budding was the only mode of asexual propagation observed across experimental treatments. Weekly production of NPP $ind.^{-1}$ (Fig. S4) consistently exhibited values similar to half the number of BPP (i.e. BPP/2) across treatments, indicating that all buds growing on a given polyp are released approximately every 2 wk in all environments. These results suggest that individual polyps of *Aurelia* are able to alter the number of buds developing at a time in response to environmental heterogeneity, which translates to different budding rates.

Asexual fecundity correlated positively and strongly with the size of the parent polyp among and within treatments, suggesting that environmentally induced body size likely plays an important role in ultimately limiting asexual reproductive capacity (polyp + ephyra production) of polyps. These results are in line with a few previous studies showing that polyp size is directly related to the number of buds (Keen & Gong 1989, Ishii & Watanabe 2003) and ephyrae (Spangenberg 1968a, Kakinuma 1975, Kroiher et al. 2000, Ishii & Watanabe 2003) produced per individual. A size constraint could also explain why, for instance, well-fed small *Aurelia* sp.9 polyps (raised at high temperature) developed significantly fewer buds, produced fewer new polyps, and stacked fewer EPS than larger individuals (raised at cool temperature) fed half the amount of food. These results are congruent with Arnold's (1983) 'morphology-performance-fitness' hypothesis, which states that the phenotype of an organism is tightly linked to performance (i.e. the capacity to carry out a specific function), which subsequently and ultimately affects individual biological fitness (i.e. the capacity to produce more offspring). We hypothesize that in *Aurelia* sp.9 polyps, environmentally induced morphology is tightly linked to propagation performance (i.e. production of new polyps and ephyrae), which ultimately affects asexual reproductive success (i.e. biological fitness; Ayre 1995)

Investment per bud (i.e. the BUV:POV ratio) decreased as parent polyps became larger. These findings suggest that *Aurelia* sp.9 polyps exhibited different environmentally induced reproductive strategies, with large polyps investing in high numbers of relatively small buds (i.e. r-strategy), and small polyps allocating energy into few, but relatively larger buds (i.e. k-strategy). This apparent trade-off between relative size and number of buds is consistent with life history evolution theory, which states that under optimal environmental conditions individuals will tend to invest energy into more numerous, relatively small offspring. By contrast, under detrimental or sub-optimal conditions, the number of offspring produced will be reduced, but the size of each offspring will tend to increase translating into relatively higher investment per offspring. This

strategy is believed to reduce offspring mortality (Stearns 1992, Roff 2002).

The total investment into budding (i.e. the TBUV: POV ratio) not only displayed a weak correlation with polyp size, but also a reproductive trait significantly affected by genetic/maternal effects, suggesting that investment in asexual reproduction may be under strong genetic control (Pigliucci 2001). Similar results were found by Keen & Gong (1989) in polyps of *A. aurita*, showing that the total volume invested in bud production (i.e. clones) was significantly affected by genotype, and similar results have been observed in anemones (Ayre 1995) and other marine invertebrate taxa such as cladocerans (Barata & Baird 1998) and bryozoans (Hughes 1992). In cnidarians, individual polyp size is proportional to the number of cells (Schaible et al. 2011), and the initial process of budding consists of cell recruitment from a large area of the calyx of the parent polyp to the bud (Hofmann & Gottlieb 1991, Schaible et al. 2011). Those cells are then regenerated once cell recruitment stops, usually right after buds develop their first tentacle rudiments (Otto & Campbell 1977). A minimum number of cells from the parent polyp must be recruited to form a bud (Schaible et al. 2011). Thereby, asexual fecundity may be constrained by environmentally induced body size if small polyps are limited in the number of cells that can recruit into buds compared to larger polyps. Since budding in *Aurelia* polyps occurs only on the calyx (Schiariti et al. 2014), small polyps in this study may have maximized the number of cells that can be recruited to bud formation by enlarging their calyxes (Fig. 3B).

Ephyra morphology

Ephyrae released from polyps raised under different environmental conditions also exhibited morphological differences, suggesting a tight link between polyp traits and ephyra traits (Fig. 7). The size of *Aurelia* sp.9 ephyrae at release was strongly linked to (environmentally induced) polyp size at the onset of strobilation, which agrees with previous studies showing that relatively larger polyps produce larger ephyrae (Spangenberg 1968b, Ishii & Watanabe 2003). More interestingly, released ephyrae also exhibited different shapes. In swimming ephyrae, lappet morphology can compensate for temperature-induced changes in viscosity that would otherwise impede water flow around lappets and reduce propulsion efficiency (Feitl et al. 2009, Nawroth et al. 2010). In the present study, ephyrae released by polyps grown at high temperature (28°C) had smaller gap areas between lappets than individuals released by polyps raised at a cooler (20°C) temperature. Small areas between lappets could potentially benefit swimming performance of ephyrae released in a relatively high-temperature, low-viscosity environment (and vice versa) (Feitl et al. 2009, Nawroth et al. 2010). Therefore, the different morphologies observed in ephyrae released from polyps exposed to different temperatures (and food quantities) perhaps represent an evolved strategy to maximize swimming and feeding performance, and consequently fitness, of young medusae under different environmental conditions. These results, documented for the first time in Scyphozoa, indicate late responses to early environments, which are predictive of future environmental conditions (Relyea 2001).

CONCLUSIONS

Polyps of *Aurelia* sp.9 were highly plastic in terms of morphology (i.e. size and shape) and asexual propagation (i.e. asexual fecundity, propagation strategy) in response to the different environmental conditions tested. Polyp body size limited asexual reproduction, suggesting a potential environmentally induced morphological constraint of asexual fecundity. Changes in polyp morphology were reflected in ephyra morphology, indicating that environmentally induced effects on polyp traits had latent effects on subsequent phases of the life cycle. These results are consistent with empirical evidence from previous studies showing that in species with complex life cycles, metamorphosis is not necessarily a new beginning, and environmentally induced variation in traits during a given phase can be carried over to the next phase (Relyea 2001, Giménez 2006, Pechenik 2006). This study also provides valuable insights into the potential mechanisms of *Aurelia* sp.9 medusae outbreaks in the Gulf of Mexico (Robinson & Graham 2013) and could help to better predict future jellyfish blooms in the region.

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