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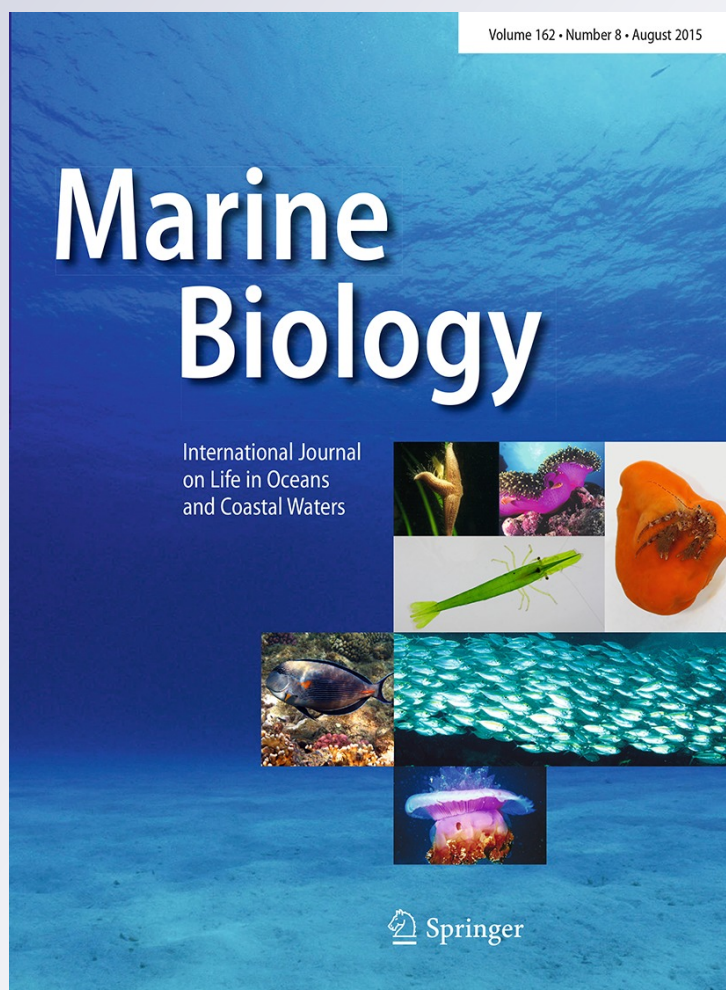
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# Density-dependent effects control the reproductive strategy and population growth of *Aurelia aurita* s.l. scyphistomae

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**Abstract** *Aurelia aurita* s.l. scyphistomae are capable of developing different asexual modes for propagation and thus present a multi-mode reproductive strategy. The reproduction rates and the reproductive strategy they adopt depend on a combination of various environmental parameters. We investigated the *A. aurita* s.l. polyp-to-polyp reproduction strategy and population growth in relation to polyp density. Our results confirmed that density-dependent factors control population growth of *A. aurita* s.l. scyphistomae in three different ways: (1) decreasing the polyp reproduction rate, (2) triggering the production of motile bud-like tissue particles and (3) inducing the detachment of developed scyphistomae. Whereas the decrease in the reproduction rate reduces the number of recruits, the motile particles and the detachment of scyphistomae contribute to

minimizing density-dependent effects by allowing reproductive products and scyphistomae to drift away. Thus, not only are the negative effects of intraspecific competition for space and food diminished but also the potential colonization of new substrates, and further increase in scyphistoma density is favoured on larger spatial scales. The potential capability to switch its polyp-to-polyp reproduction strategy in response to environmental clues and population density may give *Aurelia* high adaptability in the temperate coastal waters where they commonly live and where they may be exposed to wide-ranging and fluctuating environmental variables that affect their survival and longevity. Considering these features, as well as the wide tolerance of *Aurelia* scyphistomae (and medusae) to environmental parameters, it is not surprising that the species/lineages of *Aurelia* are cosmopolitan and exhibit the most frequent bloom events worldwide.

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## Introduction

The moon jellyfish *Aurelia aurita* s.l. (Linnaeus) is the most common scyphozoan species in terms of its cosmopolitan distribution and frequent blooms (Lucas 2001; Purcell 2007; Hamner and Dawson 2009). Problematic blooms of *Aurelia* species (Dawson and Martin 2001; Purcell 2007; Ki et al. 2008; Kogovšek et al. 2010; Ramšak et al. 2012) have been reported from a variety of coastal and shelf marine environments particularly in Europe (Baumann and Schernewski 2012; Malej et al. 2012), Asia (Uye and Ueda 2004) and North America (Greenberg et al. 1996). *Aurelia* species have a metagenetic life cycle comprising an alternation of generations between asexual benthic polyps (i.e., *scyphistomae*) and sexual pelagic medusae (Arai 1997). Whereas the medusae are the “problematic”

and conspicuous stage, the inconspicuous and tiny polyps play a key role in determining the timing and intensity of blooms by producing and releasing ephyrae into the water column through a process known as *strobilation*. Therefore, factors controlling polyp density may influence the magnitude of medusa blooms (e.g., Willcox et al. 2008; Purcell et al. 2009; Jarms 2010; Han and Uye 2010; Lucas et al. 2012).

Regardless of planulae settlement success, polyp density results from the balance between polyp population growth and mortality rates (i.e., *survivorship*; Lucas et al. 2012). Several environmental factors such as temperature, salinity, food supply, light intensity, hypoxia and pH have been reported to affect polyp survivorship (reviewed in Lucas et al. 2012). In addition, it has been suggested that the population growth of *Aurelia* sp. scyphistomae is regulated by a combination of environmental conditions including density-dependent factors like intra- and interspecific competition for space and food (Willcox et al. 2008).

Scyphistomae of the genus *Aurelia* are capable of developing different asexual modes for propagation and so present a multi-mode reproductive strategy (see Schiariti et al. 2014). There are several descriptions of the development of these modes (e.g., Berrill 1949; Kakinuma 1975; Gröndahl 1988; Vagelli 2007; Adler and Jarms 2009; Han and Uye 2010; Schiariti et al. 2014; Melica et al. 2014). However, environmental control over the number and type of reproduction modes displayed and their relative importance to polyp density (i.e., *reproductive strategy*, see Schiariti et al. 2014) are very poorly understood. It has been observed that *Aurelia* sp. scyphistomae reach highest densities at “warm” temperatures (ca. 20–25 °C) and with a “high” food supply (Willcox et al. 2008; Han and Uye 2010; Schiariti et al. 2014) colonizing available substrate mostly by means of non-motile buds (NMB) and stolons (ST) (Schiariti et al. 2014; Melica et al. 2014). In addition, density-dependent effects appear under space-limiting conditions, lowering the population growth of *Aurelia* sp. (Coyne 1973; Willcox et al. 2008). On the other hand, under poor feeding conditions not only does population growth sharply diminish (through reduction in reproduction rates; Schiariti et al. 2014) but also the reproductive strategy is modified because encystment is triggered (Han and Uye 2010; Thein et al. 2012). Therefore, it seems that different combinations of temperature, food supply and polyp density affect not only reproduction rates but also the reproductive strategy they adopt.

In addition to the NMB, ST and podocysts (POD), *A. aurita* s.l. also develops motile bud-like tissue particles (MP) (Vagelli 2007; Adler and Jarms 2009). In contrast to the NMB and ST, where new polyps remain attached close to the mother polyp, MP are released before polyp development and may swim, or drift, colonizing more distant sites.

Therefore, this mode represents a strategy to gain dispersion, thereby reducing the negative effects of competition for space and possibly also for food. However, very few studies reported the presence of MP and, among them, only Schiariti et al. (2014) tested the possible effects of environmental conditions on MP specific production rates. They found that the production of MP of different *Aurelia* species was not negligible regardless of food supply and temperature (i.e., between 15 and 25 °C).

Based on the hypothesis that the production of MP is triggered under space-limiting conditions (Schiariti et al. 2014), we aimed to investigate the effects of polyp density on population growth, polyp-to-polyp reproduction rates and asexual reproduction strategy of *A. aurita* s.l. The null hypotheses were that polyp density does not affect (1) population growth of *A. aurita* s.l. polyps, (2) the total number of reproductive products developed per polyp (i.e., reproduction rates) or (3) the proportions of the types of each asexual product.

## Materials and methods

Fifteen live *Crassostrea gigas* oysters with attached *Aurelia aurita* s.l. polyps were collected by scuba diving from dock pillars in the Port of Koper, Slovenia (45.5648°S, 13.7446°E), at depths between 4 and 5 m. Once in the laboratory of the Marine Biology Station in Piran Slovenia, oysters were opened and cleared of the soft body part. Once the shells were separated, the flattest empty ( $n = 5$ ) and the flattest rich ( $n = 5$ ) in *A. aurita* s.l. polyps were selected and placed in an aquarium with freshly collected seawater with similar temperature (9 °C) and salinity (37) as the site of sample collection. They were maintained under light aeration. Since the shells came from an environment characterized by high sedimentation, it was chosen to not keep samples in the same water for avoiding hypoxic conditions. The five oysters rich in polyps were assigned to high-density treatment (HD). On the other hand, the five empty oysters were placed in a beaker filled with marine water. Then, 10 polyps previously detached from another oyster were added using a plastic pipette to each beaker. Scyphistomae were allowed to reattach to the empty oyster and acclimate to the new experimental conditions for 7 days. These oyster shells were assigned to low-density treatments (LD). The number of attached polyps at the beginning of the experiment varied between 186 and 244 for HD treatments and between 1 and 5 polyps per oyster in the LD ones. Beakers were kept under dark conditions except during observation and manipulation times which never exceeded 40 min.

Although there were other organisms attached to the oysters (mostly algae), interspecific competition was considered of minimal impact. Most of the algae died within



a few days of the start of the experiment, and no other organisms developed during the experimental period. The 10 oysters (five HD + five LD) were placed individually in glass beakers, and the beakers were maintained in a temperature controlled chamber for another acclimation period of 9 days. The oysters, fixed by rubber bands tied to wooden sticks, hung down from the top of the beaker and were completely submerged in 250 ml of glass fiber filtered (GF/F pore size 0.7  $\mu\text{m}$ ) sea water. Beakers were covered with plastic wrap to avoid evaporation. During the entire acclimation period, polyps were not fed. The temperature was increased to 22 °C by raising it 2 °C per day and salinity was lowered to 34 by dripping distilled water during the whole acclimation process. No aeration was provided during the experimental period. Experimental conditions (temperature, salinity, food supply and darkness), proven to be favorable for *Aurelia scyphistomae* reproduction (Schiariti et al. 2014), were chosen.

The experiment lasted for 42 days. Polyps were fed twice weekly with newly hatched *Artemia* nauplii *ad libitum*. The polyps were fed for 3 h, after that time seawater, debris and uneaten food were discarded and replaced with filtered seawater at the conditions described above. The presence in all cases of uneaten food items after feeding periods guaranteed *ad libitum* conditions in all experimental units.

Immediately prior to each feeding event (i.e., twice weekly), the following response variables were registered: (1) polyp density (PD): number of polyps per  $\text{cm}^2$ ; (2) observed asexual reproduction modes; (3) number of total reproductive products; (4) number of each type of reproductive product; (5) number of polyps out of original substrate (i.e., the outer/convex side of the shell = unattached polyps + polyps attached to the inner/concave side of the shell + polyps attached to the bottom or walls of the beaker).

Data regarding number of polyps and reproductive products were recorded by counting directly under a stereoscope for each replica of LD treatment, whereas for replicates of HD treatment, three pictures were taken before feeding using the compact camera Canon PS ELPH 300 HS. The polyps and reproductive products were counted from photographs as described in Melica et al. (2014) using the public domain image processing program ImageJ provided by WCIF (Abramoff et al. 2004). The three counts per oyster were averaged. Although the procedure of counting the polyps was different between the treatments, oysters from the two treatments were agitated equally. At the end of the experiment, the oysters were photographed outside the water beside a ruler and the area was calculated using ImageJ. Since the flattest oysters were chosen at the beginning of the experiment, PD (# of polyps  $\text{cm}^{-2}$ ) was calculated by dividing the number of polyps by shell area [mean

area  $\pm$  SD:  $28.16 \pm 3.51 \text{ cm}^2$  (LD);  $27.68 \pm 1.62 \text{ cm}^2$  (HD)]. Differences in shell area between treatments were not significant (Student *t* test;  $P > 0.05$ ). Variables (3) and (4) were utilized to estimate the overall reproduction rates (Rr) and specific reproduction rates, respectively. These rates were calculated by summing up the total number of reproductive products and dividing by the corresponding number of polyps.

Univariate repeated measures ANOVA was used to examine the effect of polyp density on (1) rate of population growth and (2) the percentage of migrant polyps. Variables were transformed ( $\log_{10}$ ) for analysis. One-way ANOVA was performed to examine the effects of polyp density on reproduction rates. If the overall ANOVA results were significant, Bonferroni's pairwise comparisons were made. Assumptions for normality and heterogeneity of variance of the data were tested in all cases using Kolmogorov–Smirnov and Bartlett, respectively.

The asexual reproduction modes and reproductive particles were identified following the description of Adler and Jarms (2009) and Schiariti et al. (2014). Although typical lateral budding and lateral budding by means of stolons were observed in all replicates, they were pooled as NMB because the discrimination among them was inaccurate in HD treatments. Furthermore, we considered both modes as ecologically equivalent since they produce sessile buds right beside the mother polyp and appeared to respond to the same environmental clues (see Han and Uye 2010; Schiariti et al. 2014). Given the scarce information available about this reproductive mode, some MP were separated into a petri dish using a pipette in order to make detailed observations of their development and to confirm identification. Petri dishes were maintained under the same temperature and salinity conditions described above.

The term *population* might be controversial for species with metagenetic life cycles. To avoid misinterpretations, we considered the scyphistomae population as all the polyps attached to a specific substrate or area. In our study, population growth is equivalent to the variation through time in the number of polyps attached to the same oyster shell.

## Results

### Polyp density (PD)

The effects of PD on population growth were significant (*repeated measures ANOVA*,  $F(1, 16) = 79.28$ ,  $P = 0.00002$ ). PD increased in LD from, on average, 0.1 polyps  $\text{cm}^{-2}$  at the beginning to 1.7 polyps  $\text{cm}^{-2}$  at the end of the experiment. In contrast, a slight decrease in PD (from 8 to 6 polyps  $\text{cm}^{-2}$ ) was observed in HD treatments

during the first week of the experiment. After that, the average PD remained between 5 and 6 polyps  $\text{cm}^{-2}$  (Fig. 1).

Scyphistomae were observed in all cases under good/healthy conditions with no evidence of shrinkage of their bodies or tentacles, suggesting mortality was negligible in all treatments.

### Asexual reproduction modes

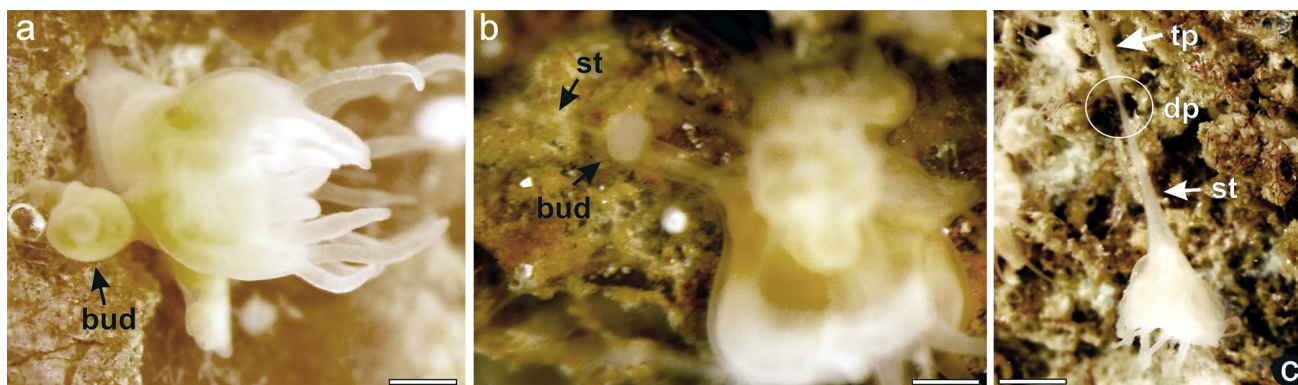
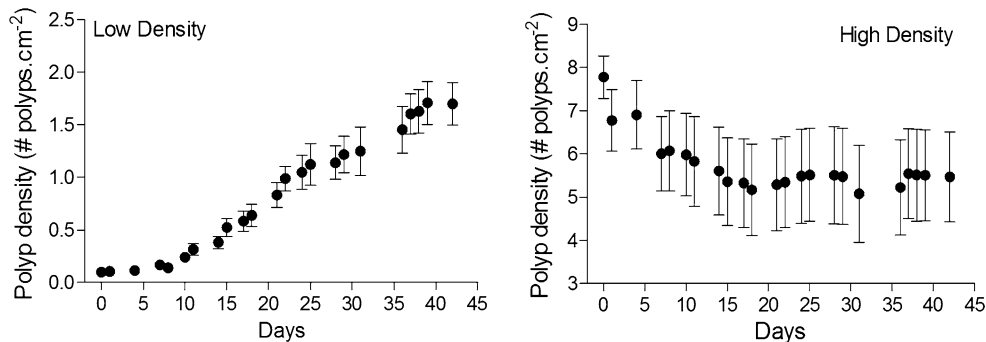
Three polyp-to-polyp asexual reproduction modes were observed: non-motile buds (NMB) (Fig. 2a, b), reproduction from parts of stolons/stalks (ST) (Fig. 2c) and motile bud-like tissue particles (MP) (Fig. 3). MP development began at the junction point of calyx to stalk (Fig. 3a). Its appearance and size was variable but mostly spherical reaching from 0.3 to 0.9 mm in diameter. Sometimes cylindrical or pear-shaped buds were observed (Fig. 3b–d). Detachment from the mother polyp always occurred prior to further development. Once released, MP presented a rotating movement and low motility mostly sinking to the bottom of the beaker in the following hours probably due to the still water conditions. Within 4–7 days, proboscis and tentacles appeared (Fig. 3e). Formation of

the stalks occurred after 3–10 days. Fully developed polyps bearing more than 20 tentacles appeared between 14 and 19 days after detachment of MP. No strobilation was observed.

### Reproduction rates (Rr) and polyp-to-polyp reproductive strategy

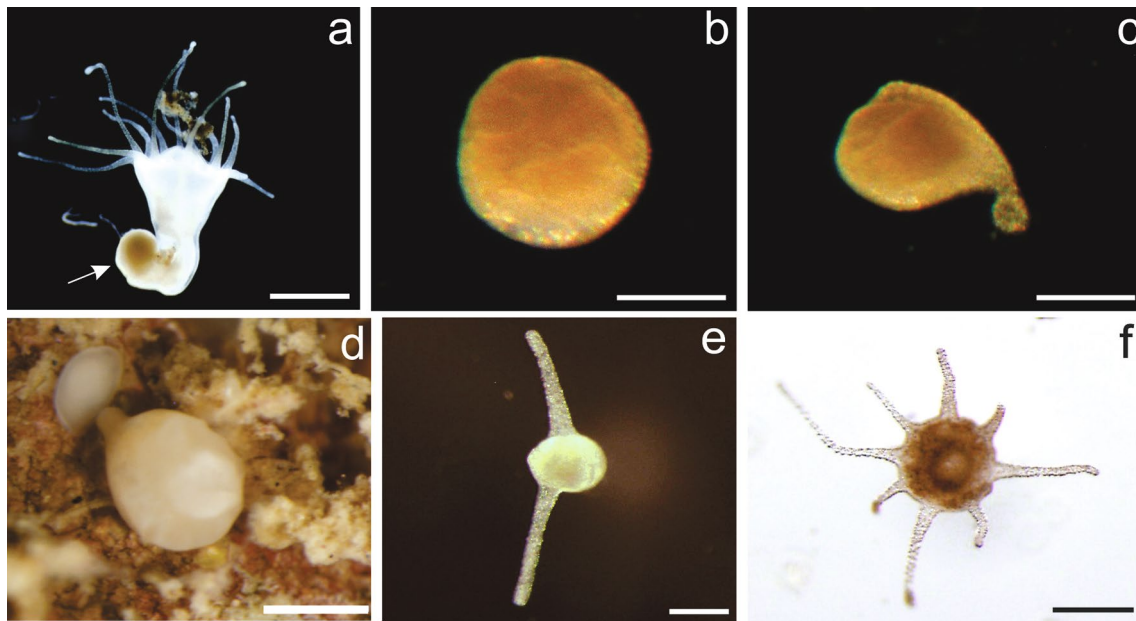
The effects of polyp density on reproduction rates of *A. aurita* s.l. were significant (ANOVA,  $F(7, 32) = 9.11$ ,  $P = 0.000004$ ). Polyps reached higher Rr in LD than in HD (Bonferroni's pairwise comparison,  $P = 0.0017$ ) (Fig. 4). In both treatments, NMB were the most frequent mode utilized for polyp-to-polyp reproduction (Bonferroni's pairwise comparison, all  $P < 0.0017$ ) (Fig. 4). However, it is worthy of note that MP were almost exclusively observed in HD treatment. In addition, MP were first observed within the first week in HD treatment, whereas they appeared after 30 days in LD treatment. The production of MP was significantly higher in HD (18 % of the total reproductive particles produced) than in LD (2 % of the total reproductive particles produced) (Bonferroni's pairwise comparison,  $P = 0.03$ ) (Fig. 4).

**Fig. 1** Effects of polyp density on the population growth of *Aurelia aurita* s.l. polyps (mean  $\pm$  SD)



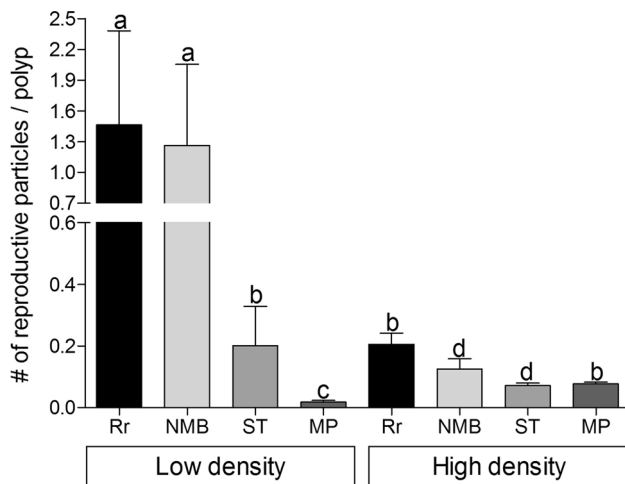
**Fig. 2** *Aurelia aurita* s.l. scyphistoma. Non-motile buds (a typical lateral budding; b lateral budding by means of stolons) and c reproduction from parts of stolons/stalks. st stolon, dp disruption point at

the stolon, tp tissue particle that will remain after stolon disruption. Scale bars = 0.5 mm (a, b) and 0.8 mm (c)

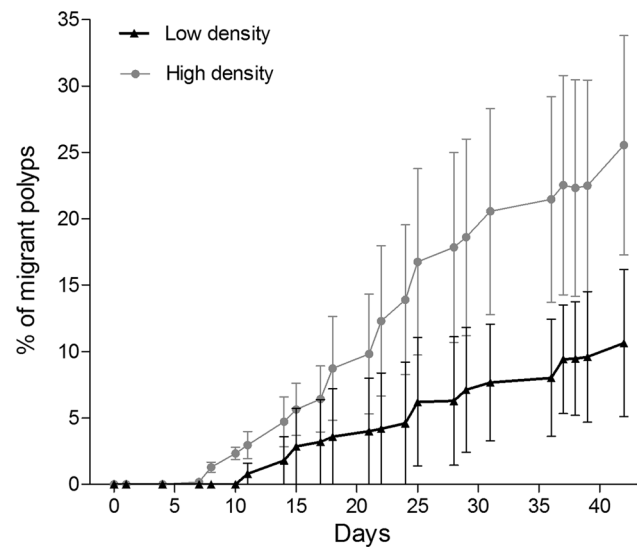


**Fig. 3** *Aurelia aurita* s.l. scyphistoma. Development of motile bud-like tissue particles. Bud before detachment (a), newly released bud (b), recently settled bud (c, d), newly scyphistoma with developing

tentacles (e, f). Scale bars = 2 mm (a), 0.3 mm (b–d), 0.5 mm (e, f). Picture a: Alejandro Vagelli



**Fig. 4** Effects of polyp density on the overall (Rr) and specific (NMB, ST, MP) reproduction rates of *Aurelia aurita* s.l. scyphistomae. The mean numbers (+SD) are represented. NMB non-motile buds, ST reproduction from part of stolons/stalks, MP motile bud-like tissue particles. Different letters (a, b, c, d) express significant differences (Bonferroni's post hoc comparisons,  $\alpha = 0.05$ )



**Fig. 5** Variation of the percentage of migrant polyps (number of migrant polyps standardized to the numbers of polyps attached to the original shell valve) over time. The mean (+SD) numbers are represented. See details in the text

### “Migrant” polyps

In both treatments, some fully developed polyps were observed attached to the inner/concave side of the valve, to the bottom and walls of the beaker, or unattached. These polyps simply detached from the outer/convex side of shells and drifted within the beaker till finding a new

attachment place. Migrant polyps, capable of feeding while drifting, maintained their normal morphology, body shape and tentacles.

The percentage of migrant polyps increased in both treatments during the experimental period (*repeated measures ANOVA*,  $F(1, 16) = 22.18$ ,  $P = 0.00152$ ) (Fig. 5).

However, they appeared sooner and reached higher numbers in HD treatments than in LD (*repeated measures ANOVA*,  $F(1, 16) = 10.03$ ,  $P = 0.0132$ ) (Fig. 5).

## Discussion

Our results confirm that polyp density controls the population growth of *A. aurita* s.l. scyphistomae in three different ways: (1) by slowing down reproduction rates; (2) by triggering the production of motile bud-like tissue particles; (3) by inducing the detachment of developed scyphistomae. Whereas the decrease in Rr reduces the number of new recruits to the substrate, the production of MP and the detachment of polyps contribute to minimizing the density-dependent effect by allowing reproductive products and polyps to drift away. This way, not only are the negative effects of intraspecific competition for space and food diminished but also the potential colonization of new substrates, and a further increase in scyphistoma density away from the source is favored on larger spatial scales. The increased population size of the benthic stage would, once strobilation is triggered, enhance the magnitude of medusae blooms by increasing strobilation rates through a higher number of the potential strobilae.

Different environmental factors have been identified as influencing the development of new scyphistomae in *Aurelia* species/lineages. Among them, temperature and food availability appear to be the most important factors that synergistically affect scyphistoma reproduction and, subsequently, population growth in a positive or a negative way (see Schiariti et al. 2014). In general, polyp-to-polyp reproduction rates increase with temperature and food supply (Lucas 2001; Lucas et al. 2012; Purcell et al. 2012; Pascual et al. 2014). Within optimal ranges of these two key parameters, *Aurelia* scyphistomae propagate almost exclusively through NMB and ST, colonizing bare substrate very rapidly (Han and Uye 2010; Schiariti et al. 2014; Melica et al., 2014; present study). However, available substrate, i.e., room for expansion, soon reaches a limit. Therefore, it is likely that availability of habitable space controls population size, reproductive output and survival of scyphistomae as it does for many other sessile marine invertebrates (Purcell 2007; Müller and Leitz 2002).

The few studies that have considered scyphistoma density (or inversely, substrate availability) as an experimental factor found that population growth of *Aurelia* scyphistomae is limited by substrate availability even under optimal values of temperature and food supply (Chiba 1969; Coyne 1973; Willcox et al. 2008; present study). In this way, dense aggregations of polyps have been found to inhibit “budding” (interpreted as a synonym of asexual reproduction) (Chiba 1969). Accordingly, Willcox et al.

(2008) observed that density-dependent factors control “budding” and recruitment of new scyphistomae to the substrate when populations were dense and space limiting. Moreover, Coyne (1973) reported that *Aurelia* scyphistomae populations with high initial density had lower growth rates than those with low initial density exactly as we observed in our experiment. The reasoning is quite simple and suggests that, if there is no habitable substrate, there is no space for new polyps. As a consequence, polyp-to-polyp reproduction rates and population growth may decline.

Coyne (1973) reported that *A. aurita* scyphistoma population grows following a trend toward a sigmoid curve. Based on the same experimental data set analyzed in the present study, Melica et al. (2014) demonstrated that population growth of *A. aurita* s.l. scyphistomae can be modeled by the basic density-dependent logistic (Verhulst) ordinary differential equation and that polyp density grows until reaching what can be considered as the *carrying capacity* of the population (Melica et al. 2014) (see Fig. 1). The gathered evidence suggests that once the carrying capacity of the population is reached, available substrate becomes a limiting factor. At this point, Coyne (1973) speculated that reduction in polyp population growth at higher densities appears to be mediated by some soluble substance produced by polyps themselves and released into the medium thus hampering population growth by inhibiting reproduction rather than by inducing regression of already formed polyps. Although we did not test for the presence of chemical triggers, we demonstrated that density-dependent factors control not only reproduction rates but also the reproductive strategy adopted by scyphistomae to develop new polyps and its capacity of avoiding crowded areas by just detaching from the substrate. Although NMB and ST were the most frequent modes in both treatments, it is evident that the MP were almost exclusively produced in HD treatment. Furthermore, while they were first observed within the first week in HD treatment, they were noticeable only after 30 days in LD treatment. Furthermore, the same response was observed for the migrant polyps which appeared before and reached higher numbers under space-limiting conditions.

Benthic sedentary invertebrates, among which scyphistomae are included, are most frequently found in dense clusters. These “colonies” are formed as a result of planulae preferences for settling in particular substrata, and by the asexual propagation of initial settlers. This gregarious behavior has several advantages, but it is not without cost (Müller and Leitz 2002). The benefits of gregariousness for scyphistomae could be at least twofold: (1) polyps reproducing by non-motile particles (NMB and ST) remain in a habitat that is more likely to support growth than if they are released and drift away;



(2) proximity increases the chances of synchronize strobilation with further benefits for pelagic stages success. On the other hand, among the disadvantages we can include that (1) predators find them faster and infections spread readily through the community and (2) polyps must compete for food reducing individual fitness. In this way, the production of MP and the detachment of polyps produce a decrease in polyp density—on a local scale—which may balance the number of polyps around a density equilibrium, given by the specific carrying capacity, and so reach a trade-off between advantages and costs. It is interesting to note that if additional bare substrate is deployed, the density-dependent factor disappears and reproduction rates return to “normal” values (Willcox et al. 2008). In this way, the increased habitable substrate area may disrupt the equilibrium toward the initial condition of high reproduction rates dominated by the non-motile particles.

The multi-mode reproduction strategy allows *Aurelia* to colonize the available substrate rapidly when conditions are favorable (the development of NMB and ST), to encyst and withstand starvation and other adverse conditions (e.g., the presence of predators, see Lucas et al. 2012) (podocyst formation) and to develop MP or to detach to facilitate dispersion and avoid the disadvantages of too dense areas mentioned above. The potential capability to switch its polyp-to-polyp reproductive strategy in response to environmental clues and population density gives *Aurelia* high adaptability in the temperate coastal waters where they commonly live and where they may be exposed to wide-ranging and fluctuating biotic and abiotic environmental variables that affect their survival and longevity. *Aurelia* scyphistoma strobilate repeatedly, are perennial and can produce new polyps and medusae for years (Arai 1997). During each strobilation event, polyps can produce as many as 40 ephyrae per polyp (Lucas et al. 2012; Pascual et al. 2014), and it is thus believed that asexual reproduction is a key driver of medusae blooms in coastal areas. Considering these features, in addition to the wide tolerance of *Aurelia* scyphistomae (and medusae) to environmental parameters (Lucas 2001; Lucas et al. 2012), it is not surprising that the species/lineages of *Aurelia* are cosmopolitan and exhibit the most frequent bloom events.

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