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Contribution to the Theme Section 'Jellyfish bloom research: advances and challenges'

Seasonal fluctuations in population dynamics of *Aurelia aurita* polyps *in situ* with a modelling perspective

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ABSTRACT: Benthic polyps are important in jellyfish outbreaks, which seem to have become more intense and are causing increasing problems for humans. We studied annual and seasonal changes of the moon jellyfish, *Aurelia aurita* s.l., polyp population dynamics *in situ*. Over 3 yr, we took monthly photographs to quantify the abundance and occurrence of asexual reproduction of polyps attached underneath oysters on pillars in the Port of Koper (Slovenia) and simultaneously collected data on seawater temperature, salinity, light radiation and pH to test the effects of abiotic factors. The 3 yr *in situ* study enabled us to establish a clear trend in seasonal dynamics in density and asexual reproduction of polyps. Polyp density averaged ~21 ± 6 polyps cm^{-2}, differed among seasons and increased with increasing temperature and decreasing salinity. Several hypotheses were tested. Asexual reproduction (buds and stolons) was highest when temperatures were above 25°C, but was significantly lower at high polyp density (≥30 polyps cm^{-2}). Most strobilae, which asexually produce medusae, were formed when temperature was <15°C. The *in situ* data enabled us to estimate the average monthly growth rate r (1.16 mo^{-1}) and carrying capacity K (37.4 polyps cm^{-2}) using a (mechanistically derived) non-autonomous logistic model with seasonality in asexual reproduction rate (λ). This model enables calculation of average life-history parameters of all polyp populations *in situ* with seasonal forcing and permits comparisons among populations to understand environmental and anthropogenic effects on polyp populations and the resulting intensity and frequency of medusa outbreaks.

KEY WORDS: Jellyfish bloom · Polyp density · Asexual reproduction · Scyphozoa · Population model · Carrying capacity · Growth rate · Northern Adriatic

INTRODUCTION

The underlying conditions in the abiotic and the biotic environment greatly affect the population dynamics of *Aurelia aurita* polyps (reviewed by Lucas et al. 2012). When environmental variables exceed important biological bounds for the population in a natural environment, blooms may occur (Denny et al. 2009, Benedetti-Cecchi et al. 2015). Blooms of *A. aurita* s.l. medusae have been regularly present in the northern Adriatic Sea over the last 200 yr; in recent decades, their frequency and intensity have increased (Kogovšek et al. 2010, Malej et al. 2012).

Jellyfish blooms can affect ecosystem dynamics (Purcell et al. 2010, Uye 2011, Tinta et al. 2012) and services that are linked to socio-economic benefits or disturbances (Graham et al. 2014), which in turn directly or indirectly contribute to the intensity and

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frequency of the blooms (Arai 2001, Richardson et al. 2009, Purcell 2012, Malej et al. 2014). Most scyphozoan medusa populations arise each year from the polyp populations. There are only a few studies that exist about the factors that determine the abundance of polyps, particularly for polyps in a natural environment over a long period of time (Miyake et al. 2002, Willcox et al. 2008, Purcell et al. 2009, Malej et al. 2012, Makabe et al. 2014). The scarcity of this information is mostly due to the unknown locations for polyps of most scyphozoan species (van Walraven et al. 2016) and the challenges of long-term monitoring.

Polyps *in situ* can be found on natural hard substrates (Russell 1970, Miyake et al. 2004) as well as on artificial ones (Hernroth & Gröndahl 1985a,b, Hoover & Purcell 2009, Feng et al. 2017). The planula larvae of jellyfish strongly prefer the undersides of substrates for settlement, which is beneficial for survival and reproduction for developed polyps (Holst & Jarms 2007). The polyp generation has a variety of asexual reproductive modes, including vegetative budding, stolon formation and pedal laceration, by which they enlarge the population and can influence the intensity of blooms through strobilation that liberates small medusae (ephyrae) (Berrill 1949, Kakinuma 1975, Arai 1997, reviewed by Lucas 2001). A polyp in the genus *Aurelia* can strobilate several times and produce up to 30 ephyrae in one strobilation process (Berrill 1949).

Polyps *in situ* are exposed to a seasonally varying environment, where the density-independent and -dependent factors may vary considerably between seasons and years (Miyake et al. 2002, Willcox et al. 2008, Purcell et al. 2009). Temporal and spatial variability of density-independent or environmental factors such as temperature (Miyake et al. 2002, Willcox et al. 2007, Purcell 2007, Purcell et al. 2009, Feng et al. 2017), salinity, temperature–salinity interaction (Purcell 2007), food variability (Hernroth & Gröndahl 1985b), and dissolved oxygen concentration levels (Ishii et al. 2008) affect the asexual reproduction rates. The asexual reproduction rates can differ among populations of *A. aurita* (Pascual et al. 2015), probably due to genetic differentiation and local adaptation (Dawson & Martin 2001). Additionally, differences in the amount and timing of asexual reproduction types may reflect on the polyp population density (Willcox et al. 2008, Purcell et al. 2009, Hočevar 2013). When the density of the population approaches the carrying capacity (Melica et al. 2014, Schiariti et al. 2015), the density-dependent processes of intraspecific competition for space, such as inhibition of budding (Chiba 1969), competition for food (Willcox et al. 2008), and cannibalism (Kakinuma 1975, Gröndahl 1988) become stronger.

Moreover, ecological populations are dynamic systems and state variables, such as population density, change with time (Turchin 1995). In mechanistic modelling, in which changes in population dynamics are based on processes at an individual-based hierarchical level (Geritz & Kisdi 2004, Eskola & Geritz 2007, Eskola 2009), known density-independent and -dependent mechanisms influencing individuals can be incorporated with existing data to estimate parameter values to describe these dynamics (Otto & Day 2007). We used a non-autonomous logistic equation, based on a mechanistically derived (autonomous) logistic model to estimate the average annual growth rate (r) and carrying capacity (K) of *A. aurita* polyps that were observed for 3 yr *in situ*. We primed the model by previously testing several null hypotheses (H_0) on underlying density-independent and -dependent mechanisms of polyp population dynamics.

MATERIALS AND METHODS

Field work

The study was conducted in the Bay of Koper (Slovenia) in the northern-most part of the semi-enclosed Adriatic Sea, where *Aurelia aurita* s.l. polyps were found *in situ*. The polyp population we studied was located on one of the 575 pillars in the Port of Koper. The pillar is covered by numerous oysters *Crassostrea gigas*, under which the polyps are attached.

We followed polyps on the lower surface of 4 marked oysters between March 2010 and March 2013. Each oyster had a code that represented its depth (in metres) and whether its attachment was protected (P) or unprotected (U). Marked oysters were located at depths between 2 and 6 m (Table 1). Oysters O2U, O4U, and O6U were attached on the

Table 1. Position, depth and photographed surface area of each oyster with the observed population of *Aurelia aurita* s.l. polyps. Codes of the oysters indicate depth (2, 4, 6 m) and protected (P) or unprotected (U) location

Oyster	Depth (m)	Area (cm^2)
O2U	2.2	45
O4U	4.1	49
O6U	6	55
O2P	2.2	42

western or 'front' side of the pier, at depths of 2, 4, and 6 m, respectively. Those oysters faced the open sea and were more exposed to external disturbances (unprotected, U). Oyster O2P was attached on the eastern or 'inside' side of the pier, facing the coastline and was more protected (P) than the others.

The entire undersurface area of each marked oyster was photographed once a month (except on June 2010 and September 2010). Underwater photographs were taken using a Nikon D2X camera with 60 mm/macro lens, SEALUX housing. The visibility underwater varied among months, presumably due to water quality, which necessitated photographs being taken at different focal depths. Photographs had the dimensions of 4288 × 2848 pixels, and the clearest images were selected and analysed with Adobe Photoshop CS5. For better visualization, magnification of photographs on the computer screen was necessary. The polyps were counted by eye always by the same person.

We collected data on (1) the abundance of single polyps attached to each oyster, (2) the number of polyps with asexual forms of buds and stolons, and (3) the number of strobilating polyps (strobilae). When visibility was too poor to accurately determine if a polyp was a stolon, strobilae, or budding polyp, we counted it as a polyp without specifying any asexual form. A ruler was placed next to each photographed oyster, enabling us to convert pixels into centimetres and calculate the surface area of the oyster and density of the polyps per unit area (cm^2).

To test the accuracy and variance of the counts, polyps of 3 replicate photographs from different focal depths for each oyster were counted in 2 periods: November 2010 to January 2011 and March 2012 to August 2012. The number of polyps counted among the replicates were not significantly different (1-way analysis of variance, ANOVA) ($F_{2,129} = 0.32$, $p = 0.726$). The rest of the photographs of each observed oyster for each month were counted once. For the purpose of the analysis, the missing data for June 2010 and September 2010 were replaced by the arithmetic means of data for the adjacent months (May and July 2010 and August and October 2010, respectively). For the purpose of interannual and seasonal dynamics analyses, data of all locations were pooled. For all data, additional separate analyses between sides of the pillar were conducted.

Temperature, salinity, pH, fluorescence, and photosynthetically active radiation (PAR) measurements were recorded using a conductivity-temperature-depth data profiler (CTD, SeaBird) concurrently with the photographs. We tested temperature from the CTD against data from a nearby oceanographic station in Koper that monitored temperature continuously. The high correlation between those temperatures ($R^2 = 0.99$) enabled us to use temperature data from the Koper station in the analysis.

Data analysis

Empirical data were tested for normality and equality of variances. The variables that did not pass the Shapiro-Wilk test (Shapiro & Wilk 1965) for normality were $\log_{10}$ transformed. To separately examine the effects of each categorical variable (year, season), we used an ANOVA test (Girden 1992) and the year was defined as a 12 mo observation period starting in March and ending in February the next year (March 2010–February 2011 = Year 1, March 2011–February 2012 = Year 2, March 2012–March 2013 = Year 3). Months were grouped into 4 seasons: spring (March, April, May), summer (June, July, August), autumn (September, October, November), and winter (December, January, February). When the means differed significantly ($p < 0.05$), a post hoc Tukey-Kramer HSD (honestly significant difference) test was additionally conducted. For tests of variance with proportion data (budding polyps, polyps with stolons, and strobilating polyps), the nonparametric Kruskal-Wallis test was used (Kruskal &Wallis 1952).

Relationships between polyp density and abiotic factors were explored with simple linear regression (Kenney & Keeping 1962). In addition to the linear regression, Pearson's product moment correlation coefficient (r) was estimated to quantify the strength of the linear association between 2 random variables (Pearson 1895).

A population dynamics model

To interpret the model parameters in terms of individual behavior (Geritz & Kisdi 2004, Eskola & Geritz 2007), we used a mechanistically derived non-autonomous logistic equation to model the dynamics of polyp density (Verhulst 1838): specifically, the continuous-time interference competition model (Geritz & Kisdi 2004, S. Geritz pers. comm.). This model assumes that (1) an individual asexually reproduces at a rate λ, (2) an individual dies at a rate μ, and (3) 2 individuals of the same kind engage in competition at a rate ν. One of the individuals loses the competition and dies. These individual-based assumptions give rise to the equation:

$$\frac{dN}{dt} = \lambda N - \mu N - \frac{1}{2}\nu N^2 \quad (1)$$

where $N(t)$ denotes the population density at time t. Eq. (1) can be written in a more familiar form:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad (2)$$

where

$$r = \lambda - \mu \quad (3)$$

and

$$K = \frac{2(\lambda - \mu)}{\nu} \quad (4)$$

Before including seasonality in the interference competition model, data of *in situ* dynamics of polyp populations were gathered and several null hypotheses tested, in order to determine if the instantaneous carrying capacity K and growth rate r of polyp populations *in situ* were affected by seasonal changes. Finally, average annual values of the growth rate $r(t)$ and carrying capacity $K(t)$ were assessed.

For analysis of the non-autonomous logistic model, open-source software RStudio was used (R Development Core Team 2013). We used R package 'deSolve' v.1.13 to solve and integrate the initial value problems of ordinary differential equations (Soetaert et al. 2010). We addressed the non-linear least squares problems using the standard technique Levenberg-Marquardt algorithm with the package 'minpack.lm' v.1.1-9. Models were fitted to data with inverse modelling using the 'FME' package v.1.3.2., which includes Monte Carlo analysis and parameter identifiability and provides a Markov-chain-based method to estimate confidence intervals of the parameters (Soetaert & Petzoldt 2010).

RESULTS

Interannual and seasonal variation of polyp density and asexual reproduction

Polyp densities ranged between 7 and 50 polyps cm^{-2} (Fig. 1A) and averaged 21.4 ± 6.4 (SD) cm^{-2}, with lower average density on the unprotected side (18.3 ± 0.7 cm^{-2}) and higher on the protected side (31.0 polyps cm^{-2}). We tested the following null hypotheses: H_1: polyp densities did not differ among years; H_2: polyp densities did not differ among seasons. Variance in polyp density was not significantly different among the 3 observation years (1-way ANOVA, $F_{2,34}$ = 1.27, p > 0.05); therefore, H_1 could not be rejected. Differences in the average polyp densities were significant among seasons (1-way ANOVA, $F_{3,33}$ = 11.29, p < 0.001). Polyp densities in summer and autumn (24.8 ± 4.3 and 24.7 ± 4.3 polyps cm^{-2}, respectively) significantly differed from those in spring and winter (16.7 ± 3.1 and 18.6 ± 3.1 polyps cm^{-2}, respectively) (post hoc Tukey test). H_2 was rejected.

Budding and stolon production were the prevalent forms of asexual reproduction from February to October, while strobilation started in November and lasted until April (Fig. 1B). The proportions of budding polyps, with an overall average of 1.4 ± 0.3 (SD) %, did not differ among years (Kruskal-Wallis rank test, χ^2 = 2.325, df = 2, p > 0.05). The proportions of budding differed significantly among seasons (Kruskal-Wallis rank test, χ^2 = 15.68, df = 3, p < 0.005), with significantly higher values in spring (2.0 ± 1.0 %) and summer (1.9 ± 0.8 %) than in autumn (0.8 ± 0.4 %) and winter (0.7 ± 0.8 %). The highest proportion of budding polyps was observed in May 2010 when 8.5 % of polyp population formed buds.

Production of stolons differed among years (Kruskal-Wallis, χ^2 = 9.47, df = 2, p < 0.05), with an overall average of 0.6 ± 0.3 % of polyps producing stolons. In Years 1 and 2, 0.4 % of polyps produced stolons, and 0.9 % in Year 3. Unlike budding, stolon production did not differ significantly among seasons (Kruskal-Wallis, χ^2 = 5.42, df = 3, p = 0.14); however, total average values ranged from 0.3 % of polyps produced stolons in winter to 0.9 % in summer (mean 0.6 ± 0.2 %).

Strobilation was found on all oysters. The strobilation pattern was similar among years, but with significant differences among seasons (Kruskal-Wallis, χ^2 = 14.53, df = 3, p < 0.005). Strobilation started in Year 1 and Year 2 in November and in Year 3 in October (Table 2). The highest total number and density of polyps, and proportion of the polyp population strobilating were on O2U (538, 11.9 polyps cm^{-2}, and 63.4 %, respectively) in November 2010. Overall, the majority of polyps strobilated in late autumn and in winter months (Table 2). In contrast to the other years, in Year 3, 11 strobilae were noted in April, 2 in May, and 1 in July and August.

Polyp density effects on asexual reproduction

The percentage of budding was highest in the spring, which could be related to the low density of polyps providing more available space for new individuals. Thus, we tested 2 null hypotheses: H_3: the proportion of polyps budding was independent of the density of polyps; H_4: the proportion of polyps

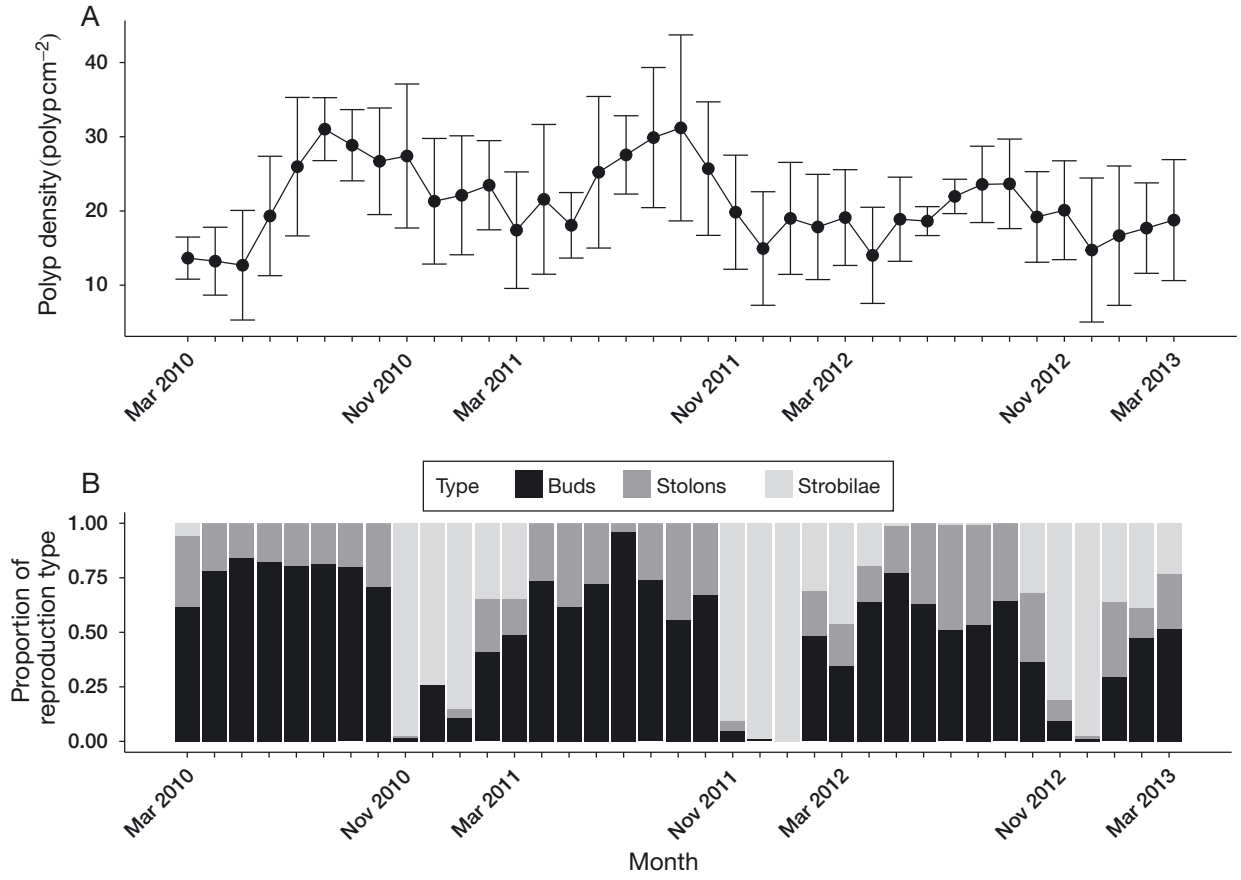

Fig. 1. Interannual variation of (A) *Aurelia aurita* s.l. polyp density on 4 oysters with means and standard deviations (polyps cm^{-2}) and (B) proportions of asexual reproduction forms (buds, stolons and strobilae) *in situ* from March 2010 to March 2013

forming stolons was independent of the density of polyps. Budding was negatively correlated with polyp density (Pearson correlation, r = –0.235, p < 0.005) and was lower when polyp density was >30 polyps cm^{-2} (Kruskal-Wallis, χ^2 = 9.125, p < 0.05); therefore, H_3 was rejected. Stolon production also was reduced significantly with higher polyp density (Pearson correlation, r = –0.204, p < 0.05). Similar to budding, stolon production was lower when polyp density was >30 polyps cm^{-2} (Kruskal-Wallis, χ^2 = 15.482, p < 0.001). H_4 was rejected. Moreover, bud and stolon production were positively correlated (Pearson correlation, r = 0.499, p < 0.001).

We tested a fifth null hypothesis: H_5: the proportion of strobilae was independent of the density of polyps. Strobilation did not show a significant linear relationship with polyp density (Pearson correlation, r = –0.110, p > 0.05); however, comparison among the

Table 2. Numbers (totals from 4 oysters) and proportions (%) by month of all *Aurelia aurita* s.l. polyps strobilating from 4 oysters and temperature data (°C) by month (2010/11 = Year 1, 2011/12 = Year 2, 2012/13 = Year 3). Thus, the monthly proportions total 100% for each year

Month	Year 1			Year 2			Year 3		
	(no.)	(% ± SD)	(°C)	(no.)	(% ± SD)	(°C)	(no.)	(% ± SD)	(°C)
Mar	2	0.2 ± 0.4	9.4	47	5.2 ± 7.6	8.7	84	10.0 ± 13.2	8.9
Apr–Sep	0	–	14.2–25.5	0	–	10.9–26.3	15	1.8 ± 1.9	12.0–27.4
Oct	0	–	18.9	0	–	19.8	21	2.5 ± 2.3	19.3
Nov	1152	89.0 ± 26.2	13.9	381	42.3 ± 26.6	16.5	253	30.1 ± 14.1	17.0
Dec	20	1.5 ± 4.1	12.8	311	34.6 ± 27.6	13.2	393	46.7 ± 37.4	11.6
Jan	79	6.1 ± 12.6	9.9	117	13.0 ± 18.2	10.8	23	2.7 ± 1.4	9.9
Feb	41	3.2 ± 14.4	8.1	44	4.9 ± 7.5	6.3	52	6.2 ± 6.7	8.7

ranges of polyp density (<20 polyps cm^{-2}, 20–30 polyps cm^{-2}, >30 polyps cm^{-2}) indicated significant variance (Kruskal-Wallis, $\chi^2 = 16.677$, $p < 0.001$). The polyp density range <20 polyps cm^{-2} was significantly different from the others (Dunn's test), indicating that strobila production occurred when polyp density was lower. Thus, we rejected H_5. High strobilation and polyp densities < 20 polyps cm^{-2} were found from November to March on oysters located on the unprotected side of the pier. Additionally, when present, strobilae were negatively correlated with budding (Pearson correlation, r = −0.260, $p < 0.05$) and stolon production (Pearson correlation, r = −0.266, $p < 0.05$).

Polyp density, asexual reproduction, and environmental factors

The environmental factors temperature, salinity, PAR, and pH were monitored to better understand variations of polyps *in situ* (Fig. 2). Temperature data exhibited seasonality typical for the northern Adriatic Sea, ranging from 6.3°C in late winter to 27.4°C in summer. We tested H_6: the population density of polyps is independent of the temperature and found a significant positive correlation of temperature with polyp density (Pearson correlation, r = 0.37, $p < 0.001$); therefore, H_6 was rejected. H_7: the population density of polyps is independent of the salinity was also rejected because salinity had a significant negative correlation with the density of polyps (Pearson correlation, r = −0.268, $p < 0.001$). We tested H_8: the population density of polyps is independent of the PAR. PAR was positively correlated with the polyp density (Pearson correlation, r = 0.20, $p < 0.05$), and H_8 was rejected. The final tested hypothesis was H_9: the population density of polyps is independent of the pH and found a non-significant correlation of pH with polyp density (Pearson correlation, r = 0.06, $p > 0.05$); therefore, H_9 was not rejected.

Production of buds and stolons both differed significantly among different temperature ranges (Table 3) (<10°C, 10–15°C, 15–20°C, 20–25°C, >25°C) and were highest when temperatures were >25°C.

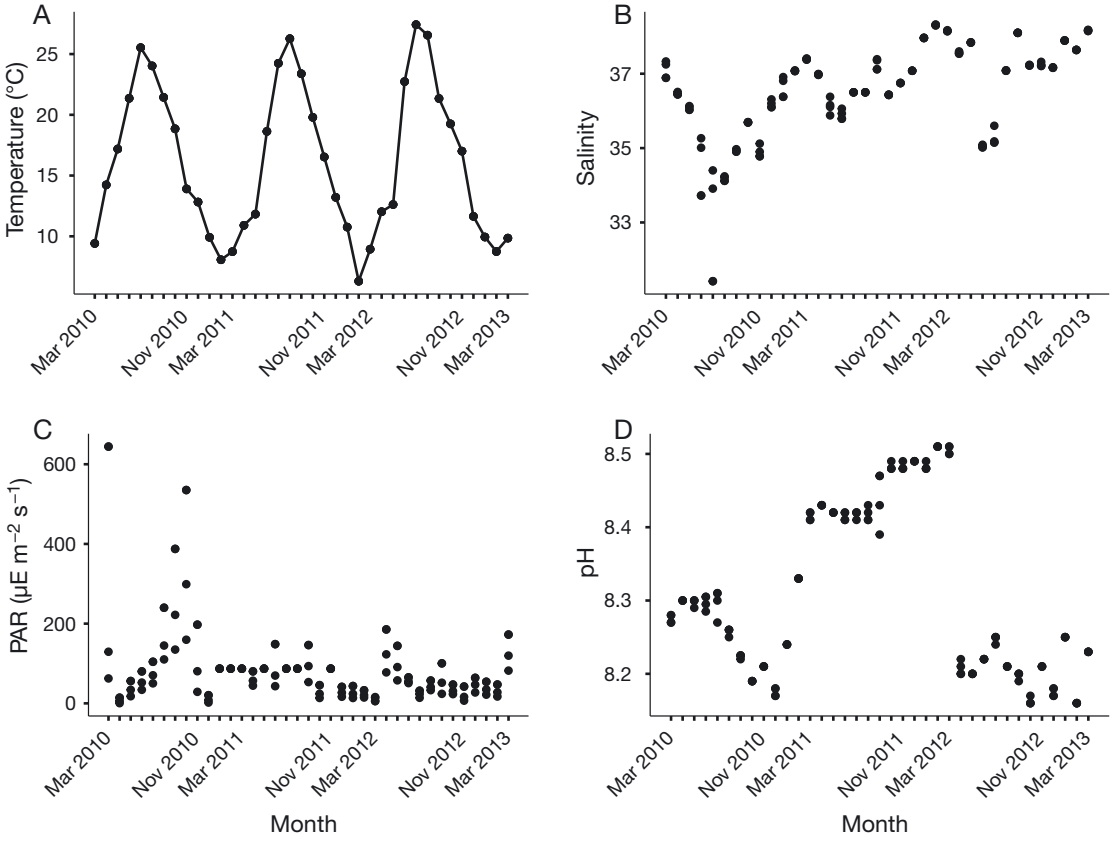

Fig. 2. (A) Temperature, (B) salinity, (C) photosynthetically active radiation (PAR), and (D) pH recorded in the Bay of Koper once per month from March 2010 to March 2013

Table 3. Means and standard deviations of *Aurelia aurita* s.l. polyp density and percentages of asexual reproduction forms (buds, stolons and strobilae when present) on all oysters from 3 years of observation, and variance among polyp density and asexual reproduction forms with different multiple comparison groups or temperature ranges (< 10°C, 10 – 15°C, 15 – 20°C, 20 – 25°C, > 25°C). Temperature was the independent variable for each test. Data were tested with a Kruskal-Wallis test. $p < 0.05$ was considered significant

Dependent variable	Mean (± SD)	d.f.	χ^2	p
Polyp density (polyps cm^{-2})	21.4 ± 8.2	4	24.10	< 0.001
Buds (%)	1.4 ± 1.2	4	16.49	< 0.005
Stolons (%)	0.6 ± 0.7	4	14.70	< 0.01
Strobilae (%)	6.0 ± 11.0	3	10.98	< 0.05

During the period when strobilae were present (Table 2), the proportion of strobilae was significantly related to the temperature ranges (Kruskal-Wallis, $\chi^2 = 10.978$, $p < 0.05$). In total, 13.2% of polyps of all observed oysters in all 3 years formed strobilae when temperatures were <10°C, 65.4% at temperatures between 10 and 15°C, and 21.4% in the temperature range 15 to 20°C. Strobilae formed only twice at temperatures > 25°C and never at temperatures between 20 and 25°C.

Growth rate and carrying capacity of *in situ* polyp populations

Based on the rejected hypotheses H_2, H_3, H_4, H_6, and H_7, we conclude that carrying capacity K and growth rates r of polyps *in situ* also exhibited seasonality. Therefore, we assumed that λ (*i.e.* a polyp's individual asexual reproduction rate of buds and stolons) changed over the year, with the highest λ during summer months when production of buds and stolons were highest. In order to include seasonality in the interference competition model, we assumed that $\lambda(t)$ had the form:

$$\lambda(t) = a\sin^2(kt) + b \quad (5)$$

where a and b are positive parameters and k is a (positive) parameter related to the period of oscillations. We named this model the interference competition model with seasonality in λ. The highest asexual production or maximum would be reached in summer months when the asexual formation of buds and stolons was the highest and equaled $a+b$. Approximately 6 mo later in the winter months, the polyp's individual asexual reproduction rate λ reached a minimum (b) because formation of buds and stolons was lowest. Thus, parameter a would be the difference between the maximum and minimum asexual reproduction rates. We assumed that the parameters μ and ν would be constants; therefore, the model is

$$\frac{dN}{dt} = (a\sin^2(kt) + b - \mu)\cdot N\left(1 - \frac{N}{\frac{2(a\sin^2(kt)+b-\mu)}{\nu}}\right) \quad (6)$$

We took the same approach, assuming that individual death rate μ could be modified as a periodically changing parameter over the year (Hočevar 2016).

The interference competition model with seasonality in λ was fitted to the data. The collected empirical data enabled us to approximate the value of k and use it for the initial parameter estimation (Table 4). Parameter estimates were inserted into Eqs. (7) & (8) and integrated to obtain the average growth rate r and average carrying capacity K for the observed polyp population for all oysters and for each oyster individually (Table 5).

$$r(t) = a\sin^2(kt) + b - \mu \quad (7)$$

$$K(t) = \frac{2(a\sin^2(kt)+b-\mu)}{\nu} \quad (8)$$

Growth rates of the observed polyp populations ranged between 1.08 and 1.26 mo^{-1} and averaged 1.16 mo^{-1} (Table 5). The average carrying capacity was 37.4 polyps cm^{-2}. The oyster O2P on the protected side of the pillar facing the coastline had the highest carrying capacity (58.2 polyps cm^{-2}) relative to the others (30.0–31.3 polyps cm^{-2}), which was significantly different from those on the unprotected side (Kruskal-Wallis, $\chi^2 = 57.711$, $p < 0.001$).

Table 4. Estimations of parameters k, a, $b - \mu$ and ν, the initial values, lower and upper bounds and the final estimates of the observed *Aurelia aurita* s.l. polyps. λ: asexual reproduction rate; k: determines the period of asexual reproduction rate; a: difference between min and max asexual reproduction rate; b: min asexual reproduction rate μ: death rate, ν: competition rate

Seasonality in λ	k	a	$b - \mu$	ν
Initial values	0.3	0.2	−0.6	0.03
Lower and upper bounds	[−1,1]	[0,2]	[−1,1]	[0,1]
Oyster				
ALL	0.312	0.131	−1.000	0.057
O2U	0.305	0.401	−0.966	0.076
O4U	0.295	0.578	−1.000	0.084
O6U	0.288	0.470	−0.942	0.074
O2P	0.280	0.164	−1.000	0.037

Table 5. Estimations of r and K of the observed *Aurelia aurita* s.l. polyp populations at different depths (2, 4, 6 m) and locations (protected P, unprotected U). λ: asexual reproduction rate; $N(0)$: initial number of individuals; r: intrinsic growth rate; K: carrying capacity

Oyster	$N(0)$	r [month^{-1}]	K (polyps cm^{-2})
O2U	6.74	1.14	30.1
O4U	6.21	1.26	30.0
O6U	10.26	1.16	31.3
O2P	8.86	1.08	58.2
Average	8.01	1.16	37.4

The percentage of bud formation was higher for polyps on the unprotected side (1.5 ± 1.3% had buds) than for the protected side (1.1 ± 1.1% had buds), but the difference was not statistically significant (Kruskal-Wallis, $\chi^2 = 3.061$, $p = 0.080$); however, stolon formation on the unprotected side (0.73 ± 0.71% had stolons) was significantly higher than on the protected side (0.38 ± 0.43% had stolons) (Kruskal-Wallis, $\chi^2 = 8.047$, $p < 0.005$).

The difference in strobilation between sides was significant when all months were analysed (Kruskal-Wallis, $\chi^2 = 4.896$, $p < 0.05$). More strobilae were formed on the unprotected side (2.7 ± 8.2% strobilae) compared to the protected side (1.3 ± 4.5% strobilae), but the standard deviation was high in both. However, the difference between sides in strobila formation when only months with strobilae were analysed was not significant (Kruskal-Wallis, $\chi^2 = 0.121$, $p > 0.05$).

There were no significant results in the variations among asexual reproduction according to depth when all 4 oysters were included in the analysis. When only oysters from the unprotected side were included in the analysis, we found significant differences (Kruskal-Wallis, $\chi^2 = 13.767$, $p < 0.005$). Polyp density at 2 m was significantly different from polyp densities at 4 and 6 m (Dunn's test). Stolon production also was significantly different by depth (Kruskal-Wallis, $\chi^2 = 6.6533$, $p < 0.05$), with significant stolon production differences between 2 and 6 m (Dunn's test). Otherwise, there were no significant variations in asexual reproduction regarding depth.

DISCUSSION

Population dynamics and polyp density *in situ*

Polyps of 4 observed oysters had average densities of ~21 polyps cm^{-2}, which was similar to the average density of ~31.3 polyps cm^{-2} at Kettering site in Tasmania (Willcox et al. 2008). Those average densities were higher than those in Kagoshima Bay, Japan (7.3–17.6 polyps cm^{-2} and 3.1–18.5 polyps cm^{-2}) growing on *Mytilus* shells and polystyrene, respectively (Miyake et al. 2002), and than those in Cornet Bay Marina, USA, where density of *Aurelia labiata* averaged 9.3 polyps cm^{-2} (Purcell et al. 2009).

Polyp dynamics *in situ* had the same pattern of seasonal changes in each of the 3 observed years. Polyps were most numerous in summer with a peak in average density of ~29 polyps cm^{-2} in August. The highest density (~50 polyps cm^{-2}) was in September 2011 on O2P, on which density was consistently high, but was still lower than the highest density observed (88 polyps cm^{-2}) in Kagoshima Bay (Miyake et al. 2002).

Although polyp density minima in our study varied among the years, the average density decreased during winter to the lowest in spring, reaching the minimum average of ~17 polyps cm^{-2} in April. This was when the temperature started to increase after having reached the lowest point of 6.30 to 8.75°C in February. Water warmed to 27.42°C in July when temperature maxima were reached in 2010 and 2012. The average polyp density followed the temperature cycle with an approximately 2 mo lag and had similar dynamics to a Tasmanian polyp population with unlimited space (Willcox et al. 2008).

Of the environmental factors tested, temperature had the strongest correlation (positive) with polyp density. The opposite (negative) trend was observed for salinity. In contrast, polyp density in Tasmania decreased with increased mean daily rainfall (Willcox et al. 2008). Although polyps show a high tolerance to salinity changes (Holst & Jarms 2010), we noted that 1 mo before polyp populations were the most dense (in August 2010, ~31 polyps cm^{-2}), the average salinity dropped (minimum in July 2010 = 32.79), presumably due to heavy rainfall and runoff from nearby rivers. Moreover, that was the only occasion when polyp density increased by >5 polyps cm^{-2} mo^{-1} in summer; the greatest increases were in May and averaged ~7 polyps cm^{-2} mo^{-1}. Therefore, this suggests that changes in salinity could affect polyp populations *in situ*, as shown for other species (Purcell 2007).

Some studies implicated the predation impact on polyp mortality and thus its population density (Thiel 1962, Hernroth & Gröndahl 1985a,b). Divers who took the underwater photos never saw any polyp predator at the time of sampling. The environment of Port of Koper is probably less suitable for predators such as nudibranch gastropods due to high turbidity and disturbances of intensive maritime traffic.

Nevertheless, we did record the second largest sudden drop in polyp density in late spring on oyster O2E located at 2 m depth on the protected side of the pillar. Polyp density decreased from ~37 polyps cm^{-2} to ~24 polyps cm^{-2} in May 2011, but completely recovered and even rose higher in the next month (~41 polyps cm^{-2}). A similar summer decrease, followed by recovery, was recorded only once again in the same polyp population in June 2012 (from ~27 to ~16 polyps cm^{-2}). We can only speculate that this resulted from predation. Interspecific competition for space with other biofouling organisms (Watanabe & Ishi 2001) could also affect polyp densities in the Bay of Koper because we observed various species of biofouling organisms that shared the same oyster's surface as polyps. Genetic differentiation and local adaptation, which also control asexual reproduction and density of *Aurelia* polyps (Dawson & Martin 2001), may explain the differences in polyp density seen among populations in diverse locations (Miyake et al. 2002, Willcox et al. 2008, Purcell et al. 2009).

Effects of buds and stolons on population dynamics *in situ*

Buds and stolons were observed in the temperature range between 6.30 and 27.42°C. The proportion of budding polyps did not differ among years, but exhibited seasonality and was correlated with temperature and density of the population. Unlike budding, stolon production differed among years due to higher stolon production in the observation period 2012/13. Temperature could have contributed to this because its average values were highest in the third year 2012/13 (16.8°C) and lowest in the first year 2010/11 (14.7°C). Stolon production did not exhibit statistically significant seasonality but was correlated ($p < 0.001$) with temperature and polyp density.

Budding was highest in the spring, when the density of polyps was low and more space was available for new individuals, while average stolon formation was greatest in the summer and spring. Reproduction rates, which can differ due to adaptations to local conditions (Pascual et al. 2015), were affected by the combination of population density and temperature ($p < 0.001$). When polyp density was low, reproduction rates increased with increasing temperature (Willcox et al. 2007, Ishii & Katsukoshi 2010, Pascual et al. 2015). Difficult identification of stolons and buds at high polyp densities could also have affected these results. A density dependent relationship was also noted in the Tasmanian polyp populations at the Kettering site when space was removed as a limiting factor (Willcox et al. 2008).

An important source of food for polyps is the plankton, which is largely dependent on a high run-off of rivers generally in early spring (Mozeti et al. 2012). This run-off enriches marine waters with nutrients and results in higher plankton biomass and high food availability for young polyps. High asexual rates of buds and stolons can coincide with high availability of food, which could be a key factor for population growth (Hernroth & Gröndahl 1985b) and was noted *in situ* also by Willcox et al. (2008).

Population dynamics and strobilation *in situ*

Strobilation began in autumn when budding and stolon production rates and temperature decreased. The timing and periodicity of strobilation, for which long nutritive preparation is a necessary condition (Berrill 1949), vary among species (Pascual et al. 2015). In Tasmania and the USA, strobilation began as water temperature started to rise after the major seasonal cooling (Willcox et al. 2008, Purcell et al. 2009), while in Koper, as in some other studies (Kakinuma 1975, Miyake et al. 2002, Holst 2012), cool temperatures were shown to be related to the start. The seasonal dynamics of strobilation in Koper were similar to that in Kagoshima Bay, but with an earlier start (Miyake et al. 2002). In our study, the greatest proportion of the polyp population in all 3 years strobilated in November, which coincided with the greatest average decrease in polyp density of ~5 polyps cm^{-2} mo^{-1}. Polyp density did not have a direct significant relationship with strobilation in Cornet Bay (Purcell et al. 2009), in contrast with polyps in Tasmania where more strobilated in the high-density population with ~31.3 polyps cm^{-2} (Willcox et al. 2008). In our study, formation of strobilae was significantly higher when polyp density was <20 polyps cm^{-2}. Strobilation at lower polyp density and cooler temperature explains its significant negative correlation with stolon and bud production. The explanation is unknown for the unexpected strobilation of 15 polyps between April and August in Year 3 on oysters growing on the unprotected side of the pier.

Population dynamics model of *in situ* polyp populations

Because polyp density was correlated with both temperature and asexual reproduction rates, the carrying capacity K and growth rate r of the polyp

population *in situ* were affected by seasonal changes of the environment. Therefore, the long-term population dynamics *in situ* could exhibit seasonal oscillations that resemble a sinusoidal curve.

Asexual reproduction rates of budding and stolon production were generally high in the warm period of each year, resulting in a month or two with high population densities. Moreover, when population densities were the highest, asexual reproduction rates of buds and stolons started to decrease, possibly suggesting effects of density-dependent processes (Chiba 1969, Schiariti et al. 2015). The average annual r and K of a polyp population *in situ* were here for the first time assessed with an interference competition model with seasonality in λ (asexual reproduction rates of budding and stolon production). The estimated average growth rate r of the polyp population in the Port of Koper was 1.16 mo^{-1}, indicating that the population had an increasing trend because $r >$ 0 mo^{-1}. The average estimated carrying capacity K of the population was 37.4 polyps cm^{-2}, which is similar to the recorded carrying capacity of 30 to 43 polyps cm^{-2} of polyp populations in a transplant experiment (Gröndahl 1988). The carrying capacity *in situ* can be affected by seasonal variations of density independent processes, such as seawater temperature and food availability (Malačič et al. 2006, Mozetič et al. 2012), and also by seasonality of density dependent processes because with greater densities of polyps, intraspecific competition for space and food is greater (Gröndahl 1988, Willcox et al. 2008).

The average growth rate r of the polyp population located on the protected side of the pillar was slightly lower than on the unprotected side, which could be due to its higher polyp density. The carrying capacity K also was higher on the protected side that was less exposed to the external effects of sedimentation and hydrodynamic conditions caused by vessels in the port.

Although our *in situ* monitoring followed polyps on only 4 oysters, by detailed manual counting, we obtained monthly data on polyp abundances and their asexual reproduction over 3 yr. *In situ* studies on scyphozoan polyps are very rare, and this study represents a valuable time series and a baseline for future research on scyphozoan polyps.

Comparison of growth rates *r* and carrying capacity *K* of *in situ* and laboratory populations

Average r and K estimations of polyp population dynamics *in situ* differed from those in laboratory conditions by Melica et al. (2014). Both polyp populations originated from the same location in the Port of Koper, but the simple logistic model was used for K and r estimations of laboratory populations because they were grown under constant laboratory conditions for 42 d (Melica et al. 2014). Their population dynamics fit a sigmoid curve, which also fit the *in situ* population for a short time soon after establishment (Coyne 1973, Melica et al. 2014). Average growth rates of the *in situ* population were significantly lower than those in the laboratory (Table 6), presumably because of exposure to the changing environment and less abundant food and space than laboratory populations, which were fed *ad libitum* twice weekly with *Artemia* nauplii and had low polyp density; the mean densities with standard error at the start of the experiment were 7.78 ± 0.49 and 0.10 ± 0.02 polyps cm^{-2} for the high and low density treatments, respectively (Melica et al. 2014). In contrast, the average estimated carrying capacity of the *in situ* population was significantly higher than that of the laboratory populations (Melica et al. 2014). The authors suggested that low carrying capacity could be due to numerous factors, including stress, lack of current, food variability, and composition of bacterial biofilms, which could affect the polyp populations in the laboratory (Melica et al. 2014).

Differences between *in situ* and laboratory populations suggest that the laboratory conditions did not simulate the seasonality of the natural environment and drivers of *A. aurita* polyps. Moreover, although a simple logistic model was appropriate to estimate

Table 6. Estimations of parameters $N(0)$ (estimated initial number of polyps), r (the intrinsic growth rate) and K (the carrying capacity) with means and standard deviations for *Aurelia aurita* s.l. average polyp populations *in situ,* using Eq. (6), and for polyps monitored under reported laboratory experiment with high and low density populations, using a standard logistic model (Melica et al. 2014). λ: asexual reproduction rate

Standard logistic model	$N(0)$	r (d^{-1})	K (polyps cm^{-2})	Source
High density	7.59 ± 0.21	0.13 ± 0.03	5.35 ± 0.11	Melica et al. (2014)
Low density	0.08 ± 0.02	0.14 ± 0.01	1.81 ± 0.08	Melica et al. (2014)
Interference competition model with seasonality in λ	8.02 ± 1.88	0.04 ± 0.002	37.39 ± 13.89	Present study

a polyp population grown in laboratory conditions (Melica et al. 2014), that model did not consider environmental seasonality and is unsuitable for a polyp population in the natural environment exposed to seasonal forcing. Environmental seasonality is an important component of the polyp population dynamics, able to affect the seasonal changes of life-history parameters (Turchin 2003), such as carrying capacity K and intrinsic growth rate r, which can be assessed by a non-autonomous logistic equation, based on a mechanistically derived (autonomous) logistic model like the interference competition model with seasonality in λ. This model enables study of all polyp populations *in situ* with seasonal forcing and, thus, can be implemented in different localities.

In situ studies of polyp population dynamics from their local ecosystems around the world with different environmental and anthropogenic pressures are needed (Purcell et al. 2007, Jackson 2008, Purcell 2012, Duarte et al. 2013, Vodopivec et al. 2017). They would enable us to compare the average life-history parameters and help to recognise the main environmental and anthropogenic effects on polyp populations and thus the resulting intensity and frequency of medusa outbreaks.

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