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Seasonality and life cycle of the jellyfish *Lychnorhiza lucerna* Haeckel, 1880 (Scyphozoa) in southern Brazil

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Abstract: *Lychnorhiza lucerna*, is a species of Scyphozoa with tropical and subtropical distribution in the western Atlantic. The knowledge of its life cycle is fragmented, with little understanding of environmental factors affecting growth processes and reproduction. This study evaluated the different phases of the life cycle of this macromedusa based on laboratory experiments with the polyp phase at different temperatures and 10 years of field data for the medusoid phase. Experiments on the polypoid phase determined a longer development time for the polyp population, highlighting the upward thermal shock for the excystment of podocysts and that the higher temperature (25 °C) stimulates greater production of ephyrae. In the south of Brazil, the presence of juveniles (< 5 cm in diameter) and adults (> 15 cm) of the medusoid phase was observed in winter and spring and during the period of upward variation in water temperature (18.5 to 23.8 °C). These results confirm the annual life cycle of the species, that sporadic outbreaks (blooms) can be influenced by the stimulus of polyp strobilation. Based on the growth rates obtained in the laboratory and the population dynamics, this suggests that the organisms could be transported to the mouth of the Plata.

Key words: Pelagic jellyfish, benthic polyps, growth, reproduction, temperature, population dynamics.

INTRODUCTION

The class Scyphozoa is one of the six existing classes of cnidarians (Collins 2009), with more than 200 species, which are from marine environments and can reach 2 m in diameter (Gershwin 2016). Their bulky body favors symbiosis with other invertebrates in addition to being part of the diet of several marine vertebrates (Doyle et al. 2014). These organisms are also responsible for capturing and transporting carbon, associated with symbiosis with microalgae, as well as for deposition on the ocean floor due to the degradation of jellyfish blooms (Doyle et al. 2014, Lebrato et al. 2019, Tinta et al. 2021). In general, scyphozoans present metagenetic reproduction, with sexual reproduction in the medusoid phase and asexual reproduction in the polypoid phase (Arai 2008, Lucas et al. 2012).

According to a review carried out by Omori & Nakano (2001) and Kitamura & Omori (2010), there is a growing interest in the edible use of the order Rhizostomeae, due to its large size and robust and rigid body. Jellyfish fishing has become popular in Southeast Asia since the 1970s, expanding to other countries such as Australia, India, Mexico, Turkey, and the USA (Hsieh & Rudloe 1994, Omori & Nakano 2001, Brotz 2016). Another economic activity is the ornamental cultivation of jellyfish, which can be used for recreational and educational purposes in public aquariums (Doyle et al. 2014, Morandini 2022). Finally, some studies portray the potential use of collagen extracted from jellyfish of the order Rhizostomeae for pharmacological purposes, as they exhibit good immunological responses and hemostatic applications, capable of controlling hemorrhages (Cheng et al. 2017, Merquiol et al. 2019, Nagai et al. 1999, Sugahara et al. 2006).

Studies of the life cycle of jellyfish, especially Rhizostomeae, are often carried out in the laboratory to understand the reproductive strategies of these organisms (Fuentes et al. 2011). Cohort analyses are normally used to analyze juvenile and adult organisms collected in the field, which are intended for fisheries management of abundant species (López-Martínez et al. 2020). However, the interpretation of this information is essential for a complete understanding of the life cycle of jellyfish and can be applied both to occurrence in gradients for certain regions and to understanding outbreaks stranded on the beaches.

Lychnorhiza lucerna (order Rhizostomeae) is an abundant species distributed along the Atlantic coast of South America, mostly occurrying from Brazil to Argentina (Schiariti et al. 2018), with records also in French Guiana and Colombia (Oliveira et al. 2016). This species presents a unique strategy of asexual reproduction (mono-mode) of forming podocysts fixed to the substrate and produced by the scyphistoma (Schiariti et al. 2014). From the center of this podocyst, a new polyp may emerge, also capable of producing new podocysts and undergoing the strobilation process with the release of ephyrae. Knowledge of the reproductive biology of *L. lucerna* was originally investigated by Schiariti (2008) (later published by Schiariti et al. 2008, 2012, 2014), through the fertilization and obtaining of planula larvae and the settlement of planulocytes and description of scyphistomae in the laboratory, in addition to the monitoring until the metaephyra phase (juvenile) with a total development time of approximately 55 days. There is no information about the development time from the metaephyra to adult medusa stage, however, according to Schiariti (2008), female medusae smaller than 8 cm in diameter have a lower percentage of gonad maturation, while those above 13 to 17 cm are predominantly mature. Males smaller than 9.6 cm are sexually immature and fully mature above 17 cm in diameter.

Within the knowledge generated about the reproductive biology of *L. lucerna*, there are still doubts about the production and excystment rates of podocysts and about strobilation under the influence of temperature. The same occurs for the growth of the medusoid phases, which are supposedly associated with temperature conditions and food availability (Schiariti et al. 2014). Furthermore, comprehending the life cycle of the species in southern Brazil can help in the interpretation of population occurring at the mouth or estuary of the Rio de la Plata (continental shelf of Argentina and Uruguay), which is made up exclusively of adults, as well as helping in understanding the massive strandings of the species frequently observed and recorded in recent years (2020 and 2024) (Fig. 1) along the Brazilian coast. In this way, this work aims to respond to gaps in the knowledge of the species' biology both in field and laboratory cultivation.

MATERIALS AND METHODS

Temperature assays with polyps

Establishment of polyp cultivation

The first two polyps of *L. lucerna* were provided by Dr. André C. Morandini (Department of Zoology, Biosciences Institute of the Universidade de São Paulo, USP) and is derived from the original batch of polyps from Schiariti (2008) Thesis. The cultivation of polyps, that is, the increase

Figure 1. Records of massive strandings (Blooms) of *Lychnorhiza lucerna* on the south coast of Brazil (SC – Santa Catarina and RS – Rio Grande do Sul states) obtained on social media (Instagram and Facebook) and confirmed by online newspaper. Balneário Camboriú and Penha close to the Itajaí-açu river (Fig. 2 – b,1 and c,1) and Rio Grande (Fig. 2 – b,2).

in the number of organisms for use in assays, was carried out between August 2021 and February 2022. The objective in this first stage was to increase the number of individuals for establishing cultivation. All development was carried out in 80 mL crystallizing dishes (glass plates) in filtered seawater with a salinity of 30, feeding three times a week with newly hatched nauplii of *Artemia* sp., completely renewing the water once a week and kept in the dark. The temperature for maintaining and cultivating the polyps ranged from 20 °C to 25 °C and observed some changes in survival rates and responses to podocyst production and strobilation. Finally, preliminary thermal shock tests applied to the podocysts were performed. This initial cultivation made it possible to establish:

1) Both maintenance temperatures (20 °C and 25 °C) and 33±3 of the salinity are satisfactory for the maintenance of polyps.
2) Feeding 3 times a week allows strobilation responses and podocyst production to be stimulated. These two reproductive mechanisms occur continuously in cultivation (Schiariti et al. 2014).
3) It was observed that the most efficient response for the excystment of podocysts was obtained by thermal shock at high temperature after maintaining them at low temperatures.
4) The transfer of polyps between test plates must prioritize non-attached organisms, since removing the polyp from the substrate may make its survival unviable. Preferably, the colonization of a new crystallizing dish should be done by podocysts, structures that are more resistant to being removed from the bottom of the plates. The problems associated with the survival of polyps in culture plates determined the experimental conditions carried out in this work. Due to this, the number of test chambers was limited, which made it impossible to carry out replicate treatments. This fact determined the use of a long-term non-parametric statistical test, with paired sampling replications.

5) The genetic variability of the organisms used in the experiments and originating from two polyps was not considered an interference.

Temperature assay

Between February 7th and May 18th, 2022 (100 days), was tested the influence of temperature (20 and 25 °C in incubator) on the asexual reproduction of polyps. The maintenance conditions at both temperatures followed those described above (item 1). Two crystallizing dishes with polyps and podocysts were selected for the experiment and met the criteria of presenting an initial similar number of organisms, not showing strobilation and not producing podocysts at the beginning of the experiment.

Plate 1 (EP1) started the experiment with 5 polyps and 14 podocysts, being kept at 25 °C. Plate 2 (EP2) started the experiment with 8 polyps and 14 podocysts and was kept at 20 °C. It was decided not to equalize the number of polyps per treatment to avoid the mortality of the organisms. The number of replicates per treatment (temperature) was reduced due to the duration of the assay (4 months), observations every 2-3 days and comparison by non-parametric statistics (more robust) for dependent samples (see data treatment). Observations of the parameters were carried out 3 times a week associated with the feeding and water renewal routine of the crystallizing dish. Data processing involved parameters accumulated monthly and treated as averages for each treatment.

The data obtained over time in the experiment were: the number of polyps, number of podocysts, number of polyps with strobilation and number of ephyrae released. With these data, the following indexes were generated: production of podocysts per polyp (monthly average number of podocysts/number of polyps); excystment days (monthly average of the number of days between the appearance of groups of polyps on the culture plates); percentage of excystment accumulated in the month (total new polyps/total number of podocysts); number of polyps in strobilation (monthly average) and number of ephyrae released (monthly average of number of ephyrae/number of strobilation).

Podocyst excystment stimulation assay

A third thermal shock test was performed using a crystallizing dish containing 68 podocysts. Originally from the maintenance treatment (item 1 of the establishment of polyp cultivation) and at a temperature of 20 °C, this crystallizing dish was kept at 15°C for three weeks (05/18/2022 to 06/08/2022) and was subsequently transferred to 25 °C. The time and percentage of excystment were observed for a period of 16 days. The treatment of item 2 of the temperature test of 20 °C was used as a control and/or comparison without the thermal shock treatment.

Other information about the growth in laboratory

Additional information obtained from cultivation of the species and with the presence of few polyps was development time of polyps from their excystment to the production of new podocysts and/or their strobilation. The development time from ephyrae to metaephyrae (juveniles - filled or closed umbrella and presence of oral arms), or from 0.9 to 12.5 mm in diameter of the umbrella, was also obtained in Kreisel-type aquaria (20 L) fed three times a week with nauplii of *Artemia* sp. In all cases, maintenance temperatures varied between 20 and 25 °C, and this parameter was not investigated.

Population dynamics of *L. lucerna*

Samples of jellyfish were obtained over 96 months between February 2012 and November 2021 as a by-catch of the artisanal shrimp fishery off the north coast of Santa Catarina state and in the region surrounding the mouth of the Itajaí-açu river, between the isobaths of 8 to 25 meters within 25 Km of coast (26°45' to 27° 00' S) (Fig. 2). Daytime trawls were performed from a motorized boat, at a speed varying from 1.6 to 2.3 knots, using nets with a mesh size of 26 mm between opposite knots in the body and in the bagger, with a length of 6 meters and opening of 7 meters and 1 m in height, covering between 500 and 700 m of distance (approximate volume of filtered water ranging from 3,500 to 4,900 m^3 or m^2, for 10 minutes of trawling). All organisms occurring in the trawls were sampled. Organisms smaller than 26 mm (net mesh size) were frequent in the samples due to changes in mesh opening (shrimp net) as well as network clogging. In any case, records of small specimens (in frequency of occurrence) are important for interpretation in cohort analysis. Collections were carried out monthly between 2012 and 2018 and bimonthly between 2019 and 2021. In each field trip, one to four trawls were carried out depending on sea conditions and the occurrence of organisms in the trawls. Additionally, temperature and salinity data were obtained at a depth of 2 m at each starting point of the trawls using a Yellow Springs® model 30/10 FT Thermosalinometer. The organisms obtained were packaged in coolers. In the laboratory (EP/UNIVALI) individual data on weight and diameter of the umbrella were obtained (De Barba et al. 2016).

The biometric data were grouped into size classes, and the percentage of juvenile or immature classes (umbrella diameter < 5.0 cm) was estimated, as well as a group of organisms

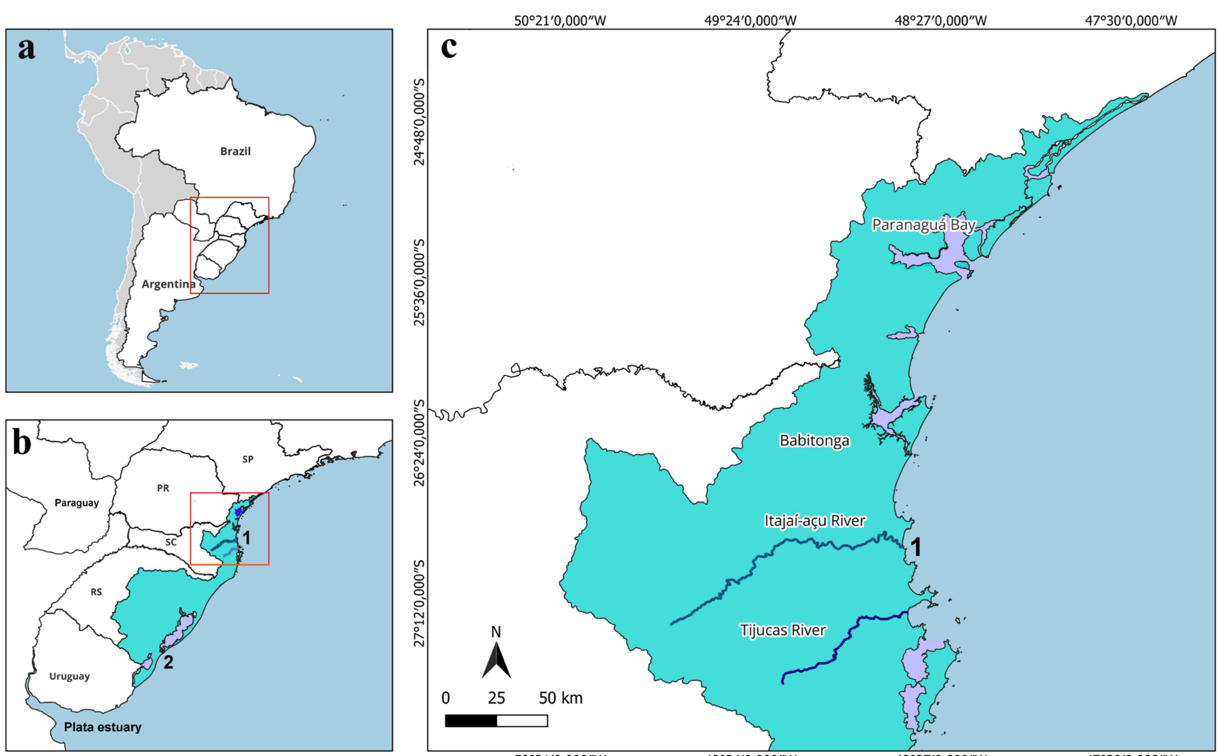

Figure 2. a - Southeast and southern regions of Brazil in South America. b - Study area (1) in the southern region of Brazil, being SP-São Paulo, PR-Paraná, SC-Santa Catarina, RS-Rio Grande do Sul, South Atlantic hydrographic basin (blue) and position of the Lagoa dos Patos estuary (city of Rio Grande) (2) and the Plata estuary. c - Northern part of the South Atlantic Hydrographic Basin with the main continental contributions and location of the study area (1 - mouth of the Itajaí-açu river and city of Itajaí).

with immature and mature representatives or intermediate class (5.1 to 15 cm umbrella diameter) and adults or all mature (umbrella diameter > 15.1 cm), as an average of 10 years of data, in order to evaluate the population dynamics of the species. To identify the *L. lucerna* cohort in the environment, the event dates of the different size classes were considered. The beginning of the cohort was considered as the month of the first occurrence of juveniles, followed by the date of increase in the percentage (representation) of the intermediate class and ending with the date of the first occurrence of adults. The diameter and weight ratio of the organisms were used to assess the existence of seasonal variations and as a comparison with other studies and regions of the South Atlantic.

Data analysis

For laboratory experiments at temperatures of 20 °C and 25 °C (temperature assays), the parameters of Podocyst production per polyp; Days of excystment; Percentage of excystment; Number of strobilations and Number of ephyrae released per polyp were subjected to a non-parametric statistical test of Signals, used for paired/related samples. The parameters were obtained each month and for 4 months and between two treatments, in this case, the replication obtained temporally. The sample distribution was considered binomial, due to the fact that $n < 30$, adopting as a null hypothesis (H0) that the temperature of 25 °C has no influence on the tested parameters, accepting it when the probability of each parameter was higher than 0.975 probability (Siegel & Castellan Jr 2006).

For field and fishing data, monthly averages of 10 years of collection (used as averages due to gaps in *L. lucerna* occurrences - 27.7% in 101 trips) were calculated for the frequency of occurrence of the different size classes of *L. lucerna* and compared with the average temperature and salinity parameters for the same periods. The seasonality of the seawater temperature and salinity parameters obtained during collection were tested by ANOVA according to Zar (2010). The exponential correlation between the weight and the diameter of the umbrella was also obtained to evaluate any seasonal difference that would affect the growth rate of the species, with the data classified into summer/autumn and winter/spring, grouping a minimum number of observed pairs.

RESULTS

Asexual phase laboratory assays

After a period of 100 days of experiment, monthly averages were obtained for each parameter of polyp reproductive activity for the two temperatures tested. The Sign Test applied to the 20 °C and 25 °C treatments indicated significance for the influence of temperature on the excystment time and the number of ephyrae released ($p>93\%$). However, for the other parameters, the probability associated with the influence of temperature was greater than 70% (72% for the production of podocysts per polyp and 84% for the increase in the number of polyps, the excystment time and the number of strobilations) (Table I). The EP1 plate (25 °C) started the experiment with 5 polyps and 14 podocysts, reaching the end of the experiment with 35 polyps and 199 podocysts. Plate EP2 (20 °C), which began the experiment with 8 polyps and 14 podocysts, reached the end of the experiment with 12 polyps and 68 podocysts.

In the thermal shock test a 24% rate of emergence of polyps from podocysts was obtained, while at a constant temperature of 20 °C (previous experiment) the maximum percentage of excystment was 11.5% in 30 days

Table I. **Monthly averages obtained for each parameter in the asexual reproduction of *L. lucerna* polyps at temperatures of 20 °C and 25 °C for 100 days. *Parameters with significant differences depending on temperature (p<0.025).**

Month/ Year	Number of Polyps	Production of Podocysts per Polyp	Excystment Days*	Excystment Percentage (%)	Number of Strobilations	Number of Ephyrae Released per Polyp *
25 °C						
02/2022	05	3.4	15.3	10.0	3.0	3.3
03/2022	15	3.2	26.6	20.0	6.0	4.1
04/2022	27	4.1	26.0	5.0	10.0	4.2
05/2022	33	5.1	35.0	1.8	5.0	7.5
Average	**21**	**4.0**	**25.7**	**9.2**	**6.0**	**4.8**
20 °C						
02/2022	08	2.1	15.5	11.5	0.0	0.0
03/2022	12	3.2	34.0	7.3	10.0	3.2
04/2022	14	4.5	28.0	1.5	9.0	4.1
05/2022	14	4.8	47.0	0.0	2.0	3.5
Average	**12**	**3.7**	**31.1**	**5.1**	**5.3**	**2.7**

(Table I). It is also noteworthy that the podocysts used in the heat shock experiment were, on average, older than those compared to the constant temperature of 20 °C.

Information on the development time and asexual reproduction of polyps and growth from ephyrae to metaephyrae are summarized in Table II. Due to the limited number of observations on these development phases, which required individual monitoring, treatments at different temperatures were not applied. Thus, the range of 20 °C to 25 °C was considered in polyp cultures and the temperature of 23.5 °C in ephyra cultivation (maintenance laboratory temperature for Kreisel-type tanks). In any case, both the time for the production of podocysts by the polyps and the time for the growth of the ephyrae to juveniles (growth rate of 0.8 mm day^{-1}) involved a period of more than one month, while the strobilation of the polyps was observed. from two weeks after excystment.

Population dynamics of *L. lucerna*

Sampling carried out in the period 2012-2021 showed a higher occurrence and abundance of *L. lucerna* in spring, extending into summer (October to January). The distribution of size classes of *L. lucerna* indicated the presence of juveniles (< 5.0 cm in diameter) from the end of winter to the first two months of spring, suggesting a period subsequent to the strobilation of polyps present in the environment (Fig. 3). In this same period, the variation in water temperature showed a marked seasonality (ANOVA, $F (11.83) = 33.3361$, $p<0.001$) with values on an ascending gradient from July and August (18.5 °C and 18.7 °C) to December (25.0 °C). For salinity, no defined pattern was observed, varying from 30 to 33, except for the

Table II. Development time and growth rate for different phases of the life cycle of *L. lucerna* in the laboratory (polyps and ephyrae) and in the field database between juveniles and adults, with estimated temperatures, according to Schiariti (2008), Puente-Tapia et al. (2024) and those obtained in this study.

Phases (Laboratory)	Schiariti (2008)	This study
Young polyp → Podocyst production	20 – 25 days (22 °C)	25 – 39 days (20 - 25 °C)
Podocyst → Young polyp (Excystment)	10 – 60 days (22 °C)	16 – 47 days (20 °C) 15 – 35 days (25 °C)
Young polyp → Strobilation (Ephyra)	25 – 33 days (22 °C)	18 – 49 days (20 - 25 °C)
Ephyra → Metaephyra (Juvenile)	10 – 15 days (≈ 0.8 mm day^{-1}) (22 °C) (1.4 to 14 mm)	14 dias (0.8 mm day^{-1}) (23.5 °C) (0.9 to 12.5 mm)
Phases (Field)	**Estuary of the Río de la Plata (Uruguay and Argentina) Puente-Tapia et al. (2024)**	**South of Brazil (this study)**
Juvenile → Adult	-	≈ 10 months (0.6 mm day^{-1}) (18.5 – 26.9 °C, average 22.7 °C) (3.1 to 22.8 cm in diameter)
Mature adult	January/February (0.3 mm day^{-1}) (20 – 23 °C) (12.5 – 19.0 cm in diameter)	-

month of August, where salinity below 30 was recorded (Fig. 4).

For cohort analysis, it is suggested that the emergence of the juvenile class (<5.0 cm in umbrella diameter) observed in September led to an increase in the frequency (%) of the intermediate class (5.1-15 cm) in December, which caused the emergence of adults (>15.1 cm) in July. This class delimitation would result in a growth rate of 0.6 mm day^{-1} over a period of 10 months, with the growth rate being similar between the three size classes (Table II).

Finally, no change was observed in the patterns of the relationship between the diameter of the umbrella and the weight of the organisms for the different times of the year (Fig. 5). Most of the organisms sampled (70%) weighed less than 0.5 kg and measured less than 10 cm in diameter. The largest organism captured in trawls during the 10 years of study weighed 4.6 kg and measured 39 cm in diameter and was sampled in September 2021.

DISCUSSION

The results obtained from the population dynamics of *L. lucerna* based in the field and in the laboratory observations suggest that the life cycle of the species is associated with the seasonality of temperature in the environment. Following the chronology of abundance events of the juvenile class (< 5.0 cm in diameter), mainly in spring, and the highest abundance of organisms in the intermediate classes (5 cm to 15 cm) in spring/summer, and based on the polyp development time (podocysts and strobilation) and growth of ephyrae, it is suggested that the beginning of polyp population growth (excystment) and strobilation in the environment begins in winter, between the months of June to August and continues until November when the juveniles class still persisted in the sampling, also being the period of an ascending thermal gradient of 5.4 °C.

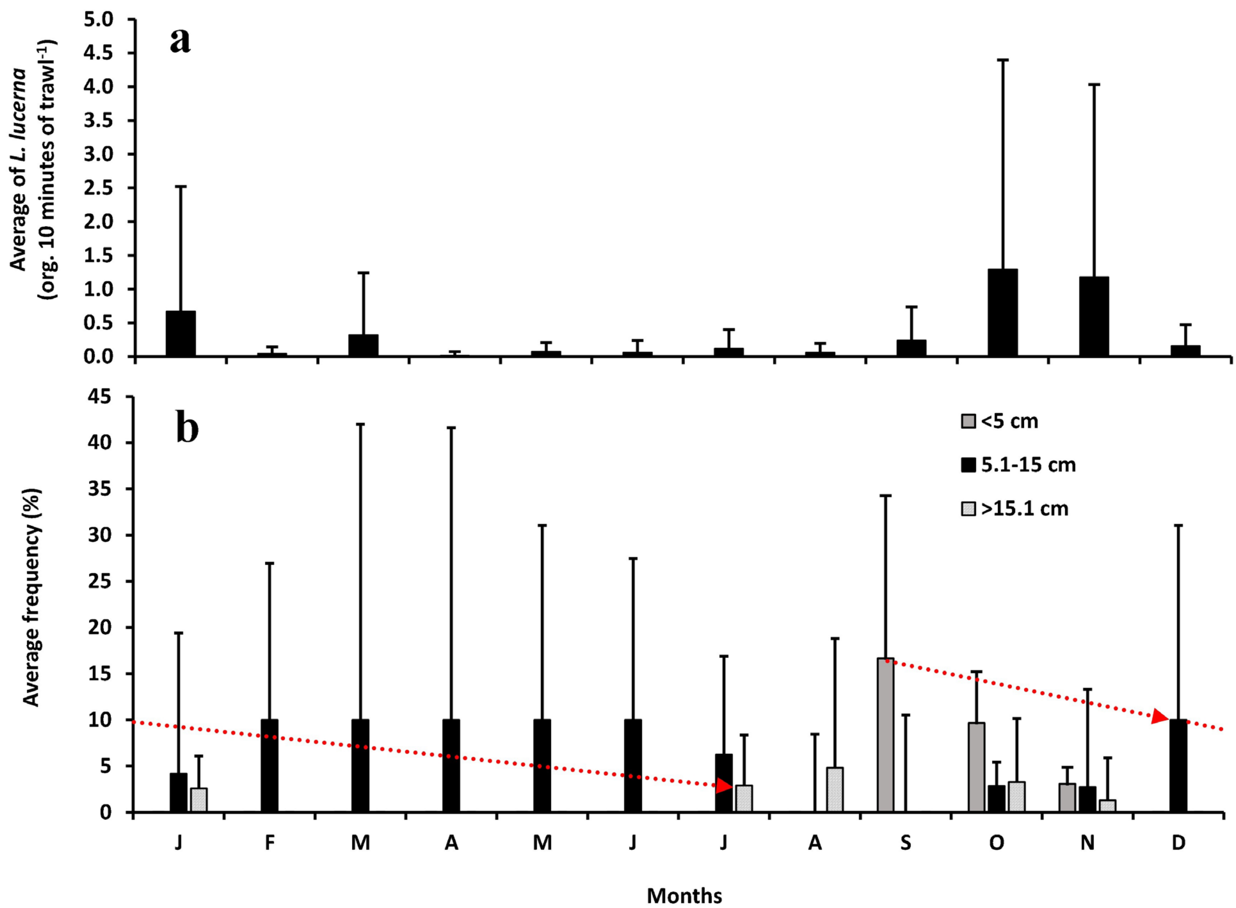

Figure 3. a - Average values (bars) and standard deviation (lines) of the relative abundance of *L. lucerna* (org.10 minutes of trawl^{-1}) and b - average frequency of occurrence (%) of three umbrella diameter classes occurring monthly between the years 2012 to 2021. The red dotted line represents the possible development of a cohort over the year.

Although the range of temperature tested for thermal shock to induce podocyst excystment was not applied considering the environmental conditions, this result, however, can be used as a model to stimulate excystment, as constant temperatures close to 30 °C also have the same effect (data not shown). Temperature proved to be decisive in the results for the excystment rate of podocysts in thermal shock experiments. The high frequency of the juvenile class in the environment during this period may be stimulated by the increase in the polyp population and, subsequently, by strobilation at the increasing temperatures observed at the end of winter. Making a comparison with the life cycle presented by Schiariti et al. (2008) and filling some gaps (Table II) highlights clarifying issues in the life cycle of the species despite some variability between authors results. Temperature is known as a determining factor for scyphozoans, involving excystment time (Schiariti et al. 2014) and strobilation, as well as salinity (especially in the fertilization success of eggs in the sexual phase, Schiariti pers. comm.) and mainly diet (Kawahara et al. 2012, Schiariti 2008, Schiariti et al. 2014, Thein et al. 2012). However, despite these factors influencing the asexual reproduction of rhizostome polyps, there is a high variability in reproductive behavior. Lee et al. (2017) in a study with *Nemopilema nomurai*,

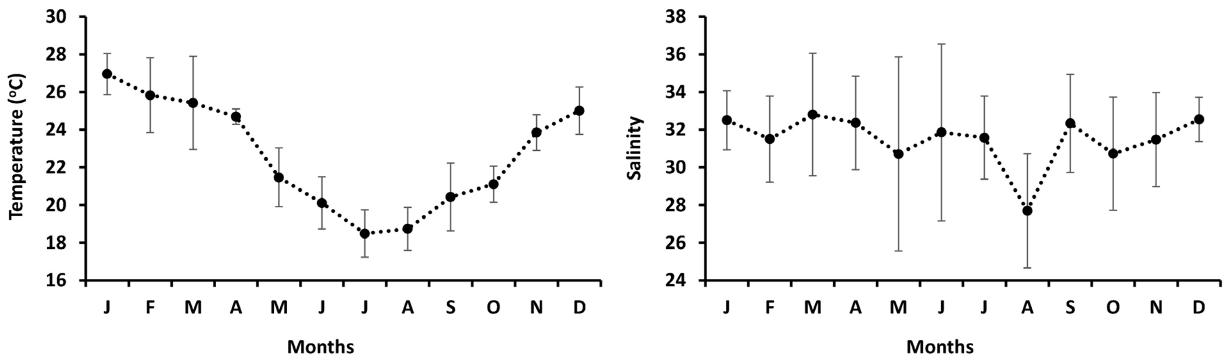

Figure 4. Average values (points) and standard deviation (lines) of temperature (°C) and surface salinity in the study area per month between the years 2012 to 2021.

a well-researched rhizostome species, highlights that, unlike salinity, higher temperatures stimulate the production of podocysts, while strobilation and the release of ephyrae occurred at low temperatures.

According to Schiariti et al. (2014) the mono-mode reproductive strategy of *L. lucerna*, which is dependent on podocysts, might be a limitation to the record of outbreaks (blooms) of the species and less dependent on sexual reproduction of the medusoid phase. Considering podocysts as the unique mode of asexual reproduction to increase the polyp bank of a species, their production is dependent on survival of polyps, diet and excystment which is negatively correlated with their age (Arai 2008, Blanquet 1972, Cargo & Schultz 1966). Due to this, polyp population growth is slower, and it is believed that the species' bloom processes are more related to the triggers of strobilation. According to Schiariti et al. (2008), the strobilation process of *L. lucerna* can also be triggered by thermal shock.

Additionally, in this work, the number of ephyrae released per polyp was stimulated by the highest temperature (25 °C) and could reach 6 ephyrae per polyp. Moreover, the species produces ephyrae continuously in cultivation. The seasonal change of environmental features would stimulate the beginning of the reproductive cycle of *L. lucerna* based on the temperature data recorded in this study. Under these conditions, the growth of the polyp population would involve more than a month considering the production and excystment of podocysts and the time required for the release of ephyrae would be two to three weeks (Table II). It is interesting to highlight that the occurrences of Scyphozoa outbreaks or blooms are more controlled by the strobilation and survival of ephyrae than by the growth of the polyp population (Xie et al. 2021, Fernández-Alías et al. 2023).

The finding of polyp populations in the natural environment faces difficulties in sampling on consolidated substrate due to the fragile and small size of the organisms (Vodopivec et al. 2018). In any case, the polyp population would only be subject to thermal shocks and higher temperatures that would stimulate the occurrence of outbreaks (blooms) if they are located at shallower depths, an environment where there is also a high supply of food (mesozooplankton). Furthermore, as the blooms observed for the species are sporadic (Fig. 1), there is a need for population growth of polyps under low predation to allow the production of ephyrae for a given region. Another possibility would be for the strobiliation process to prevail over the production of podocysts, which could

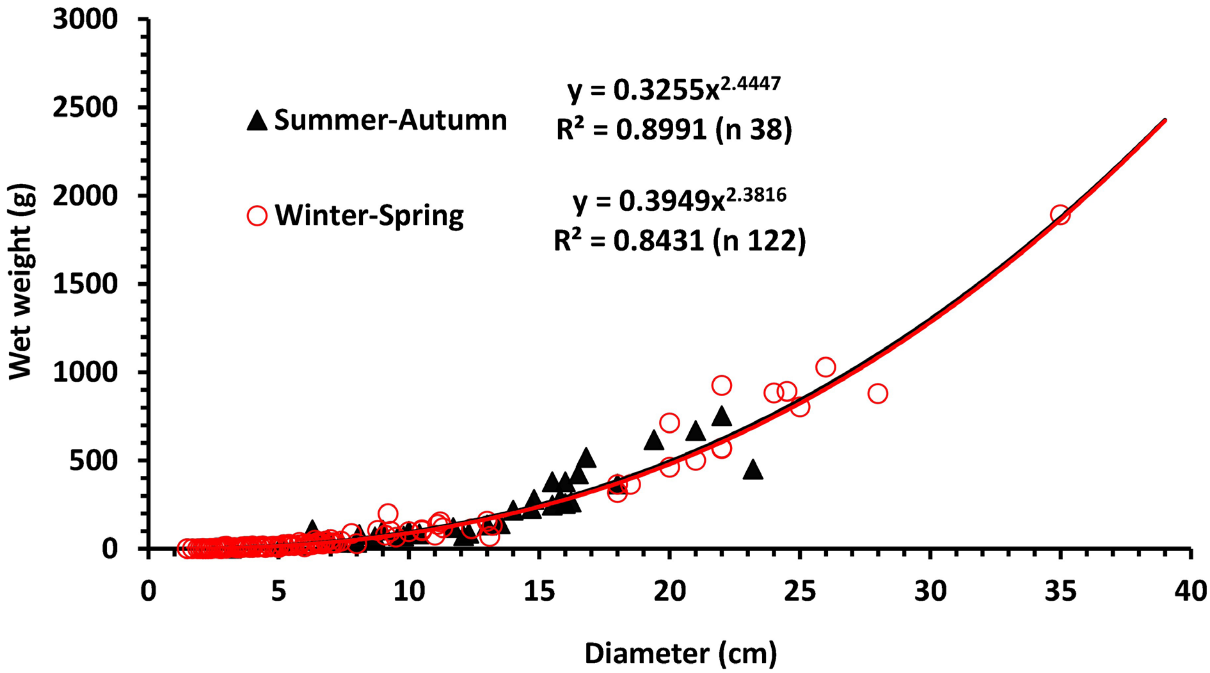

Figure 5. Relationship between umbrella diameter (cm) and wet weight (g) of *L. lucerna* captured between 2012 and 2021 on the south coast of Brazil. The data were grouped into organisms captured in summer/autumn (▲) and winter/spring (○) to estimate the exponential function.

occur shortly after the emergence of polyps following the sexual reproduction of medusoid forms.

The presence throughout the year of the intermediate size class of *L. lucerna* (5.1-15.0 cm) somewhat confirms the continuous release of ephyrae into the environment, but also highlights that their increased representation at the end of spring and beginning of summer, one to two months after the occurrence of juveniles, responds to the lowest growth rate of this phase in relation to ephyrae (from 0.8 to 0.6 mm day^{-1} between ephyrae and juveniles). The lack of seasonality in the relationship between the weight and diameter of the organisms, as observed in this study, draws attention to the inability to define periods for the growth and maturation of the gonads (greater weight of mature organisms), which may also explain the lower growth rate for this size class. However, even this intermediate size class presents a percentage of mature organisms that can release larvae into the environment (Schiariti et al. 2008) and that may also be favored by the presence of consolidated substrates that are abundant on the coasts of Santa Catarina, Paraná and southern São Paulo (Fig. 2). Additionally, this coast is also characterized by the largest supply of continental waters, which interfere with local salinity and the responses of the species' fertility rate and planktonic (food) production (Resgalla Jr. 2011).

For the Rio de la Plata estuary, Puente-Tapia et al. (2024) presented 20 years of catch data for *L. lucerna* in industrial fishing. Highlighting the abundance of adult individuals in summer and the diameter/weight ratio (slope 2.5-2.6) being larger than observed in this study (slope 2.3-2.4), lower growth rate (Table II), characterized by adults whose metabolism is more focused on reproduction and with a reduction in size of organisms with the arrival of autumn. Unlike in southern Brazil, adults of *L. lucerna* (> 15 cm in diameter) presents information limitations in the field because or they present active gregarious behavior (Kaartvedt et al. 2015) or the typically low density of this size class and its associated dispersion.

Although the population at the Río de la Plata estuary is composed of adult and mature specimens, the absence of consolidated substrates in the region has been used as justification for the absence of juvenile classes in the region (Schiariti 2008, Schiariti et al. 2018). According to these authors it is suggested that these organisms originate in the north (southern Brazil) due to the dominant flow of platform waters to the south, accumulating older organisms in the Rio de la Plata estuary.

In practice, it would take at least 10 months for individuals of *L. lucerna* to grow to reach the size of organisms in the Plata region and being transported by coastal currents from the southern Brazilian shelf (Costa & Moller 2011). However, this displacement is neither continuous nor unidirectional (Zavialov et al. 2002), and can be altered by southerly winds, including convergence towards the coast and even promote massive strandings on beaches. The strandings shown in figure 1, observed in the years 2020 and 2024, were associated with winds from the southern quadrant and occurred up to 24 hours before the events.

The occurrences of ephyrae of the species in field samples in the Lagoa dos Patos estuary (Nagata et al. 2021), as well as the presence of juveniles (metaephyrae or juveniles) in the central region (Nogueira Jr. et al. 2010) and north (this study) of the state of Santa Catarina, confirm breeding areas for the species in southern Brazil. Finally, a molecular study at the population level would be the most applicable to confirm the relationship between the locations where the species occur.

CONCLUSIONS

This study presents evidence of the influence of temperature on the asexual reproduction of Scyphozoa *Lychnorhiza lucerna*, making the excystment of podocysts shorter, or stimulating the production of ephyrae. The data obtained from field sampling and the different size classes of these organisms demonstrate agreement with these results when comparing environmental temperature variations. The results suggest that the population increase of the species can be attributed both to the thermal gradient and to the increase in water temperature influencing the strobilation process. Addiotionally, it is suggested that the species has an annual cycle, with a well-defined period of asexual reproduction, with strobilation and the release of ephyrae being factors that stimulate the occurrence of blooms. Southern Brazil can be considered a breeding area for the species and a point of dispersal of organisms to the south of the continent.

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