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Cryptic life stages in scyphozoan jellyfish: Larval settlement preferences of the South American sea nettle *Chrysaora plocamia*

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ABSTRACT

Bloom forming jellyfish have received considerable attention over the past years. And while the eye-catching medusa is well studied, little is known about its small, inconspicuous and hard to find polyp-counterpart. In fact, so hard to find that polyps of most scyphozoan species have not been detected in their natural habitat. Considering the important roles polyps may play in jellyfish bloom formation, identifying the criteria for planulae to select suitable microhabitats that warrant the well-being and survival of polyps is a key issue. In order to find clues on the characteristics of natural habitats of *Chrysaora plocamia* polyps, settlement preferences of planulae were determined in a laboratory study. The settlement density, geotaxis and colour preferences were assessed, using a three-dimensional substrate that provided settlement areas of different orientation, levels of shelter and colours. Planulae exclusively colonized horizontal surfaces in an upside down position, tended to settle in sheltered areas and showed significant preferences for green and red substrates. If planulae of the jellyfish *C. plocamia* display similar preferences in the field, polyps should be found on protected substrates that provide overhangs, small caves, crevices or roof-surfaces, and green or red substrates, like stipes and blades of macroalgae, or crustose coralline algae.

1. Introduction

Due to interactions with humans and population proliferations worldwide, the interest in jellyfish research has grown substantially over the past decade (Condon et al., 2012; Graham et al., 2014). The complex life cycle of scyphozoans (e.g., Ceh et al., 2015) generally comprises a pelagic medusa and a benthic polyp generation. The pelagic planulae, product of the sexual reproduction of medusae, sink to the benthos, seek suitable settlement substrates and metamorphose into benthic polyps. Here they undergo various body-plan changes and through a process called strobilation produce pelagic medusae again.

Owing to their high productivity and impressive repertoire of asexual reproductive strategies, polyps have been recognized as a potent agent for population-blooms (Purcell, 2007; Lucas et al., 2012). However, due to the difficult quest to detect polyps in their natural environment, information on in situ polyp generations is lacking and reliable predictions on jellyfish proliferations are thus hard to make. As such, laboratory experiments that focus on factors that affect the survival of these cryptic life stages may facilitate us to locate polyp stages in their natural environment and therefore open a new avenue of in situ polyp research.

In sessile marine invertebrates, the selection of larvae for suitable settlement sites is a crucial process for the success of survival and reproduction. The colour of ambient light guides coral larvae to suitable microhabitat (Strader et al., 2015), and geo- and phototaxis might play important roles in settlement choices in medusozoan planulae: planulae attached upside down to floating substrates on the water surface (Raskoff et al., 2003), or tended to settle at the edges of a settlement vessel (Brewer, 1976). Species like *Aurelia aurita*, *Cyanea capillata*, *Ptychogena lactea* are light sensitive and settle under opaque objects (Custance, 1964; Brewer, 1978; Brewer, 1984). While these studies mainly focused on the type and textural properties of settlement surfaces, they did not pay attention to the role colour may play in the process of habitat selection in planulae.

The South American sea nettle *Chrysaora plocamia* (Lesson 1832) is an abundant species in the Humboldt Current System of Chile and Peru (Quiñones et al., 2013; Ceh et al., 2015). It generally occurs from late spring to late summer (October to February), and is recognized for its negative effects on human industries, e.g., pelagic fisheries and tourism in the area (Mianzan et al., 2014). In order to narrow down possible natural habitats that may host wild polyps, a laboratory study was performed to assess fine scale settlement preferences of *C. plocamia* planulae. Settlement preferences were investigated using a three–

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dimensional substrate that provided different settlement choices for orientation, shelter and colour.

2. Materials and methods

2.1. Study location and organism

Planulae were collected from the oral arms of two female *C. plocamia* medusae, captured 20 km North of Antofagasta Bay (28° 27′ 30.35″S, 70° 36′ 08.36″W), Chile in January 2015. Permits for collecting jellyfish were not needed as the study animal *C. plocamia* is considered a pest.

2.2. Experimental design

Fifty planulae, randomly selected from the two adults collected, were counted into each of four experimental units (200 mL plastic vessels of 8.5 cm depth), containing seawater and a settlement substrate (6.4×4.8 cm^2 in size), that was placed upside down on the water surface. Each of four settlement substrates were assembled from toy-LEGO bricks (The LEGO Group, Billund, Denmark); LEGO is made from ABS (acrylonitrile butadiene styrene), a thermoplastic polymer comprised of three monomers, acrylonitrile, 1,3-butadiene and styrene. According to the manufacturer the colours and materials in ABS plastic do not rub off or leach and meet the same material standards for safety that are required of plastic eating utensils. All four plastic vessels were equal but settlement substrates were constructed differently in terms of colours (i.e., different colours in different positions); however, each colour- shelter combination was similarly represented within substrates (see Suppl. Info. 1). Straight as well as sloped bricks were used to assess the preferred settlement orientation of planulae, i.e., horizontal, vertical or sloped, upside down or right side up. To test for shelter preferences (e.g., crevices and edges), each substrate was built with three different levels of depth (Suppl. Fig. 1), where the first and deepest level was considered the most sheltered settlement area, the second medium sheltered and the third exposed. The difference in depth between levels was determined by the height of one brick (9.6 mm). Seven different colours of bricks (yellow, white, red, blue, black, green, brown) were used to detect colour preferences. Settlement substrates were not pre-conditioned in sea water before the treatment.

The settlement units were kept at 18 °C under a 12:12 light dark regime (roughly following the conditions in Riascos et al., 2013) and examined under a dissecting microscope every 8 h until >50% of all planulae had settled, which occurred within 48 h. Settlement was considered complete when planulae had attached to the substrate and metamorphosed into scyphistomae. Hereafter, the settlement structures as well as the plastic vessels were examined for numbers of established polyps, distinguishing between types of orientation, levels of shelter and colours planulae settled on.

2.3. Data analysis

A two-way ANOVA model, followed by a Tukey HSD test for pairwise comparisons was used to test for differences in settlement density (planulae cm^{-2}), between levels of shelter (factor 1, three levels) and between colours (factor 2; seven levels). The interaction term (shelter × colour) was also included in the statistical model. Data on settlement density were first transformed ($Y = \log(X + 1)$) to meet the assumption on normality of distribution for this parametric test. The type of orientation was not included in the analysis, neither areas with sloped bricks, because settlement only occurred on horizontal surfaces. Statistical analyses were performed using the software JMP 10.0.0 (SAS Institute Inc., Cary, NC, United States). This study was approved by the ethics commission "Comité de Ética de la Universidad de Antofagasta."

3. Results

At 48 h of incubation time > 50% of planulae had settled in each of the four experimental units. Out of fifty planulae added per unit, 29, 26, 25 and 26 planulae settled on the provided structures, corresponding to an average settlement density of 0.9 planulae per cm^2. <5 planulae per experimental unit settled on the bottom of the plastic vessel, whereas the remaining planulae were still swimming and searching at 48 h.

On the provided structures planulae settled exclusively upside down on horizontal surfaces; vertical areas and slants were never colonized. Planulae tended to settle more in sheltered areas than on medium sheltered and more in medium sheltered than in exposed areas; however, no significant differences were found between levels of shelter (Fig. 1; Table 1). Moreover, planulae settled more often on specific colours, preferring red and green (Fig. 2, Table 1), which was confirmed by the statistical analysis showing significant differences between colours, independent of the level of exposure. Post-hoc tests showed differences in settlement density between red/green and blue surfaces and between red/green and brown surfaces (Table 2). Comparing the settlement density of planulae on different colours to the wavelength spectrum of visible light, planulae of *C. plocamia* displayed no significant differences in settlement density within the 500 to 700 nm range, i.e., between green/red and yellow (Fig. 2).

4. Discussion

This is the first study reporting on settlement preferences of planulae for the scyphozoan jellyfish *C. plocamia*, providing information on the settlement density and on preferences for orientation, shelter and colours of planulae.

The settlement density was homogenous between replicate settlement structures. Considering the growth into an adult polyp and the expansion through podocyst formation, one polyp per cm^2 might indicate the average natural settlement density and corroborates with results of previous experiments for this species (unpubl. data).

On the substrates planulae attached exclusively upside down and only on horizontal surfaces. Negative geotaxis combined with negative phototaxis has been reported to play an important role for the orientation of planulae settlement in scyphozoans (Brewer, 1976; Brewer, 1978; Cargo, 1979; Kikinger, 1992; Pitt, 2000). It has been hypothesized for marine invertebrate larvae that negative geo- and phototaxis may be an evolutionary adaptation to avoid mortality through solar irradiation, sedimentation, and predation by settling below overhangs and in concealed habitats (Svane and Dolmer, 1995). Moreover, a certain distance from the bottom may reduce the risk of anaerobic conditions

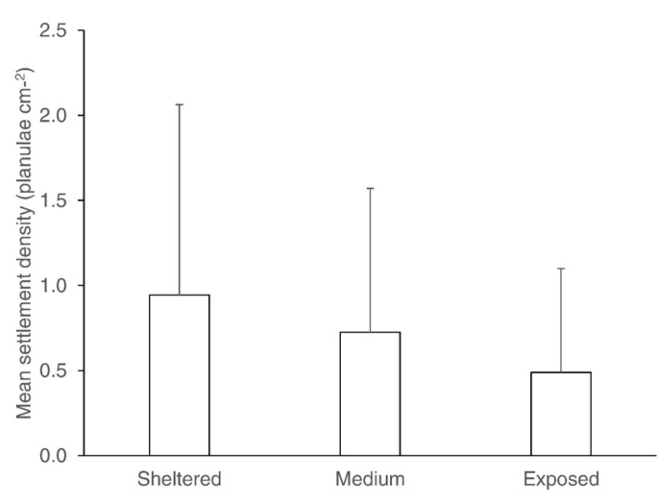

Fig. 1. Mean settlement density of *Chrysaora plocamia* planulae per cm^2 on different exposure levels. Bars denote standard deviations around the mean.