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The effect of light intensity and tidal cycle on the hatching and larval behaviour of the muricid gastropod *Chorus giganteus*

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ABSTRACT

Encapsulation is a common strategy observed among marine caenogastropods. Although the capsule confers protection for embryos, its rigidity and strength pose a significant challenge as the larvae hatch. The factors that drive hatching among these benthic marine gastropods have scarcely been studied. In this study, we experimentally evaluated whether the capsule plug opening and larval release processes were synchronised with day/night or tidal cycles in the muricid gastropod *Chorus giganteus*. In addition, we tested the effect of different levels of light intensity on the swimming behaviour of pre- and post-hatching larvae. The results showed that capsule plug rupture occurred in synchronous pulses of capsule groups during both day and night. A periodogram analysis did not show circatidal rhythmicity in either the plug rupture or total number of capsules hatched. The highest percentage of larvae hatched at sunset and during the night (82.9%), whereas only 17% of them hatched during the day. These results demonstrate a circadian pattern. The swimming activity of the larvae decreased significantly with light intensity. In the darkness, over 80% of the larvae actively swam in the tank and the majority of the larvae initially moved toward the water surface. No swimming activity was observed at 500 $\mu E * m^{-2} * s^{-1}$ of photon flux density. These results suggest that *C. giganteus* larvae present negative phototropism behaviour and that capsule plug degradation occurs by other processes like internal physical enzymatic actions.

1. Introduction

Encapsulation is a mode of parental protection commonly observed among marine invertebrates, in which the embryos are enclosed in capsules of various shapes and chemical compositions (Pechenik, 1979). Protection against desiccation, osmotic changes, UV light or predation are examples of the numerous advantages of this strategy (for a review, see Przeslawski, 2004). Inside the capsules, the embryos may either advance or complete their development, thus determining indirect or direct life cycle strategies, respectively (Averbuj and Penchaszadeh, 2010; Hawkins and Hutchinson, 1988; Ilano et al., 2004; Pechenik et al., 1984). Although the capsule confers protection to the embryos, its rigidity and strength pose an important challenge to the hatching larvae. At the end of the encapsulation period, the larvae must open the capsule and synchronise their hatching time with their developmental stage. Under this scenario, hatching would depend on the complex chemical, physical and behavioural larval traits.

The capsules of marine gastropods are mainly composed of protein and carbohydrates (Bayne, 1968; Hawkins and Hutchinson, 1988; Sullivan and Maugel, 1984). Observations with optical and electron microscopy have shown that the capsule walls of gastropod species are multi-laminated structures that typically consist of more than four layers (D'Asaro, 1988; Garrido and Gallardo, 1993; Hawkins and Hutchinson, 1988; Sullivan and Maugel, 1984; Tamarin and Carriker, 1967). This configuration provides resistance to mechanical damage and biological deterioration (Hawkins and Hutchinson, 1988). In addition, in muricid species, the ovicapsules have a protein plug in the apex where the embryos hatch. Therefore, hatching from the ovicapsule may be divided in two continuous steps: 1. the degradation and rupture of the capsule plug and 2. larval release. The osmotically induced uptake of water and chemical dissolution are the main mechanisms that open the plug (Hancock, 1956; Hawkins and Hutchinson, 1988; Kennedy and Keegan, 1992; Pechenik, 1975). Additionally, direct mechanical action of the enclosed embryos on the plug has been reported (Leiva et al., 1998; Vaughn, 1953). Typically, a combination of the above-mentioned mechanisms may be observed. For example, Hawkins and Hutchinson (1988) recorded the osmotic and enzymatic mechanisms in capsule openings for the marine gastropod *Ocenebra erinacea*.

In contrast, the larval release process in marine gastropods has been studied to a lesser degree. Larval hatching in some marine invertebrates is synchronised with environmental cues such as day–night cycles, tidal cycles or moon phases (Cancino et al., 1994; Forward, 1987; Morgan, 1995; Morgan and Christy, 1995; Saigusa, 1988; Ziegler and Forward, 2005). In crustacean species, larval release is typically synchronised with the circadian cycle but also may be related to the tidal cycle (Ziegler and Forward, 2005). For example, larval release of the subtidal

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crab *Neopanope sayi* and the intertidal crab *Sesarma cinereum* occurs principally during high tides (De Vries and Forward, 1989). The tidally rhythmic behaviour observed even in subtidal species suggests that hydrostatic pressure variation may stimulate larval activity (Naylor, 1985). In viviparous sponges, larval release concentrates in the morning, which suggests a diurnal periodicity (Amano, 1986), whereas in brooding corals, larval release responds to the lunar cycle (Johnson, 1992; Stimson, 1978; Tanner, 1996). In this manner, patterns of light–dark cycles and/or the tidal cycle are the environmental cues that appear to promote larval release among intertidal and subtidal marine invertebrate species.

In addition, larval response to the light after hatching has been associated with larval type (Thorson, 1964). Thus, larvae with long pelagic phase, such as planktotrophic larvae, would respond positively with greater frequency to light, migrating to the surface layers during day until metamorphic competence occurs (i.e. Poulin et al., 2002; Romero et al., 2012; Thorson, 1964). This nocturnal diel vertical migration could be related to food availability and predation risk (Morgan, 1995; Ohman et al., 1983; Poulin et al., 2002). In contrast, demersal larvae or larvae with short pelagic life, such as lecithotrophic pediveliger larvae, would show negative phototropism with high swimming activity at low light intensities. This may be related to the poor light condition at the benthic substratum experimented by benthic larvae, in order to promote the search of suitable substrata for metamorphosis immediately after hatching (Gallardo, 1981; González and Gallardo, 1999; Thorson, 1964).

Chorus giganteus is an endemic species of the Chilean coast and occurs sub-tidally on soft sediments and in areas with small rocks. Embryonic development in *C. giganteus* occurs between 60 and 100 days inside of semi-transparent ovicapsules that are attached to the substratum. The females deposit nurse eggs inside the capsules to be consumed by the larvae at the trochophore stage. At the completion of the encapsulated development, 150–300 lecithotrophic pediveliger larvae with a 900–1000 μm shell length emerge from each ovicapsule (Gallardo, 1981; González and Gallardo, 1999; Leiva et al., 1998). Before hatching, the capsule plug gradually dissolves at the end of the intracapsular period and becomes transparent in colour and decreases in thickness (González and Gallardo, 1999). These observations suggest a chemical mechanism of the plug degradation. In addition, Leiva et al. (1998) observed that the embryos aggregate beside the capsule plug and force its rupture through direct mechanical action. The subsequent larval release is a slow process that may require many hours (González and Gallardo, 1999). However, little is known regarding the factors that drive the hatching process, although some results on the morphology and behaviour of post-hatching larva have been reported.

After hatching, the pediveliger larvae of *C. giganteus* extend a tetralobular velum approximately 1650 μm on each side. The larvae alternate periods of active swimming using the velar cilia and periods of crawling on the seabed facilitated by retracting the velum inside of the shell and utilising a well-developed foot (González and Gallardo, 1999; Leiva et al., 1998). The pediveliger has statocysts and ocelli, which orient the larva in response to gravity and light, respectively. According to previous experimental studies, newly hatched larvae alternate between swimming and bottom-crawling during 2–5 days until the larva becomes competent and metamorphosed into a juvenile (Gallardo, 1981; González and Gallardo, 1999; Leiva et al., 1998). These observations suggest that larvae of *C. giganteus* search for suitable setting benthic substrates immediately after hatching promoted by a negative phototropism behaviour. Based on the evidence exposed above, we suggest that the light and tidal cycles promote the rupture of the capsule plug and the hatching of *C. giganteus* by influencing the behaviour of the pre-hatching larvae inside of the capsules. We experimentally evaluated three questions in this study: 1. whether the final plug rupture is synchronised to the light–dark or artificial tidal cycles, 2. whether the pattern of larval release is synchronised with the light–dark cycle and 3. Whether the swimming activity of the artificially hatched embryos and pediveliger larvae changes with different light intensities.

2. Materials and methods

2.1. The effects of light and tide on capsule plug rupture

Adults *C. giganteus* were collected from the Gulf of Arauco, Chile (37° 10′S; 74° 25′S), maintained with a constant flow of seawater and air, and fed ad libitum in the coastal laboratory of the Universidad Católica de la Santísima Concepción at Lenga in central Chile (36° 45′ S, 73° 10′ W). Capsules spawned by females were collected and maintained in flow-through seawater tanks between 12 and 15 °C. Once the embryos reached the pre-hatching veliger stage, 150 capsules were randomly transferred to an artificial tidal cycle system with a 12:12 light/dark photoperiod. Tidal cycles of 6 h were simulated using water pumps that produced a tidal variation of 1 m. As *C. giganteus* is a subtidal species, capsules were maintained underwater during the entirety of the experiment. This allowed for the simulation of only hydrostatic pressure changes at low and high tidal periods while discarding confounding factors such as desiccation and oxygen level. Simultaneously, other groups of 150 capsules (the control group) were maintained underwater with an identical photoperiod. For both treatments, the capsules were maintained in a vertical position inside a transparent container to simulate natural conditions and facilitate outside observation. Three replicates (transparent containers) with 50 capsules per replicate were cultivated in seawater (approx. 35 ppm) maintained at a constant temperature (13 °C) and aeration. The experiments were performed for seven days, and the number of opened capsules was recorded every 3 h. We correlated the hatching pattern with the artificial tidal cycle using a spectrogram analysis to evaluate synchronicity. In addition, an ANOVA was used to compare the percentage of opened capsules between the treatments with and without tidal cycles. The effect of light on the percentage of opened capsules was evaluated with a Wilcoxon test. All analyses were performed using Statistica 10 software (StatSoft, Inc.).

2.2. The timing of the larval release

The pattern of larval release was evaluated in nine capsules containing embryos at the pre-hatching stage. The capsules were obtained from 9 different females (1 capsule per female) and individually cultivated in glass jars with 300 ml of filtered seawater (1 μm) in a cultivation chamber maintained at 13 °C (±1) with a natural photoperiod, which was measured in situ using a light meter. The water inside of the jars was stirred by a paddle system with an oscillating movement at a speed of 1.82 ± 0.15 $cm * s^{-1}$. The water was changed every second day. Once the hatching began, the larvae were collected with a Pasteur pipette and counted every 3 h until all larvae had hatched from the capsule. A time series analysis (periodogram) was performed to explore the synchronicity pattern of larval release with the circadian rhythm using Statistica 10 software (StatSoft, Inc.).

2.3. Responses of the larvae to light intensity and light/dark conditions

The responses of the larvae to the light were evaluated in 663 newly hatched larvae collected from a pool of capsules from different females. Groups of 16–42 larvae randomly chosen were transferred from the aquarium to a Petri dish that was 5 cm in diameter and contained 10 ml of filtered (1 μm) seawater. The larvae were acclimated for 30 min in the dark and then exposed to five different levels of photon flux density: 0, 10, 40, 240 and 500 $\mu E * m^{-2} * s^{-1}$. After 60 min, the larval behaviour was recorded and classified into two different categories: 1. larvae with the velum extended and actively swimming and 2. larvae with the velum retracted and crawling on the bottom of the Petri dish.

The percentage of larvae in the different groups was analysed using an ANOVA after an arcsine square root transformation.

In addition, we compared the behaviour of pre- and post-hatching larvae in regard to the light/dark stimuli. The pre-hatching larvae were obtained from a capsule containing pediveliger larvae approximately one week before hatching. To collect the pediveliger larvae, the capsule plug was carefully cut with a scalpel and the larvae were transferred to a Petri dish using a Pasteur pipette. We recorded the swimming behaviour for 140 min in three replicates per treatment (light/dark) consisting of 30–35 larvae. During the 140 min, the larvae were exposed to light (120 $\mu E * m^{-2} * s^{-1}$) for the initial 70 min and then placed under dark conditions for the remainder of the recording. The swimming behaviour was recorded every 20 min and categorised as in the previous experiment (the swimming and crawling larvae). For the control groups, we recorded the swimming behaviour of larvae that were exposed to constant light (120 $\mu E * m^{-2} * s^{-1}$) or dark period. Between 3 and 5 replicates per treatment were performed. All of the experiments were performed at 15 ± 1 °C.

3. Results

3.1. The effects of light and tide on capsule plug rupture

A total of 113 capsules (37.7%) hatched during the experiments. The capsule plug rupture occurred in highly synchronised pulses during the day and night periods (Fig. 1). The time series analysis showed that the capsule opening was unsynchronised with the simulated tidal cycle (Fig. 2). In addition, the percentage of hatched capsules did not differ between the treatments with (37 ± 6%) and without (38 ± 15%) a tidal effect (ANOVA: $F_{1,4} = 0.005$; $p = 0.94$). Similarly, no significant differences were observed between the day (19 ± 6.7%) and night (18 ± 5.5%) periods (Wilcoxon Test: $n = 6$; $T = 7.5$; $z = 0.63$; $p = 0.53$).

3.2. Timing of the larval release

A total of 1347 larvae were released from the nine experimental ovicapsules (150 ± 16 larvae per capsule). The frequency distribution of the larval release was unimodal and strongly influenced by the light cycle (Fig. 5). The highest percentage of larvae hatched at sunset and during the night (82.9%), whereas only 17% of the larvae hatched during the day (Fig. 3). The periodogram analysis showed a circadian pattern of larval release with a maximum spectral density of larval released in 24 h period (Fig. 4).

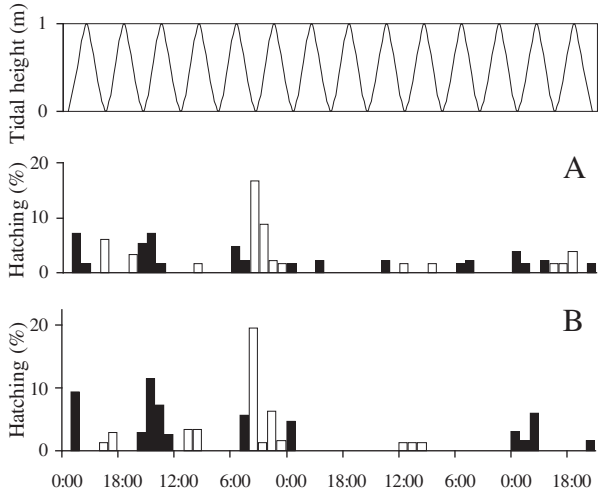

Fig. 1. The mean hatched capsules of *C. giganteus* as a function of both light–dark and tidal cycles (A) and as a function of light–dark without tidal effects (B). Each bar represents the mean of 3 replicates (± 1 SD), white and black bars represents hatching occurring during night or day respectively.

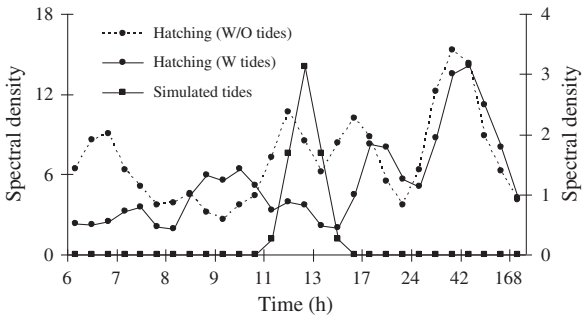

Fig. 2. Periodograms of the percentage of capsules hatching in the treatments with (W tides) and without tidal (W/O tides) effects. An additional periodogram of the simulated tidal cycle is shown with an obvious peak at 12 h.

3.3. Responses of the larvae to light intensity and the light/dark conditions

The swimming activity of the larvae decreased significantly with light intensity (ANOVA: $F_{4,17} = 37.5$; $p < 0.01$; Fig. 5). In the dark, over 80% of the larvae actively swam in the tank and most initially moved toward the water surface and then to the middle of the water column. Fewer larvae remained swimming close to the bottom of the tank. No swimming activity was observed at 500 $\mu E * m^{-2} * s^{-1}$ of photon flux density (Fig. 5). The behavioural patterns were similar between the naturally and artificially hatched larvae, as both groups showed high swimming activity during the dark periods and inactivity under light period (Fig. 6). The larvae that were continuously exposed to dark or light showed similar behavioural patterns (activity during the dark periods and low activity during the light periods) in all experiments (Fig. 7).

4. Discussion

Larval hatching in encapsulated gastropod's embryos includes two different and consecutive steps: capsule plug degradation and larval release. In this study, we examined the assumption that both steps in *C. giganteus* might be uncoupled with capsule openings occurring under both the dark and light conditions; in contrast, larval release was observed mainly at night, which shows a circadian rhythm. The swimming activity decreased at a higher light intensity in pre- and post-hatching larvae with total inhibition at 500 $\mu E * m^{-2} * s^{-1}$. These results suggest that the rupture of the capsule plug in *C. giganteus* was controlled by intrinsic factors and that larval hatching occurred because of external stimuli.

In this study, plug degradation and the opening of the capsules in *C. giganteus* did not present a tidal or circadian pattern. Among

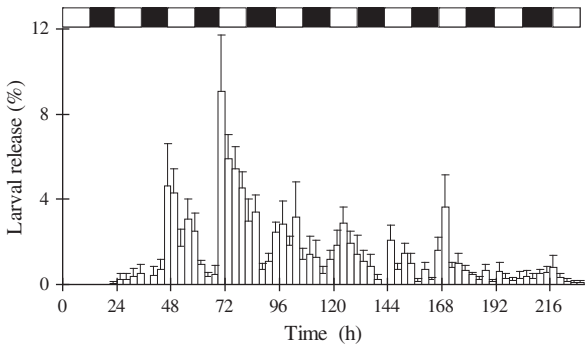

Fig. 3. The mean daily release (± 1 SD) of *C. giganteus* larvae in the laboratory as a function of the natural photoperiod ($n = 9$ capsules, a total of 1437 larvae).

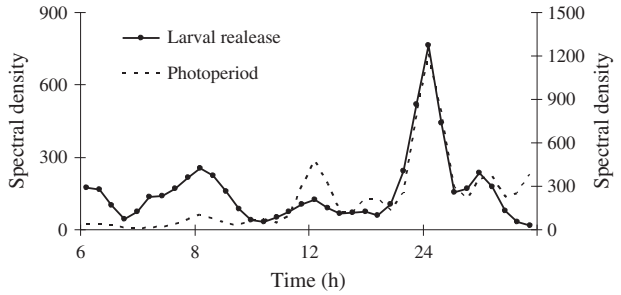

Fig. 4. Periodograms of the number of larval released (solid line) and of natural photoperiods (broken line) measured in situ using a light meter.

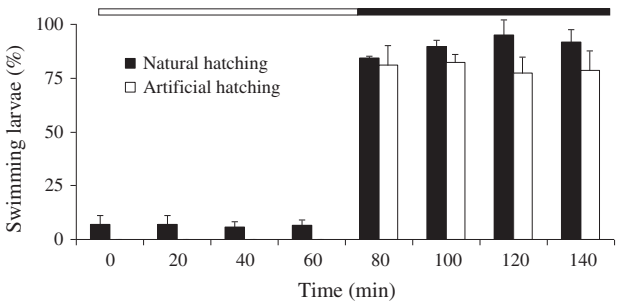

Fig. 6. The percentage of active larvae of *C. giganteus* before and after the change from light (120 $\mu E*m^{-2}*s^{-1}$) to dark conditions. Solid bars represent the naturally hatched larvae; open bars represent the artificially hatched larvae. The values provided are averages ± 1 SD (n = 3).

marine invertebrates, capsule opening is attributed to external factors, such as maternal action (in species with brooding behaviour; King, 1976; Oyarzun and Strathmann, 2011), and internal factors, such as changes in the intracapsular osmotic pressure, enzymatic degradation and/or mechanical actions of the larvae (osmotic and chemical action: Hancock, 1956; Hawkins and Hutchinson, 1988; Kennedy and Keegan, 1992; Pechenik, 1975; mechanical action: Leiva et al., 1998; Vaughn, 1953). Observations of the intracapsular larval behaviour of *C. giganteus* showed that the larvae swim upward inside the capsule mainly at night and most likely exert pressure on the plug, which may support the mechanical action hypothesis. However, capsule plug rupture was also evident during the day when the larvae showed low swimming activity. This finding suggests that capsule opening may be attributed not only to the mechanical effect of the larvae but also to enzymatic action. Our results support previous studies on *C. giganteus*, which suggest that the enzymatic and mechanical processes led by the larvae produce capsule plug ruptures in this species (González and Gallardo, 1999; Leiva et al., 1998). However, the capsule opening time in marine gastropods may also be controlled by external environmental factors, thus showing a high plasticity. For example, Miner et al. (2010) reported that hatching in the direct developing *Nucella lamellosa* is delayed in capsules that are exposed to the water-borne chemicals of predators, whereas the presence of adult conspecifics accelerates hatching. The differences in hatching time affect the body size of juveniles. In this manner, the evolution of an optimal capsule opening strategy is driven by a complex interplay between internal and external factors, which determine the developmental mode and larval survival.

The larval behaviour of *C. giganteus* was strongly influenced by the light conditions. Larval release showed a clear circadian pattern, with maximum values observed at night. These results were consistent with the negative relationship between larval swimming activity and light intensity. The pre- and post-hatching *C. giganteus* larvae were highly active during the dark periods and showed extensions of the velum and ciliary activity. High light intensities had an inhibitory role on larval swimming, and at 40 $\mu E*m^{-2}*s^{-1}$, the majority of the larvae (more than 80%) had retracted velums, sank to the bottom of the tank and displayed a crawling behaviour. The tendency of the larvae to swim toward the capsule plug and then to the water surface, particularly at night but also during the day, suggests a negative geotactic response. These results contrast with previous suggestions of positive phototactism in *C. giganteus* larvae (González and Gallardo, 1999). Although the light conditions of the experiments were not reported by González and Gallardo (1999), our reinterpretation indicates it is possible that the experiments were performed at low light intensities, therefore promoting an increase in the swimming activity of the larvae toward the surface, which may be misinterpreted as positive phototactism. Similarly, our study observed a doubling of time in the larval release process (48 ± 12 h) in comparison with the results of González and Gallardo (1999). This finding may be explained by differences in the experimental light conditions. It is possible that the low light intensity stimulated larval swimming activity and accelerating hatching.

Many pelagic larval stages of some fish and invertebrate species exhibit daily vertical migrations (Forward et al., 1996a, 1996b; Poulin et al., 2002; Shanks, 1986). The most common diel vertical migration type corresponds to a deeper distribution of larvae during the daytime and surfacing at night, although a reverse pattern may be observed in some species (Morgan, 1995; Ohman et al., 1983; Poulin et al., 2002; Richards et al., 1996). The larval behavioural response and diel vertical migration may be attributed to many factors, including anti-predatory response, dispersal capacity, and food availability (Morgan, 1995; Ohman et al., 1983; Poulin et al., 2002). Given the negative effect of light on the swimming activity of *C. giganteus* larvae, it is likely that the larvae would present the typical diel vertical migration in the field. The highly developed foot in the hatched pediveliger of *C. giganteus* would allow the larvae to crawl on the bottom substrate during the day. A similar pattern of day/night migration is observed in larvae of some *Crepidula* species, in which the negative phototactism overcomes the geotactic response during the day, whereas the opposite occurs at night (Young and Chia, 1987). Other species show a contrasting pattern. For example, the released larvae of *Turritella communis* aggregate near the water surface, thus showing positive phototactism. The

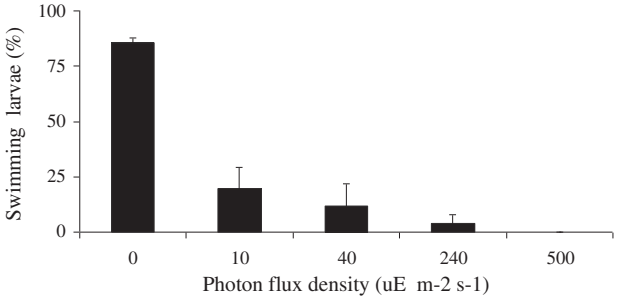

Fig. 5. The larval swimming (%) in *C. giganteus* as a function of photon flux density. The values provided are averages ± 1 SD (n ranges from 3 to 5).

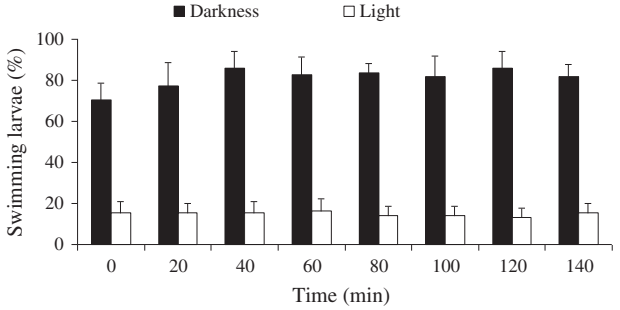

Fig. 7. The percentage of active *C. giganteus* larvae in two different light environments: light (120 $\mu E*m^{-2}*s^{-1}$) and dark. The values provided are averages ± 1 SD (n = 3).

response develops gradually in this species because on day 1, only 1% of the hatched larvae swim to the surface of the water, whereas over 50% of the larvae show a similar behaviour by day 11 (Kennedy and Keegan, 1992). Similarly, in the muricid *Concholepas concholepas*, field sampling resulted in a higher frequency of veliger larvae at the water surface during the day (Poulin et al., 2002). Exposure to sunlight imposes important challenges for larvae to protect against UV radiation (Miner et al., 2000). In *C. concholepas*, as in other epineustonic invertebrate larvae with positive phototactism, the development of large chromatophores on larval structures and a dark larval shell provide efficient protection against UV radiation (DiSalvo, 1988; Poulin et al., 2002). It is possible that the light colour of *C. giganteus* larvae shells and a less pigmented velum may reduce its resistance to high levels of light radiation and promote the sinking of larvae during the day.

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References

Amano, S., 1986. Larval release in response to a light signal by the intertidal sponge *Halichondria panacea*. Biol. Bull. 171, 371–378.
Averbuj, A., Penchaszadeh, P.E., 2010. Reproductive seasonality, oviposition and development of the nassariid whelk *Buccinanops cochlidium* (Dillwyn, 1817) in Patagonia, Argentina. J. Molluscan Stud. 76, 25–32.
Bayne, C.J., 1968. Histochemical studies on the egg capsules of eight gastropod molluscs. Proc. Malacol. Soc. Lond. 38, 199.
Cancino, J.M., Hughes, R., Orellana, M.C., Hayward, P., Ryland, J., Taylor, P., 1994. A comparative study of larval release in bryozoans. Biology and Paleobiology of Bryozoans. Olsen and Olsen, Fredensborg, Denmark, pp. 41–45.
D'Asaro, C.N., 1988. Micromorphology of neogastropod egg capsules. Nautilus 102, 134–148.
De Vries, M.C., Forward Jr., R.B., 1989. Rhythms in larval release of the sublittoral crab *Neopanope sayi* and the superlittoral crab *Sesarma cinereum* (Decapoda: Brachyura). Mar. Biol. 100, 241–248.
Disalvo, L., 1988. Observations on the larvae and post-metamorphic life of *Concholepas concholepas* (Bruguiere, 1789) in laboratory culture. Veliger 30, 358–368.
Forward, R.B., 1987. Larval release rhythms of decapod crustaceans: an overview. Bull. Mar. Sci. 41, 165–176.
Forward Jr., R.B., Burke, J.S., Rittschoft, D., Welsh, J.M., 1996a. Photoresponses of larval Atlantic menhaden (*Brevoortia tyrannus* Latrobe) in offshore and estuarine waters: implications for transport. J. Exp. Mar. Biol. Ecol. 199, 123–135.
Forward Jr., R.B., Tankersley, R.A., Burke, J.S., 1996b. Endogenous swimming rhythms of larval Atlantic menhaden, *Brevoortia tyranus* Latrobe: implications for vertical migration. J. Exp. Mar. Biol. Ecol. 204, 195–207.
Gallardo, C., 1981. Posturas y estadios de eclosión del gastrópodo muricidae *Chorus giganteus* (Lesson, 1829). Stud. Neotropical Fauna Environ. 16, 35–44.
Garrido, O., Gallardo, C.S., 1993. Ultraestructura de la cápsula ovígera de *Concholepas concholepas* (Bruguiere, 1789) (Gastropoda: Muricidae). Rev. Biol. Mar. 28, 191–201.
González, K., Gallardo, C.S., 1999. Embryonic and larval development of the muricid snail *Chorus giganteus* (Lesson, 1829) with an assessment of the developmental nutrition source. Ophelia 51, 77–92.
Hancock, D., 1956. The structure of the capsules and the hatching process in *Urosalpix cinerea* (Say). Proc. Zool. Soc. London 127, 565–571.
Hawkins, L., Hutchinson, S., 1988. Egg capsule structure and hatching mechanism of *Ocenebra erinacea* (L.) (Prosobranchia: Muricidae). J. Exp. Mar. Biol. Ecol. 119, 269–283.
Ilano, A.S., Fujinaga, K., Nakao, S., 2004. Mating, development and effects of female size on offspring number and size in the neogastropod *Buccinum isaotakii* (Kira, 1959). J. Molluscan Stud. 70, 277–282.
Johnson, K.G., 1992. Synchronous planulation of *Manicina areolata* (Scleractinia) with lunar periodicity. Mar. Ecol. Prog. Ser. 87, 265–273.
Kennedy, J., Keegan, B.F., 1992. The encapsular developmental sequence of the mesogastropod *Turritella communis* (Gastropoda: Turritellidae). J. Mar. Biol. Assoc. U. K. 72, 783–805.
King, K.M., 1976. The life history of *Boccardia proboscidea* Hartman (Polychaeta: Spionidae). Master of Arts Thesis, Department of Biology, California State University, Long Beach.
Leiva, G.E., Muñoz, J.E., Navarro, J.M., 1998. Desarrollo intracapsular y mecanismos de eclosión del caracol trumulco *Chorus giganteus* (Lesson, 1829) (Gastropoda: Muricidae), bajo condiciones de laboratorio. Rev. Chil. Hist. Nat. 71, 157–167.
Miner, B.G., Morgan, S.G., Hoffman, J.R., 2000. Postlarval chromatophores as an adaptation to ultraviolet radiation. J. Exp. Mar. Biol. Ecol. 249, 235–248.
Miner, B.G., Donovan, D.A., Andrews, K.E., 2010. Should I stay or should I go: predator- and conspecific-induced hatching in a marine snail. Oecologia 163, 69–78.
Morgan, E., 1995. The timing of larval release. In: McEdward, L. (Ed.), Ecology of Marine Invertebrate Larvae. Marine Science Series. CRC Press, Florida.
Morgan, E., Christy, J.H., 1995. Adaptative significance of the timing of larval release by crabs. Am. Nat. 145, 457–479.
Naylor, E., 1985. Tidally rhythmic behaviour of marine animals. Symp. Soc. Exp. Biol. 39, 63–93.
Ohman, M.D., Frost, B.W., Cohen, E.B., 1983. Reverse diel vertical migration: an escape from invertebrate predators. Science 220, 1404–1407.
Oyarzun, F.X., Strathmann, R.R., 2011. Plasticity of hatching and the duration of planktonic development of marine invertebrates. Integr. Comp. Biol. 51, 81–90.
Pechenik, J.A., 1975. The escape of veligers from the egg capsules of *Nassarius obsoletus* and *Nassarius trivittatus* (Gastropoda, Prosobranchia). Biol. Bull. 149, 580–589.
Pechenik, J.A., 1979. Role of encapsulation in invertebrate life histories. Am. Nat. 114, 859–870.
Pechenik, J.A., Chang, S.C., Lord, A., 1984. Encapsulated development of the marine prosobranch gastropod *Nucella lapillus*. Mar. Biol. 78, 223–229.
Poulin, E., Palma, A.T., Leiva, G., Narvaez, D., Pacheco, R., Navarrete, S.A., Castilla, J.C., 2002. Avoiding offshore transport of competent larvae during upwelling events: the case of the gastropod *Concholepas concholepas* in central Chile. Limnol. Oceanogr. 47, 1248–1255.
Przeslawski, R., 2004. A review of the effects of environmental stress on embryonic development within intertidal gastropod egg masses. Molluscan Res. 24, 43–63.
Richards, S.A., Possingham, H.O., Noye, J., 1996. Diel vertical migration: modeling light-mediated mechanisms. J. Plankton Res. 18, 2199–2222.
Romero, M.R., Walker, K.M., Cortez, C.J., Sanchez, Y., Nelson, K.J., Ortega, D.C., Smick, S.L., Hoese, W.J., Zacherl, D.C., 2012. Larval diel vertical migration of the marine gastropod *Kelletia kelletii* (Forbes, 1850). J. Mar. Biol. http://dx.doi.org/10.1155/2012/386575.
Saigusa, M., 1988. Entrainment of tidal and semilunar rhythms by artificial moonlight cycles. Biol. Bull. 174, 126–138.
Shanks, A.L., 1986. Vertical migration and cross-shelf dispersal of larval *Cancer* spp and *Randallia ornata* (Crustacea: Brachyura) off the coast of southern California. Mar. Biol. 92, 189–199.
Stimson, J., 1978. Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. Mar. Biol. 48, 173–184.
Sullivan, C., Maugel, T., 1984. Formation, organization, and composition of the egg capsule of the marine gastropod, *Ilyanassa obsoleta*. Biol. Bull. 167, 378–389.
Tamarin, A., Carriker, M.R., 1967. The egg capsule of the muricid gastropod *Urosalpinx cinerea*: an integrated study of the wall by ordinary light, polarized light, and electron microscopy. J. Ultrastruct. Res. 21, 26–40.
Tanner, J.E., 1996. Seasonality and lunar periodicity in the reproduction of Pocilloporid corals. Coral Reefs 15, 59–66.
Thorson, G., 1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophelia 1, 167–208.
Vaughn, G., 1953. Effects of temperature on hatching and growth of *Lymnaea atagnalis appressa* Say. Am. Midl. Nat. 25, 407–408.
Young, C.M., Chia, F.S., 1987. Abundance and distribution of pelagic larvae as influenced by predation, behaviour and hydrographic factors. In: Giese, A.C., Pearse, J.S., Pearse, V.B. (Eds.), Reproduction of Marine Invertebrates, IX, Generals Aspects: Seeking Unity in Diversity. Blackwell Scientific, Palo Alto, and the Boxwood Press, Pacific Grove, CA.
Ziegler, T.A., Forward Jr., R.B., 2005. Larval release rhythm of the mole crab, *Emerita talpoida* (Say). Biol. Bull. 209, 194–203.