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Further observations on the strobilation of the coronate scyphozoan *Linuche unguiculata* (thimble jellyfish)

Observaciones adicionales sobre la estrobilación del escifozoario coronate *Linuche unguiculata* (medusa dedal)

Lourdes Segura-Puertas[1],*
Karina Orduña-Novoa[1]
and Edgar Heimer de la Cotera[2]

[1] Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología,
Unidad Académica Puerto Morelos, P.O. Box 1152, 77501, Cancún, Q. Roo, México
[2] Universidad Nacional Autónoma de México, Instituto de Neurobiología-Campus Juriquilla, 76230 Querétaro, México
* Corresponding Author: lsegura@mar.icmyl.unam.mx

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ABSTRACT

In nature, strobilation of *Linuche unguiculata* is triggered by an increase in water temperature. However, the results showed that under laboratory conditions, it can be induced when scyphistomae are submitted to a sudden drop of 5 °C.

Key words: Scyphomedusa, thimble jellyfish, strobilation, life history, Caribbean Sea.

RESUMEN

En condiciones naturales, la estrobilación de *Linuche unguiculata* es desencadenada por un incremento en la temperatura del agua. Sin embargo, los resultados mostraron que en condiciones de laboratorio, este proceso puede ser inducido al someter a los escifistomas a un descenso brusco de la temperatura de 5°C.

Palabras clave: Escifomedusa, medusa dedal, estrobilación, ciclo de vida, Mar Caribe.

Linuche unguiculata (Swartz, 1788) is a small warm-water symbiotic scyphomedusa, very abundant in the tropical western Atlantic region (Mayer, 1910; Kramp, 1961). Its whole life cycle was described in detail under laboratory conditions (Ortiz-Corp's *et al*., 1987). The life cycle includes a benthic polyp, the scyphistoma, which reproduces asexually through strobilation to produce ephyrae. The ephyrae grow and develop into dioecious adults that subsequently reproduce sexually to produce the motile planula larvae that settle to produce benthic scyphistomae. Silveira & Morandini (1998a, 1998b) added new information on the asexual reproductive mechanism by the formation of planuloids through strobilation, and the occurrence of resting stages in this scyphozoan species. These authors based their study on cultures of scyphistomae of *L. unguiculata* collected from south-east Brazil, and they consider these new reproductive mechanisms as an adaptation of the species to subtropical waters, where no ephyrae or medusae of *L. unguiculata* have been observed in plankton and suprabenthic samples.

According to Arai (1997), strobilation is a process by which occurs a series of anatomical changes in the scyphistoma resulting in the formation and release of the ephyrae. Strobilation is controlled by endogenous factors (Spangenberg, 1965). However, the time and rate of strobilation are also influenced by exogenous chemical and physical factors including iodinated compounds, polypeptides, temperature, light and nutrition. These two last factors can be interrelated in symbiotic species (Arai, 1997).

In the laboratory, strobilation in a variety of scyphozoan species can be induced by changing the water temperature. Custance (1966) found that the scyphistomae of *Aurelia aurita* (Linné, 1758) could strobilate if the water temperature was increased gradually from 12 to 15°C. Rahat & Adar (1980) showed that temperatures higher than 20°C and endosymbiotic algae act synergistically to induce strobilation in *Cassiopea andromeda* (Forskål, 1775). These authors also observed that strobilation of that species were definitely temperature dependent, and occurred only above 25°C. This requirement of elevated temperature to induce strobilation has also been observed by Sugiura (1965) for the symbiotic scyphomedusa *Mastigias papua* (Lesson, 1830) and by Loeb (1972) for the nonsymbiotic species *Chrysaora quinquecirrha* (Desor, 1848). In both cases, the scyphistomae were maintained at 20°C for several weeks for later strobilation at 22 and 26°C, respectively. On the contrary, in the scyphistomae of *Rhopilema nomadica* Galil *et al.* 1990 a rapid strobilation was observed between 18 and 20°C, declining considerably when the temperature was raised to 24 or 26 °C (Lotan *et al*., 1994).

In nature, water temperature is considered the main factor for inducing strobilation, without setting aside other factors such as food availability. Since feeding by the scyphistomae ceases just before strobilation, it can be assumed that this process requires substantial nutritional reserves. Although strobilation of *Rhopilema esculenta* Kishinouye, 1891 is dependent on food availability, it is inhibited when the water temperature decreases below 15°C (Chen & Ding, 1983). A similar effect was observed in

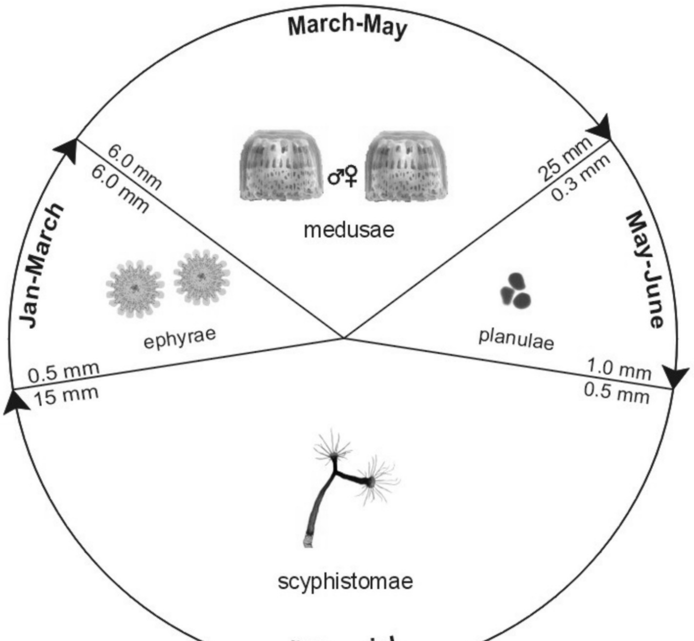

Figure 1. Life cycle of *Linuche unguiculata* (Swartz, 1788) in the Mexican Caribbean waters.

various Atlantic species of *Cyanea* and *C. quinquecirrha*; strobilation starts when the water temperature increases above 15 °C (Brewer, 1989). Water temperature thus appears to synchronize the annual occurrence of various scyphomedusae species.

Along the Mexican Caribbean waters, the occurrence of *L. unguiculata* has a chronological sequence that is observed annually, from late winter to late spring. Recently, Segura-Puertas *et al.* (2001) studied the whole life cycle of *L. unguiculata* in relation to seabather's eruption outbreaks, employing a combination of field and laboratory observations. In this region, the annual occurrence of the ephyra generation appears in late January. The ephyrae grow and mature into adults between March and May, and in May and early June the planktonic planulae of the next generation appear in abundance, the planulae settle on the substrate, remaining the species as polypoid form (Fig. 1).

The three free-swimming stages of the life cycle (ephyra, medusa and planula) can be observed sequentially, overlapping from late winter until late spring.

The onset of strobilation of *L. unguiculata* occurs when water temperature increases in the spring, leading to large swarms of ephyrae. However, under laboratory conditions, strobilation can be induced by submitting the scyphistomae to thermal stress. During the observations of *L. unguiculata* reared, it was noted that some scyphistomae strobilated when they were transferred from ambient temperature to controlled temperature, into the laboratory. These cultures had been established from planulae obtained after fertilization of mature medusae collected in the reef lagoon of Puerto Morelos on 19 March, 1998. Fifteen colonies, each with 2 to 15 scyphistomae were reared from 14 April to 25 October 1998. The colonies were maintained in glass dishes (19 cm wide and 7cm high). The scyphistomae were fed with newly hatched *Artemia* nauplii at two-day intervals, and their sea water was changed daily.

On 17 June 1998 five colonies kept at ambient temperature (29 ± 2°C) were transferred into the laboratory (24°C) by cleaning and removing the filamentous algae adhered to the scyphistomae tubes. After two hours, the first scyphistoma (64 days old) strobilated releasing 10 ephyrae. Strobilation was monitored from 17 June to 25 October 1998. During this period, other 24 scyphistomae strobilated. The number of ephyrae released by each scyphistoma varied from 10-45 individuals, releasing as many as 503 ephyrae. Duration of the strobilation of each scyphistoma was 3-5 days. The scyphistomae regenerated within 5-15 days. The strobilation process was similar to that reported for this scyphomedusa by Ortiz-Corp's *et al.* (1987).

The ephyrae from strobilating scyphistomae were transferred into glass dishes containing 0.25, 0.5, 1 and 8 L of filtered sea water, and reared to mature medusae. They were fed daily with newly hatched *Artemia* nauplii, and after feeding, they were removed and placed in fresh sea water. From the 503 ephyrae reared, only 64 (those released in 17 and 22 June 1998) reached the adult stage in 112 and 108 days, respectively.

The ephyrae reared present some variations in the number and size of certain structures. The development of the marginal tentacles was delayed, and their number and size were smaller that those ephyrae collected in plankton samples, and in some cases, they were absent. It was also observed ephyrae with fusion of two lappets when they had reached a size between 3.2 and 6.4 mm in diameter (36 and 52 days old, respectively). The eight rhopalia were not fully developed. The gonad primordia appears at about 47 days (4.3 mm in diameter) and all appeared to be females. The young medusae reached a diameter of 10 mm, and all died before reaching the sexual maturity.

These results show that thermal stress (a sudden drop in temperature of 5 °C) can induce the strobilation in *L. unguiculata* scyphistomae. The capacity of scyphistomae to release ephyrae, under unfavorable conditions of temperature, could be interpreted as a mechanism of ensuring the survival of a cohort through to the next period of strobilation. It is not sure that the drop of temperature is the only reason for the initiation of strobilation. Perhaps it is due to a combination of physical factors. Unfortunately, very little is known on the combined effects of environmental conditions in the reproductive biology of scyphozoan species.

These observations are in agreement with those reported by various authors who have shown that under laboratory conditions a lowering of temperature starts the strobilation process for *A. aurita* (Kakinuma, 1962; Spangenberg, 1968) and for various species of *Cyanea* (Cargo, 1974; Brewer & Feingold, 1991). In nature, this has also been observed for the strobilation of *A. aurita* in Tokyo Bay (Omori *et al.*, 1995).

Some of the morphological variations recorded during the development of the ephyrae reared in our laboratory had been observed by Ortiz-Corp's *et al.* (1987) in a previous study with *L. unguiculata*. These variations could reflect a response to varying culture conditions. For example, the diet employed; the ephyrae were fed with *Artemia* nauplii, exclusively. Medusae are selective feeders, and they require a great variety of food. In natural conditions, *L. unguiculata* consumes a wide range of prey including copepods, other microcrustaceans, gastropod veligers, chaetognaths and larval fish (Larson, 1979). Other causes for the morphological alterations may due to the feeding frequency. In a laboratory study of the feeding behavior of *L. unguiculata*, Larson (1979) observed that food was digested within two hours. Morandini & Silveira (2001) also observed that the medusae of *Nausithoe aurea* Silveira *&* Morandini, 1997 presented some altered structures under laboratory conditions. Unfortunately, these authors do not give any explanation for these abnormalities.

Despite their essential role in the life-history of scyphomedusae, the knowledge of the scyphistoma and its variants is still very limited. In order to understand the role of environmental conditions in the reproductive biology of the scyphozoans, further research is required in this field.

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