



## Succession of generations is still the general paradigm for scyphozoan life cycles

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**ABSTRACT.**—A recent study proposed an unorthodox view of the long-known metagenetic life cycle of scyphozoan jellyfish. We argue that misinterpretations and imprecise information generated a misleading view of such life cycle patterns. In favor of our reasoning, we present the historical understanding of metagenesis, and contend that it can still be used as a shared general life cycle pattern for Scyphozoa, as well as for other medusozoans.

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Recently, Ceh et al. (2015) published a study presenting a particular view of the classic and longstanding “model” of alternation of generations for scyphozoan jellyfishes (Agassiz 1860: 99–100, 105–106, pls. X–XI), referred to by the authors as the “metagenetic life cycle” (MLC). We contend that Ceh et al. (2015) provided imprecise information and misinterpretations of the subject, generating a misleading view of the MLC. Here, we argue that (1) the historical meaning of metagenesis, referred to as “alternation of generations” and “metagenesis”, was misunderstood by Ceh et al. (2015); and (2) metagenesis (and its derivation “MLC”) can still be used as a shared

general life-cycle pattern for Scyphozoa, as well as for other medusozoans. We also note some imprecise or erroneous interpretations from different data sources used to ground the authors' argument.

Fautin (2002: 1737–1738) highlighted that cnidarian reproduction is more variable than had been thought, and that some recent data are exceptions to relatively robust general patterns, although some of these general patterns were derived from few studies or atypical species. Knowledge of scyphozoans seems to be well established; the first life cycles described are very similar to more recent ones (e.g., Agassiz 1862, Schiariti et al. 2008). But for the cubozoans, some results are less consistent with the first described cycle (assumed as a pattern) (Werner et al. 1971, Straehler-Pohl and Jarms 2005, Toshino et al. 2015), although in general, the succession of stages is recognized.

(1) A “GENERATION SUCCESSION” MISINTERPRETED  
AS “ALTERNATION OF GENERATIONS”

There is no direct connection between the concept of the MLC and Louis Agassiz (Agassiz 1860), as assumed by Ceh et al. (2015). Cornelius (1990: 580) synthesized the history of the term “alternation of generations.” The Danish term *Generations rækker* and the German *Generationswechsel* (Steenstrup 1842a,b), meaning “generation passing” and “change of generations,” respectively, referred to the general concept of succession of stages. The German reference was eventually translated into English as “alternation of generations” by British zoologist and paleontologist George Busk (Steenstrup 1845). Agassiz (1860: 32 et seq.) subsequently reinforced the use of the concept “alternation of generations” for cnidarians, combining Sars's (1841) and Steenstrup's (1842a,b, 1845) contributions. However, Agassiz (1860) never used the term “metagenesis” or its derivative “metagenetic” in his study. Cornelius (1990: 580) correctly pointed out that “The term ‘alternation of generations’ so often associated with medusoid cnidarians has been equated with metagenesis but is different and is also inappropriate. [...] The term of course wrongly implied a two-state life-cycle rather than a succession of generations (i.e., including the planula, and ephyra), but the phrase caught on and has been widely used in cnidarian and other literature in the English language.”

Even if one assumes an incorrect equivalency between Agassiz's (1860) “alternation of generations” and a general concept of “metagenetic life cycle,” Agassiz's use (1860: 32) explicitly cited Steenstrup's (1845) definition, viz. “[...] the fundamental idea expressed by alternation of generations. It is a remarkable, and, thus far, unexplained phenomenon of nature, that an animal brings forth a brood neither similar, nor growing to be similar, to the parent, but differing from it, and producing by itself another brood, that returns to the form and relations of the mother animal, in such a manner that a mother animal does not rear the like of itself, but reappears only in its descendants of the second or third or a following generation; and this appears always, in different animals, in a definite generation, and with definite intermediate generations”. Unlike Ceh et al.'s (2015) view, no reference to environmental or seasonal conditions is implied in metagenesis. These factors are referred to elsewhere in the text (Agassiz 1860: 99), not associated with metagenesis as “[...] another feature of the species of *Acalephs* [...] these animals are periodical in their appearance and last for a short period in their perfect state of development. In our latitude [...] Among the

Hydroids there is more diversity in their periodicity [...] Some bring forth Medusae buds and free Medusae or Medusaria during winter; others, and in our latitude this is the case with by far the largest number of the Hydroids, produce their Medusae brood in the spring [...]" Evidently, Agassiz was aware that hydroids also show metagenesis (e.g., Agassiz 1860: 34–35), and therefore he was clearly not limiting the definition of metagenesis, in a broader sense, to environmental variables. The mention of different seasons and specific life-cycle stages of scyphozoans appears in Agassiz (1862: 75–78) when he was describing the habits of *Aurelia*.

## (2) PARTICULAR LESS-INCLUSIVE TAXONOMIC TRAITS DO NOT SIGNIFY THE LACK OF A GENERAL PATTERN

Disregarding the incorrect inclusion of environmental variables in the life-cycle model proposed by Agassiz (1860) for Scyphozoa, the scientific context should have been considered. Agassiz (1860) based his model on knowledge available during the mid-nineteenth century, i.e., fragmentary observations of two scyphozoan species, namely *Aurelia aurita* (Linnaeus, 1758) and *Cyanea capillata* (Linnaeus, 1758), from the same geographic region. Agassiz's generalizations are obviously outdated and should not be considered too rigidly. An example of such rigidity is the remark "These and other observations suggest that Agassiz's model does not consistently apply to all scyphozoans and that variations in jellyfish life cycle patterns might be common" (Ceh et al. 2015: 2). "Unusual patterns," i.e., special (or less frequent) features in almost every life cycle have accumulated since the mid-nineteenth century (Jarms 2010), as new life cycles continue to be revealed. This is epistemologically expected and should not be interpreted as the lack of an ancestral and basic life cycle (Marques and Collins 2004, Collins et al. 2006, Van Iten et al. 2014).

The evolutionary and ecological plasticity among cnidarians is overwhelming, and "life cycle" is a good example of these diverse expressions (Boero 1990, Fautin 2002, Jarms 2010). This is of utmost importance in cnidarian biology, making it possible for the group to be found in practically all the different marine habitats since Cambrian or even Ediacaran times (Cartwright et al. 2007, Van Iten et al. 2014). We understand that if the life cycle of a given species does not fit in the MLC model, it is because Agassiz's hypothesis was simply the basic framework for the scyphozoan life cycle. From a historical perspective, life cycles that truly contradict Agassiz's hypothesis for a general scyphozoan life cycle have been used to justify the erection of new taxa (Werner 1975, Marques and Collins 2004, Miranda et al. 2010).

Additionally, from an ecological point of view, Agassiz (1860: 99) recognized that cnidarians from other latitudes could have different production patterns in their life histories. Indeed, simple medium-term observations (e.g., periods longer than two years) show that the "appearance" of jellyfish cannot be completely predicted, and in most cases the "jellyfish season" differs in successive years, and their patterns of distribution/occurrence and abundance can change completely from one season to the next. This is actually a common phenomenon among gelatinous zooplankton (Boero et al. 2008).

## A DIFFERENT PERSPECTIVE ON SOME TOPICS DISCUSSED BY CEH ET AL. (2015)

SAMPLING METHODS AND INTERPRETATION OF RESULTS.—We have been sampling jellyfish in southeastern Brazil (SW Atlantic) since 1999, and we have learned that different sampling methods can mask background patterns. The majority of our samples have been taken using artisanal shrimp trawls (10–20 m depth, 2–3 cm mesh size) and visual observations on the water surface (0–3 m depth), almost always on a monthly basis (for larger specimens) and accompanied by plankton tows (200–300  $\mu\text{m}$  mesh size) (for smaller individuals). Curiously, no ephyra was commonly found in the plankton samples, except once (Tronolone et al. 2002), and the smallest jellyfish sampled (3–4 cm bell diameter) were found only when mangrove leaves clogged the trawl net. Evidently, we all agree that the sampling method is not the most accurate for small medusae. Also, the choice of the sampling location can be an important factor to find different developmental stages. Image-based methods are more accurate for this type of study and, in certain cases, the results obtained for other species are opposite to those shown by Ceh et al. (2015)—see discussion in Billett et al. (2006). Similar examples can be found in the Rio de la Plata estuary, where no ephyrae of any of the abundant scyphozoan species described for the region (*Lychnorhiza lucerna* Haeckel, 1880 and *Chrysaora lactea* Eschscholtz, 1829) were ever found after examination of more than 3000 plankton samples collected over a period of >8 yrs (Schiariti 2008).

Size as an indication of sexual maturity can introduce some bias, especially considering that, under unfavorable conditions, scyphomedusae can shrink in size (degrow) and then can regrow when conditions become favorable again (Hamner and Jenssen 1974). Maturity has been interpreted at the tissue level by some authors (Schiariti et al. 2012). Although specimens may appear to have fully grown gonads, they sometimes are not ready to spawn and might require some special stimulus (Ohtsu et al. 2007). Ceh et al. (2015) reached interesting conclusions about the sexual reproduction patterns of *Chrysaora plocamia* (Lesson, 1830), but without explaining how they identified sexually mature specimens, besides their size. Specifically, they wrote: “Animals were classified as either immature (no mature gonads) or mature (with either ripe testes or ovaries)”, but the criterion is incomplete without an explanation of what they considered a “mature gonad.” As comprehensively discussed in Schiariti et al. (2012), conclusions can vary considerably depending on the criterion adopted. On the other hand, determining sexual maturity from bell size could also lead to erroneous interpretation of the reproductive patterns, because both bell size and sexual maturity may be strongly affected by environmental conditions (Hamner and Jenssen 1974, Schiariti 2008, Schiariti et al. 2012).

The data presented for the appearance of larger specimens in the beginning of the “jelly season” clearly show that these specimens correspond to a cohort from the previous year. However, the presence of late adults in a given season might be fairly common, as occurs with *Stomolophus meleagris* L. Agassiz, 1860 off the southeastern USA (Kraeuter and Setzler 1975).

Feeding data for *C. plocamia* demonstrating the existence of benthic items in the gut contents call attention to a special habit of this species that might be further investigated. This species has long oral arms, and a large individual of about 40 cm diameter might have arms 2 m long. In shallow waters, individuals may occasionally prey on certain items without being in close contact with the sea bottom.

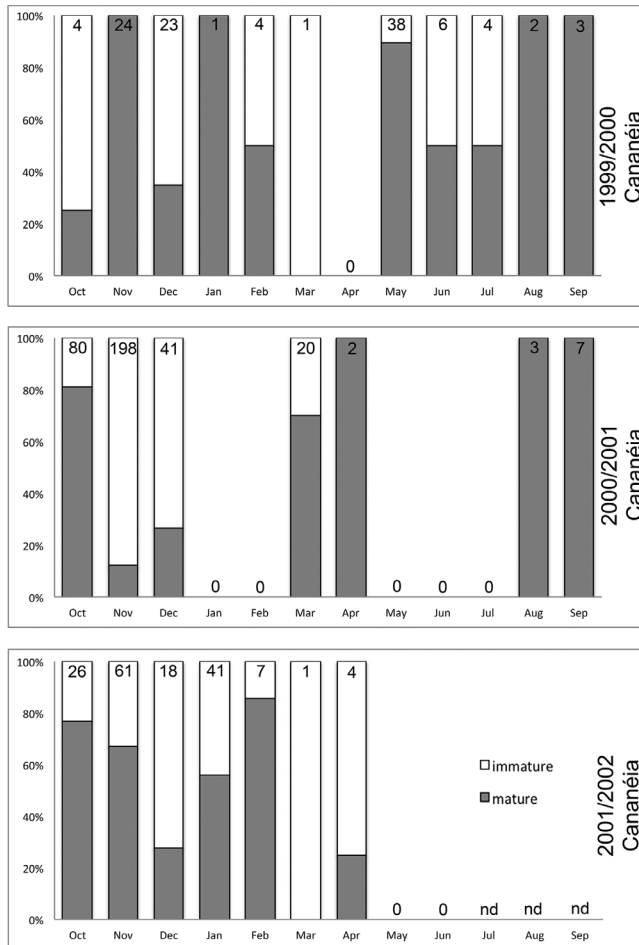


Figure 1. Percentage of mature vs immature *Lychnorhiza lucerna* medusae in three successive sampling years. Sampling was conducted in the Cananéia estuary (SE Brazil) (data from first author's PhD thesis). The criterion used to distinguish between mature and immature specimens was the presence of gonadal tissues surrounding the central stomach, which usually occurred when the specimens reached 10 cm in bell diameter. Numbers above panels represent the number of jellyfish sampled. Zeroes indicate absence of medusa, and "nd" indicates that no sampling occurred in that month. Note: this figure was intentionally constructed to resemble Figure 2 of Ceh et al. (2015) to facilitate comparison of the data interpretation.

Occasionally, some scyphozoan species may "overwinter" in deeper layers and also consume benthic prey; however, a recent study has shown that predation on animals near or at the bottom can reduce the dead jelly mass very rapidly (Sweetman et al. 2014). Additionally, stable isotope analysis can improve understanding of the connections among several levels of trophic webs in different environments, and also demonstrate the consumption of benthic species by some jellyfish (Nagata et al. 2015).

Raw data (number of individuals collected and proportion of specimens with presumed developed gonads) for the rhizostome *L. lucerna* vary considerably in the southwestern Atlantic Ocean. Whether one considers the same region in successive

sampling years (Cananéia, Brazil) (Fig. 1), or compares different areas in different years (Barra de São João and Guarujá, Brazil), it is not possible to determine a precise period of occurrence.

**IMPRECISE DATA FROM LITERATURE.**—The table presented by Ceh et al. (2015) neglects the members of the order Coronatae, for which many studies will support the “MLC” presumed model, and also several species that show deviations from the presumed model (Jarms 2010). At the end of the second paragraph, the authors mention the genus *Stephanoscyphistoma* as an example of suppression of the medusa stage. This is incorrect, because this genus was proposed to accommodate species of uncertain generic identity (Jarms 1990, 1991) based solely on the polyp stage. Accurate examples would be the species *Nausithoe planulophora* (Werner, 1971) or *Thecoscyphus zibrowii* Werner, 1984, in which the medusa stage is suppressed in different ways, or *Nausithoe racemosa* (Komai, 1936) or *Nausithoe eumedusoides* (Werner, 1974), which have reduced, non-swimming medusoids.

The review of types of asexual reproduction is not complete, and neglects a recent comprehensive study (Adler and Jarms 2009) that summarizes several observations on *Sanderia malayensis* Goette, 1886 that can serve as a guideline to identify the different modes of propagation.

The statement by Ceh et al. (2015: 2): “The exact timing of these processes is not well understood but it is likely to be different between species as well as between individuals of the same polyp colony” quoting (Arai 2009) is extremely important and summarizes what we should expect when studying and interpreting a certain species life cycle. The next sentence by the authors: “The MLC model implies that the occurrence of medusae is restricted to a season in the year and that polyp- and medusa generations alternate and are temporally and spatially separated in scyphozoans” should not be taken as “absolute truth.” As the preceding sentence implies, there might be some variation around the general MLC pattern. Besides, as the polyps are presumed to be potentially perennial, regardless of a few exceptions, polyps and medusae are not temporally separated [as observed for *Chrysaora quinquecirrha* (Desor, 1848) off southeastern USA (Calder 1972, 1974; Kraeuter and Setzler 1975)].

**RESULTS FROM LABORATORY OBSERVATIONS.**—Ceh et al. (2015) also stated that when conditions are favorable, the pelagic stage (jellyfish) is prevalent, and when there are limitations in resources and degrading environmental conditions, the sessile stage (polyp) is prevalent. This is not completely correct, and some laboratory experiments have shown that under favorable conditions (food in abundance and higher temperature), the sessile form can flourish and increase in abundance as seen for the rhizostomes *Cassiopea* sp., *Cephea cephea* (Forskål, 1775), *Rhizostoma pulmo* (Macri, 1778), and the semaeostomes *Aurelia* spp., and *S. malayensis* (Schariti et al. 2014, 2015) and that the presence of dissolved organic material in seawater can provide sufficient nutrition for the polyps to continue producing jellyfish normally (Shick 1975). Thus, both stages (polyps and medusae) can benefit from good environmental conditions and proliferate (and eventually bloom) (Purcell et al. 2007, Richardson et al. 2009, Schariti et al. 2014).

In the course of keeping polyps of many different scyphozoan species under laboratory conditions for several years, we observed that some of them can strobilate almost continuously. On one hand, certain species (e.g., *Nausithoe aurea* Silveira and Morandini, 1997; *Nausithoe wernerii* Jarms, 1990; some *Aurelia* populations; *L.*

*lucerna*; *S. meleagris*; and *C. plocamia*) when kept under constant temperature and food availability can produce ephyrae every month (or when the polyp is fully regenerated). On the other hand, other species [e.g., *S. malayensis*; *Phyllorhiza punctata* von Lendenfeld, 1884; *Cotylorhiza tuberculata* (Macri, 1778); and *Chrysaora pacifica* (Goette, 1886)] produce ephyrae only when certain conditions prevail (e.g., critical temperature and food levels, presence of zooxanthellae). Such observations from laboratory culture lead us to hypothesize that some species are more prone to respond very rapidly to environmental changes, while others need specific triggers.

We conclude that the interpretation provided by Ceh et al. (2015) is historically inaccurate, highly speculative, not based on general data, and lacks a general comparative perspective. The possible variations reported by the authors are not adequate to reject the current paradigm based on a shared pattern derived from hundreds of data points from other species, particularly if a thorough comparative argument is not provided. The depicted pattern is merely another case of a few peculiar patterns that fit into a general perspective of metagenesis, or MLC. The observations of Ceh et al. (2015) on *C. plocamia* are interesting and must be included in this comprehensive view of “general patterns” of scyphozoan life cycles.

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