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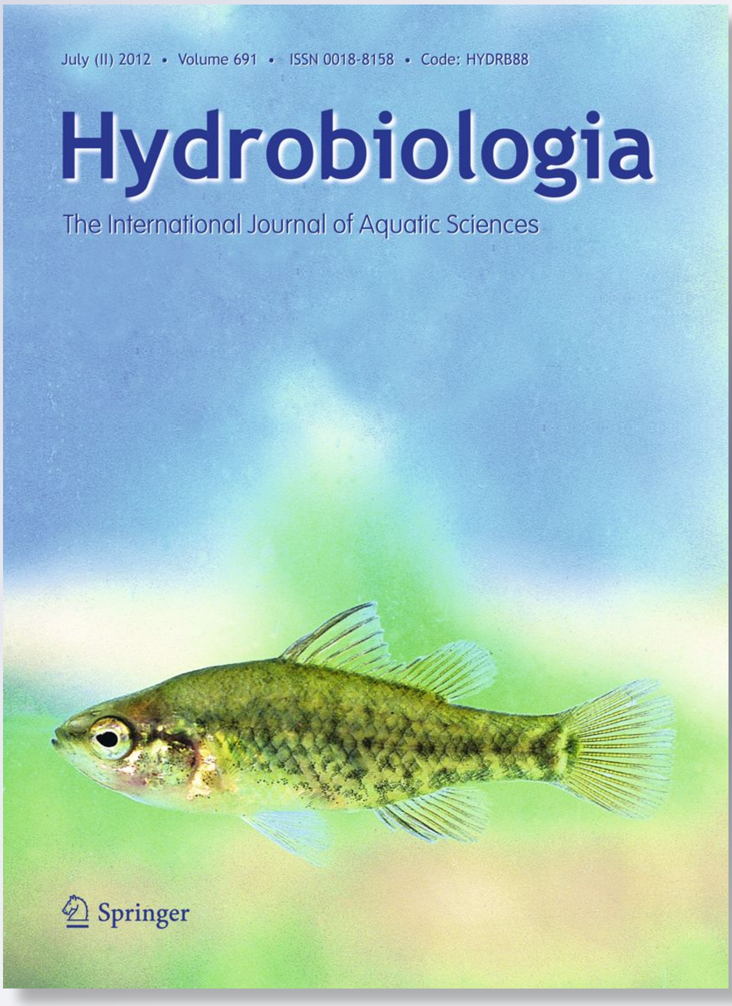

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JELLYFISH BLOOMS

Review Paper

Do Staurozoa bloom? A review of stauromedusan population biology

**Lucília S. Miranda · André C. Morandini ·
Antonio C. Marques**

Abstract The study of “jellyfish blooms” provides important data toward determining the causes and consequences of these phenomena; however, the definition of “bloom” remains controversial and different concepts have been adopted in recent works. By addressing the biological and convenience definitions, this study tested the adequacy of the different concepts of “blooms” for the Class Staurozoa (Cnidaria). From seasonal monitoring data of some species of Staurozoa, we concluded that stauromedusae bloom if we used the biological concept of “bloom”, which considers the life cycle and resulting changes in the abundances of these animals. By contrast, the small, benthic, inconspicuous, and non-harmful stauromedusae do not bloom if we use the convenience concept of “bloom”, which constrains the events to those that humans can observe and that cause damage to human activities. In other words, the same group of organisms either is or is not capable of blooming depending on which concept of “bloom” is used. In fact, previous literature has suggested that Staurozoa could not bloom, which indicates that the study of “jellyfish blooms” can be biased, considering convenience rather than biological reasoning.

Keywords Stauromedusae · Seasonality · Life cycle · Evolution

Introduction

Increases in the abundance of medusae are a phenomena of great interest, especially because of the negative impacts on ecosystem dynamics (Morandini & Marques, 2010) and human activities, such as fisheries, tourism, mariculture, and power production (Purcell et al., 2007). Several studies on “jellyfish blooms” (regarding only the medusoid stages of Phylum Cnidaria) have been carried out using different approaches, all contributing to a better understanding of the “bloom” phenomenon. Such studies have focused on methods of detection (Houghton et al., 2006; Bayha & Graham, 2009; Straehler-Pohl & Jarms, 2010), importance of different life stages (Purcell, 2007; Boero et al., 2008; Willcox et al., 2008; Arai, 2009; Bayha & Graham, 2009; Hoover & Purcell, 2009; Straehler-Pohl & Jarms, 2010), influence of climate (Dawson et al., 2001; Mills, 2001; Parsons & Lalli, 2002; Purcell, 2005; Hong et al., 2008), anthropogenic causes and subsequent consequences to

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the economy (Dawson et al., 2001; Purcell et al., 2007; Hong et al., 2008; Mariottini et al., 2008; Richardson et al., 2009), ecological (Pitt et al., 2009), and evolutionary (Dawson & Hamner, 2009; Hamner & Dawson, 2009) aspects of "blooms".

Despite the importance of these studies, the concept of "bloom" remains controversial (Table 1). Some even dispute the term "bloom", which is taken from plant ecology where it is applied to the flourishing appearance and high densities of plants, algae, and general phytoplankton in the marine environment (Smayda, 1997). The animal equivalent would be the term "outbreak", considered by some to be more appropriate to describe "…exceptional abundances (usually sudden and monospecific) of zooplankton, which can be seasonal or non-seasonal" (CIESM, 2001). Recently, an interesting perception of "bloom" emerged in the literature: the concept of "true bloom" and "apparent bloom" (Graham et al., 2001), later incorporated into evolutionary studies (Dawson & Hamner, 2009; Hamner & Dawson, 2009). In the "true bloom", there is a rapid population growth due to reproduction, and in the "apparent bloom", a stable population is re-distributed or re-dispersed as a consequence of physical, chemical, or behavioral factors (Graham et al., 2001). Thus, the term "jellyfish bloom" is common in the jellyfish literature (Table 1) and also accepted (CIESM, 2001); therefore, we will use both terms synonymously.

The study of "blooms" is often hampered by the need for appropriate methods of sampling and long-term monitoring (Genzano et al., 2008; Kogovšek et al., 2010). In addition, it is important to consider the different stages of the life cycle, such as benthic polyps, since they are crucial to understanding "bloom" dynamics (Purcell, 2007; Willcox et al., 2008; Bayha & Graham, 2009; Dawson & Hamner, 2009; Hoover & Purcell, 2009). Because "blooms" of

Table 1 Compilation of definitions of "bloom"/"outbreak" published during the last decade

References	Remarks
CIESM (2001)	"Bloom" synonymous with "outbreak", including "abnormal" and "normal (seasonal) blooms"
Benović & Lučić (2001)	"Bloom" as an abnormal event
Graham et al. (2001)	Differences between "apparent bloom" and "true bloom"
Mills (2001)	"Normal" and "abnormal blooms" ("true bloom")
Nival & Gorsky (2001)	Convenience concept of "bloom"
Parsons & Lalli (2002)	Differences between "apparent bloom" and "true bloom"
Purcell et al. (2007)	"Bloom" related to reproduction, i.e., "true bloom"
Boero et al. (2008)	"Bloom" (multispecific) is different from "outbreak" (monospecific); seasonal ("normal bloom") or unexpected ("abnormal bloom")
Daryanabard & Dawson (2008)	Differences between "apparent bloom" (aggregations) and "true bloom"
Genzano et al. (2008)	"Bloom" as an abnormal event; discussion on the convenience concept of "bloom", and differences between "apparent" and "true bloom"
Albert (2009)	Swarm and aggregation ("apparent bloom")
Dawson & Hamner (2009)	Definition of mass occurrence, "normal" and "abnormal blooms" ("true blooms"), and swarm ("apparent bloom")
Gibbons & Richardson (2009)	"Normal" and "abnormal blooms" ("true bloom") and "apparent bloom"
Hamner & Dawson (2009)	Definition of "true bloom" ("normal" and "abnormal"), "apparent bloom" (aggregations and swarms), mass occurrence, and accumulations
Lilley et al. (2009)	"Bloom" synonym of large aggregations
Purcell et al. (2009)	"Bloom" synonym of "outbreak"
Licandro et al. (2010)	"Bloom" as a synonym of "outbreak", related to the density of organisms
Purcell (2012)	"Bloom" as unusually high abundance (i.e., "abnormal bloom") synonym of "outbreak"
Brotz et al. (2012)	"Bloom" defined as increase in presence, numbers, or biomass

large medusae primarily are responsible for the negative impacts reported (Uye, 2008; Richardson et al., 2009), a biased view in the characterization of "blooms" neglects some inconspicuous groups, as the hydromedusae (Hamner & Dawson, 2009). Nevertheless, examples of hydromedusan "blooms" are in the literature (e.g., Purcell & Grover, 1990; Mianzan et al., 2000; Raskoff, 2001; Stefani et al., 2010; Purcell, 2012 electronic supplementary material).

Within the Phylum Cnidaria, the Class Staurozoa (Marques & Collins, 2004; Van Iten et al., 2006) comprises the small and inconspicuous benthic stauromedusae, some of which have a differentiated life cycle (Wietrzykowski, 1912; Kikinger & von Salvini-Plawen, 1995; Miranda et al., 2010). There are no reports of direct impacts on human activities by these animals: they do not prey on fish, and they are not harmful to humans (Davenport, 1998; Zagal, 2004a). These features make them interesting to contrast against the bias often introduced for "bloom" studies. Fortunately, long-term monitoring exists for some species (Corbin, 1979), which facilitates the study of "blooms" in this group. Thus, in this study, we test the different concepts of "bloom" for Staurozoa, discussing different applications of the term in relation to biological phenomena or human convenience.

Staurozoan population biology

Stauromedusae are small, stalked, benthic medusae that live mainly in the intertidal zone, attached to algae or rocks (Mayer, 1910; Mills & Hirano, 2007; S1. 1). They belong to the Class Staurozoa, the most recently proposed class for the Phylum Cnidaria (Marques & Collins, 2004; Collins et al., 2006; Van Iten et al., 2006; Daly et al., 2007). Although metagenetic, the general life cycle of Staurozoa is distinctive in that a planula larva attaches to the substrate and develops into a stauropolyp, which subsequently undergoes an apical metamorphosis into an adult stauromedusa. Consequently, the species do not produce a pelagic medusa, because the transformation to adult takes place without fission or budding. This developmental pattern results in a mosaic individual, in which the structures of the oral part are similar to those of an adult medusa (particularly, scyphozoans and cubozoans), whereas the basal part retains characteristics of the sessile polyp. The dioecious adult stauromedusa reproduces sexually and produces new planulae (Wietrzykowski, 1912; Kikinger & von Salvini-Plawen, 1995; Mills & Hirano, 2007).

The general life cycle described for Staurozoa states that one polyp produces directly only one adult medusa; however, they also possess a capacity for asexual reproduction, which occurs by lateral budding of the calyx (upper part of the animal) and at the distal portions of some special tentacles of the polyp (Kikinger & von Salvini-Plawen, 1995); and in the early stage of attached larvae ("microhydrula" stage) through frustulation (Jarms & Tiemann, 1996; Miranda et al., 2010). Asexual reproduction greatly increases the ability of a single individual to generate many clones. This ability was corroborated by molecular markers (16S, ITS1, and ITS2), which showed a unique haplotype for ten individuals of each population (from King George Island, Antarctica and Valdivia, Chile) of *Haliclystus antarcticus* Pfeffer 1889 analyzed (Miranda et al., 2010).

Although stauromedusae are widely distributed (Kramp, 1961), limited information exists on their biology and ecology, especially concerning their life cycle (Miranda et al., 2010). As a result, long-term monitoring data are rare, with a few exceptions (Table 2). Periods of high abundances of stauromedusae were recorded during the end of spring and summer for different species in both hemispheres (Fig. 1a; Table 2). In fact, high abundances of species of *Haliclystus* were found in the Northern Hemisphere summer by Uchida (1927), Ling (1937), Berrill (1962), and Corbin (1979), and in the Southern Hemisphere summer by Amor (1962), Davenport (1998), Zagal (2004a, b), and Miranda et al. (2009). According to Ling (1937) these animals "…occur most abundantly during the first part of August, (…) becoming quite rare by the end of October" in the Northern Hemisphere. Similarly, the population of *H. antarcticus* reached its highest density (1,405 ind m^{-2}) during the summer period in January in the Southern Hemisphere (Table 2) and then decreased drastically during the winter months (Zagal, 2004b). Additional records of stauromedusae have peak abundance in the summer, including the genera *Sasakiella* (Ling, 1937), *Manania*, and *Lucernaria* (Berrill, 1962); however, there are also exceptions, such as species of *Lucernariopsis* that peak in abundance during the autumn/winter (Corbin, 1979; Fig. 1b; Table 2).

Table 2 Life cycles and population abundances of some species of Staurozoa

Species	Generations year^{-1}	Peak abundance	Hemisphere	Season	Reference
Craterolophus convolvulus (Johnston 1835)	2	April (1st generation) September (2nd generation)	North	Spring & summer-autumn	Corbin (1979)
Haliclystus antarcticus Pfeffer 1889	1	January	South	Summer	Zagal (2004b)
Haliclystus auricula (Rathke 1806)	1	July	North	Summer	Corbin (1979)
Haliclystus salpinx Clark 1863	1	July	North	Summer	Berrill (1962)
Lucernaria quadricornis Müller 1776	1	July	North	Summer	Berrill (1962)
Lucernariopsis campanulata (Lamouroux 1815)	1	October	North	Autumn	Corbin (1979)
Lucernariopsis cruxmelitensis Corbin 1978	1	February	North	Winter	Corbin (1979)
Manania atlantica (Berrill, 1962)	1	July	North	Summer	Berrill (1962)
Sasakiella cruciformis Okubo 1917	1?	August	North	Summer	Ling (1937)

A single peak in the monitoring curve of abundance indicates that several species of stauromedusae have an annual cycle with one generation year^{-1} (Fig. 1a, b) (Berrill, 1962; Corbin, 1979; Zagal, 2004b). Corbin (1979), who monitored the variation in abundance of stauromedusae for 23 years, suggested that an annual life cycle is a common trait of Stauromedusae, with the exception of *Craterolophus convolvulus* (Johnston 1835), which has two generations year^{-1} (Fig. 1c; Table 2).

Although we do not know the exact environmental signals that synchronize these annual events (Mills & Hirano, 2007), the seasonality of stauromedusae was hypothesized to be related to the availability of suitable algal substrates; specifically, the periods of highest abundance of stauromedusae and greatest algal cover coincide, indicating optimal conditions for growth and nutrition of these animals (Zagal, 2004b). Environmental conditions are probably less favorable outside of these peak periods (Zagal, 2004b); however, species develop slightly differently from one another, and those that co-occur at one location may emerge, age, and disappear at different times of the year (Mills & Hirano, 2007).

How can stauromedusae appear in great numbers during specific seasons and then suddenly disappear? Stauromedusae are hard to find because of the relatively small size of some species, especially if they are camouflaged in color and texture against the background of macrophytes or coralline algae (Corbin, 1979; Larson & Fautin, 1989; Zagal, 2004b; S1). Moreover, the life cycle of stauromedusae includes inconspicuous creeping planula larvae that lack cilia (Otto, 1976, 1978) and stauropolyps, which are also small and difficult to observe (Wietrzykowski, 1912; Kikinger & von Salvini-Plawen, 1995). Many individuals of these "hidden" life cycle stages may occur with adult stauromedusae in the intertidal, but stauropolyps (∼0.3–0.8 mm; Hirano, 1986; Kikinger & von Salvini-Plawen, 1995) and planulae (20–100 µm; Otto, 1978) are even more difficult to find than the camouflaged stauromedusae (usually varying from 1 to 4 cm; Mills & Hirano, 2007; S1). In fact, planulae from only five species (Kowalevsky, 1884; Wietrzykowski, 1912; Hanaoka, 1934; Otto, 1976, 1978) and polyps from only nine species (Wietrzykowski, 1912; Hirano, 1986; von Salvini-Plawen, 1987; Kikinger & von Salvini-Plawen, 1995) have been recorded from a total of 51 known species of Staurozoa (Daly et al., 2007; Mills, 2011).

Migration, in which the stauromedusae move from the littoral zone to deep waters, is another possibility for their absence during some seasons of the year (Sars, 1846; Corbin, 1979; Zagal, 2004b). Literature suggests that not only the medusoid but also other staurozoan life stages migrate. Gwilliam (1956) hypothesized that "…there exists in the vicinity [of the intertidal population of stauromedusae] a permanent subtidal population which is continually supplying planulae…", and when conditions were suitable, these planulae would settle, grow, and mature on algae. The "microhydrula" stage, which occurs after planula attachment, of *H. antarcticus* was collected at a depth of about 31 m attached to bivalve shells (Jarms & Tiemann, 1996; Miranda et al., 2010), also suggesting a migratory behavior. This could be indirect evidence that intertidal

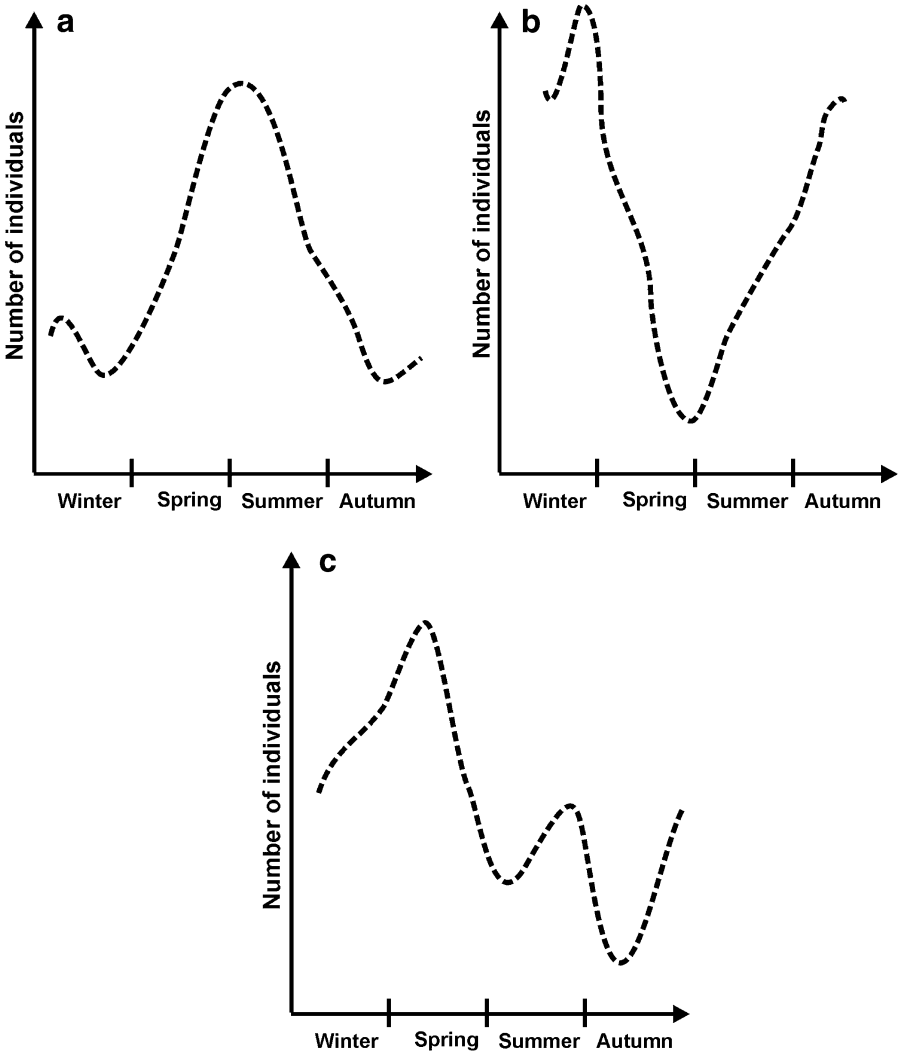

Fig. 1 Seasonal patterns of abundance of Staurozoa. **a** Spring/summer peak (annual cycle); **b** autumn/winter peak (annual cycle); **c** a biannual cycle. Adapted from Corbin (1979)

adult stauromedusae of *H. antarcticus* could co-exist with at least one other life history stage surviving in a different habitat than the adult, perhaps developing and migrating when conditions become favorable. It remains unknown whether this migration occurs actively or passively.

In addition to the planula and "microhydrula" stages, stauropolyps might also perform migration. The stauropolyp of *Haliclystus octoradiatus* (Lamarck 1816) tightly adheres to the substrate until the 4-tentacle stage, when the polyp spontaneously detaches itself, even when water conditions are calm. This was observed consistently in laboratory cultures and similar events may occur under natural conditions (Wietrzykowski, 1912), providing an opportunity for polyps to migrate from a deeper region, where the "microhydrula" stage was located, to shallow waters, where stauromedusae are observed. However, there are no other reports to corroborate that planulae and stauropolyps of Staurozoa can migrate seasonally from shallow to deep waters or vice versa (Gwilliam, 1956; Corbin, 1979; Zagal, 2004b), and there is no evidence of migratory behavior during the stauromedusa stage.

Information on the duration of each stage of the life cycle of Staurozoa, which would help in understanding the appearance of great numbers of stauromedusae, is also scarce. However, the migratory hypothesis has some support from scattered information on the life cycle of many species. The "microhydrula" stage of *H. antarcticus* was found in December at King George Island (Jarms & Tiemann, 1996) and could have been the source of the large number of adult stauromedusae recorded in late February–early March (Miranda et al., 2009). Although no further information exists for this species, some data in the literature help to deduce the life cycle. The planula stage of *H. octoradiatus* develops into a fully developed stauropolyp in about 15 days (Wietrzykowski, 1912) and the stauropolyp of *Stylocoronella* takes 2 months to become a mature stauromedusae under laboratory conditions (Kikinger & von Salvini-Plawen, 1995). Finally, Wietrzykowski (1912) observed young polyps of *H. octoradiatus* in the field during April and mature stauromedusae during July. Thus, about 3 months between December and March would be enough for planulae to become mature stauromedusae for *H. antarcticus*.

Field observations confirm that most species of stauromedusae disappear for several months before their young stages reappear, so encystment of the larvae also seems likely to occur in the field (Mills & Hirano, 2007). Although encystment or resistance stages have not been observed, when planulae of *Haliclystus salpinx* Clark 1863 settle in the laboratory, they can aggregate and become surrounded by an amorphous substance that forms packed subunits enclosing the planulae, which could be an overwintering stage (Otto, 1978). Otto (1978) suggests that the planulae of *Haliclystus* spp. probably do not develop directly after settlement in nature, but form cysts during unfavorable conditions. Interestingly, the "microhydrula" stage of *H. antarcticus* also aggregates (Miranda et al., 2010), and could represent the "resistant" stage suggested by Otto (1978). In addition, this "microhydrula" stage can produce frustules (Jarms & Tiemann, 1996; Miranda et al., 2010). In the genus *Stylocoronella*, many frustules further divide into two smaller ones during the development of some specimens, and this stage encysts, showing no further development (Kikinger & von Salvini-Plawen, 1995). These frustules could act as resting stages, later developing into stauropolyps under favorable conditions (Kikinger & von Salvini-Plawen, 1995). Probably due to their resistance, Otto (1978) was unable to trigger further development of staurozoan planulae or frustules in the laboratory. In fact, the "microhydrula" stage of *H. antarcticus* has been kept in continuous culture for nearly 20 years without further development (Jarms & Tiemann, 1996; Miranda et al., 2010).

In addition to a seasonal peak, which occurs once or twice a year depending on the species (Table 2), Corbin (1979) reported exceptional increases in abundances of certain species during specific years. On average, *Lucernariopsis cruxmelitensis* Corbin 1978, for instance, produced about 200 individuals during its peak abundance during winter. In 1968, it was estimated that this number reached 2,000 individuals in February (Northern Hemisphere winter). Corbin (1979) also detailed an event of considerable increase in abundance for different species (*Lucernariopsis campanulata* (Lamouroux 1815) and *C. convolvulus*) in 1974, which was maintained for a considerable period of time and gave "every indication of the occurrence of a population explosion of these two species" (Corbin, 1979). Corbin (1979) suggested that certain factors were especially favorable to these species at the time of spawning, prior to maturity, and continuing through the development and growth of the resulting "explosion generations". A combination of extrinsic and intrinsic factors could lead to an unusually high number of specimens.

Despite these high densities ("seasonal" or "exceptional") documented for Staurozoa, evolutionarily these animals are not considered able to bloom (either "apparent" or "true bloom"; Dawson & Hamner, 2009; Hamner & Dawson, 2009). In order to discuss the suitability of considering staurozoan "blooms", we will address different concepts of "bloom" in the literature, verifying whether or not they are applicable to Staurozoa.

Stauromedusae and the concepts of "bloom"

Biological concept

"Apparent bloom"

An "apparent bloom" is an event caused by environmental (physical and chemical) and/or biological (swimming) factors. These factors may lead to aggregations or swarms that could affect local perception of large numbers of jellyfish as a real population increase (Graham et al., 2001; Table 1).

Stauromedusae have limited capacity of movement and spend most of their lives attached to rocks or seaweeds by their peduncle; however, they can use their tentacles or anchors (adhesive structures) to restrict locomotion (Hyman, 1940; Mills & Hirano, 2007; personal observations). Their planulae do not possess cilia and so also have limited movement (Otto, 1976, 1978). Because traversing physical barriers depends on swimming (Graham et al., 2001), stauromedusae are susceptible to accumulation due to environmental variables. Currents or winds can accumulate their substrata or stauromedusae when they reach a barrier, thereby creating an “apparent bloom” of Staurozoa. Nevertheless, evolutionary analysis of “jellyfish blooms” (Dawson & Hamner, 2009; Hamner & Dawson, 2009) concluded that “apparent blooms” were “rare or absent” in the class. Contrary to this conclusion, there are records of dense stauromedusa aggregations (Collins & Daly, 2005), but insufficient information was available to conclude if these events were “apparent blooms” (Table 3).

“True blooms”

A “true bloom” can be a regular event (“normal bloom”; Graham et al., 2001). Jellyfish populations in temperate climates usually vary seasonally in abundance in a somewhat predictable manner, with their peak following the regular sequence of the phytoplankton spring pulse (CIESM, 2001). Some authors considered these seasonal, natural population phenomena to be a “true (demographic) normal bloom” (Mills, 2001; Dawson & Hamner, 2009; Hamner & Dawson, 2009; Table 1). According to those definitions, the annual pattern of abundance of a staurozoan population, with one or two annual peaks (Fig. 1) should be classified as a “normal true bloom”.

“Blooms” are one possible consequence of a metagenetic life cycle because all metagenetic cnidarians have the potential to bloom (Mills, 2001; Hamner & Dawson, 2009). Among Scyphozoa, each benthic polyp may produce many ephyrae through strobilation (asexual reproduction), and each of the ephyrae can develop into an adult scyphomedusa. Thus, one polyp can produce many medusae, contributing decisively to the formation of “blooms” (Purcell, 2007). On the other hand, one stauropolyp only produces one adult stauromedusa because it does not strobilate, but metamorphoses directly into a benthic medusa (Wietrzykowski, 1912; Kikinger & von Salvini-Plawen, 1995). Similarly in cubozoans, each cubopolyp metamorphoses directly into a single cubomedusa (Stangl et al., 2002); this was one reason to conclude that this taxon cannot form “extraordinary blooms” (Hamner & Dawson, 2009). Nevertheless, cubozoans (Werner et al., 1971; Arneson & Cutress, 1976; Yamaguchi & Hartwick, 1980) and at least some, if not all, Staurozoa can asexually reproduce in the early life cycle stages (settled planulae—“microhydrula”—and stauropolyps; Wietrzykowski, 1912; Kikinger & von Salvini-Plawen, 1995; Miranda et al., 2010). This asexual reproduction would create many new polyps, which could each metamorphose into one new medusa. Thus, even without strobilation, there could still be rapid population growth in Staurozoa due to asexual reproduction. Constraining a species' ability to bloom to only those capable of strobilation is an oversimplification of the biological question. Also, these “blooms” are not biologically homologous (e.g., strobilation in Scyphozoa and frustulation in Staurozoa); therefore, evolutionary reconstructions of the “bloom” capacity may need to consider additional biological processes/features.

Table 3 The adequacy of considering a “Staurozoa bloom”, according to the different concepts of “bloom”

Concepts of “bloom”	Do Staurozoa bloom?
Biological	
“Apparent bloom”	?
“True bloom”	
“Normal” (Regular)	Yes
“Abnormal” (Irregular)	Yes
Convenience	
Size/conspicuity	No
Plankton	No
Impact on human activities	No

Evidence indicates that Staurozoa may occur periodically at high densities. During 23 years of monitoring (Corbin, 1979), stauromedusae presented a seasonal, predictable, “normal true bloom”. This also was observed during 1 year of monitoring by Zagal (2004b). In conclusion, although data on the life cycle of Staurozoa are rare, the population dynamics of some species allows us to reject the conclusion that the Class Staurozoa does not have “normal true blooms” (Hamner & Dawson, 2009; Table 3).

“True blooms” also can be unpredictable events (“abnormal blooms”; Graham et al., 2001). Some authors suggest that the normal, seasonal increases in the abundance of individuals of a population (herein called “normal true bloom”) should not be considered a “bloom”; however, in some years, the expected occurrence of a species may exceed the usual abundance level and only then should be considered a “bloom” (CIESM, 2001; Genzano et al., 2008; Table 1). This was called an "abnormal true bloom" because it resulted from a population increase following asexual reproduction ("true bloom"; Dawson & Hamner, 2009; Hamner & Dawson, 2009) and "abnormal" because it surpassed the usual levels for the species.

In order to recognize such events as unusual, there must be good knowledge of what is "normal" abundance or biomass. Answering this question is only possible when proper baseline information, such as long-term monitoring, is available (Genzano et al., 2008). Corbin (1979) noted some years of "exceptionally high" abundances of stauromedusae. In 1968, the number of specimens of *L. cruxmelitensis* was 10-times higher than the maximum mean observed in other years. In 1974, the population of *C. convolvulus* and *L. campanulata* reached a high density, an event with "every indication of the occurrence of a population explosion" (Corbin, 1979). Zagal (2004b) also recorded remarkably high densities of *H. antarcticus*, reaching 1,405 ind m^{-2} (vs. a mean density of 385 ind m^{-2}) in summer 2002. Unfortunately in this case, the species was monitored for only 1 year, so we cannot know if those numbers were abnormal. Thus, the limited available data have shown "abnormal true blooms" in Staurozoa (Table 3), contrary to earlier conclusions (Dawson & Hamner, 2009; Hamner & Dawson, 2009).

Literature highlights different reasons for causes of "abnormal true blooms" of jellyfish, including anthropogenic sources (eutrophication), fishing pressure (overfishing), aquaculture, construction (human modification of aquatic habitats, altering coastal waters and circulation), climate change, and invasions (translocations) (Purcell et al., 2007; Richardson et al., 2009; Purcell, 2012). In Staurozoa, attempts to identify the events would be purely speculative, but likely include extrinsic factors, such as food availability, suitability of substrate, environmental water temperature, exposure, and concentration of predators; and intrinsic factors affecting more intense gametogenesis in the parent generation, higher levels of fertilization, better survival of larvae and cysts, more successful settlement, and optimal survival of post-larvae stages (Corbin, 1979).

The "convenience concept" ("biased bloom")

Convenience concepts are those not based on biological patterns and, unfortunately, they are spread throughout many biological examples including Medusozoans (Marques, 2001). Likewise, the concept of "bloom" should be based on biological aspects related to evolution or life history of the species. Nevertheless, the terms "bloom" or "outbreak" are sometimes used without considering the biological processes involved in the phenomenon.

Some authors consider a species to be blooming "…when it becomes conspicuous in the sea and when it is harmful to humans" (Nival & Gorsky, 2001; Table 1), incorporating high levels of anthropocentrism, because "…this condition depends on the size of the sample and on the sampling method used" (Nival & Gorsky, 2001). "Normal (annual) blooms" and absence of noxious species for humans do not draw attention (Benović & Lučić, 2001); therefore, most of the times they are not noticed or reported. Usually, "blooms" are observed when massive appearances of conspicuous, stinging jellyfish occur near coastal areas, significantly and visibly affecting human activities, like fisheries, tourism, and power production (Genzano et al., 2008). Hence, there is a focus on "macromedusae", mainly scyphozoans, which are individually large and cause negative impacts on various economic activities (Bayha & Graham, 2009; Richardson et al., 2009). We use the term "convenience concept of bloom" to refer to these events because they constrain "bloom" events to those observed by humans and that interfere with human activities. In other words, it is a "biased" concept.

Staurozoa are inconspicuous, often camouflaged animals (S1), in all stages of their life cycle (Wietrzykowski, 1912; Hanaoka, 1934; Otto, 1976, 1978; Hirano, 1986; Mills & Hirano, 2007). Their cnidae are not harmful to humans (personal observations), and there is no reported negative impact on human activities. Moreover, they are benthic animals, and the term "bloom" only has been applied to planktonic animals (CIESM, 2001), even though biologically they are medusae (Marques & Collins, 2004; Collins et al., 2006). Consequently, according to the convenience concept, Staurozoa do not bloom (Table 2).

Conclusion

Whether or not the Staurozoa have the capacity to bloom depends on the concept of "bloom" used (Table 1). When we considered the biological concept of "bloom", the Staurozoa do bloom according to the concepts of "true bloom" (normal and abnormal) and probably bloom according to the "apparent bloom" concept. In contrast, Staurozoa do not bloom if we use the convenience concept of "bloom", which refers to planktonic, conspicuous, and harmful to humans. Although an evolutionary analysis considered the Staurozoa to be a non-blooming clade (Dawson & Hamner, 2009), biological data reviewed here indicate that they can bloom. Consequently, the evolution of "bloom" (Dawson & Hamner, 2009) should be reviewed, as well as their phylogenetic implications.

It usually is difficult to identify the processes involved in high abundances of organisms, i.e., re-distribution of a stable population, real population growth, or both (Graham et al., 2001; Hamner & Dawson, 2009). Monitoring data are fundamental to defining such events (Genzano et al., 2008). It is also important to consider the various stages of the life cycle, such as planulae and polyps, which are often neglected in "bloom" studies (but see Arai, 2009; Dawson & Hamner, 2009; and Htun et al., 2012 on podocysts; Bayha & Graham, 2009; Astorga et al., 2012; Holst, 2012; and Purcell et al., 2012 on polyps; Straehler-Pohl & Jarms, 2010 for ephyrae detection). The biological concept of "bloom" also has weaknesses because there may be different, non-homologous processes for the origin of the "blooms". A "jellyfish bloom" is an interesting event, and if we want to be able to predict it, we need to study its whole complexity, with efforts to minimize possible biases introduced by the human point of view.

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References

Albert, D. J., 2009. *Aurelia labiata* (Scyphozoa) jellyfish in Roscoe Bay: their spatial distribution varies with population size and their behaviour changes with water depth. Journal of Sea Research 61: 140–143.

Amor, A., 1962. Sobre "Stauromedusae" do litoral Patagónico, *Haliclystus auricula* (Rathke). Notas del Museo de la Universidad Nacional de La Plata 20: 89–96.

Arai, M. N., 2009. The potential importance of podocysts to the formation of scyphozoan blooms: a review. Hydrobiologia 616: 241–246.

Arneson, A. C. & C. E. Cutress, 1976. Life history of *Carybdea alata* Reynaud, 1830 (Cubomedusae). In Mackie, G. O. (ed.), Coelenterate Ecology and Behavior. Plenum Press, New York: 227–236.

Astorga, D., J. Ruiz & L. Prieto, 2012. Ecological aspects of early life stages of *Cotylorhiza tuberculata* (Macri, 1778) affecting its pelagic population success. Hydrobiologia. doi:10.1007/s10750-012-1036-x.

Bayha, K. M. & W. M. Graham, 2009. A new Taqman© PCR-based method for the detection and identification of scyphozoan jellyfish polyps. Hydrobiologia 616: 217–228.

Benović, A. & D. Lučić, 2001. Jellyfish outbreaks: natural cycle or stress response effect? CIESM Workshop Series 14: 59–62.

Berrill, M., 1962. The biology of three New England stauromedusae, with a description of a new species. Canadian Journal of Zoology 40: 1249–1262.

Boero, F., J. Bouillon, C. Gravili, M. P. Miglietta, T. Parsons & S. Piraino, 2008. Gelatinous plankton: irregularities rule the world (sometimes). Marine Ecology Progress Series 356: 299–310.

Brotz, L., W. W. L. Cheung, K. Kleisner, E. Pakhomov & D. Pauly, 2012. Increasing jellyfish populations: trends in large marine ecosystems. Hydrobiologia. doi:10.1007/s10750-012-1039-7.

CIESM (The Mediterranean Science Commission), 2001. Gelatinous zooplankton outbreaks: theory and practice. CIESM Workshop Series 14: 112 pp. http://www.ciesm.org/online/monographs/Naples.html. Accessed 05 Nov 2011

Collins, A. G. & M. Daly, 2005. A new deepwater species of stauromedusae, *Lucernaria janetae* (Cnidaria, Staurozoa, Lucernariidae), and a preliminary investigation of stauromedusan phylogeny based on nuclear and mitochondrial rDNA data. Biological Bulletin 208: 221–230.

Collins, A. G., P. Schuchert, A. C. Marques, T. Jankowski, M. Medina & B. Schierwater, 2006. Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. Systematic Biology 55: 97–115.

Corbin, P. G., 1979. The seasonal abundance of four species of stauromedusae (Coelenterata: Scyphomedusae) at Plymouth. Journal of the Marine Biological Association of the United Kingdom 59: 385–391.

Daly, M., M. R. Brugler, P. Cartwright, A. G. Collins, M. N. Dawson, D. G. Fautin, S. C. France, C. S. McFadden, D. M. Opresko, E. Rodriguez, S. L. Romano & J. L. Stake, 2007. The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. Zootaxa 1668: 127–182.

Daryanabard, R. & M. N. Dawson, 2008. Jellyfish blooms: *Crambionella orsini* (Scyphozoa: Rhizostomeae) in the Gulf of Oman, Iran, 2002–2003. Journal of the Marine Biological Association of the United Kingdom 88: 477–483.

Davenport, J., 1998. Note on the trophic relationships of the stauromedusa *Haliclystus antarcticus* from subantarctic South Georgia. Journal of the Marine Biological Association of the United Kingdom 78: 663–664.

Dawson, M. N. & W. M. Hamner, 2009. A character-based analysis of the evolution of jellyfish blooms: adaptation and exaptation. Hydrobiologia 616: 193–215.

Dawson, M. N., L. E. Martin & L. K. Penland, 2001. Jellyfish swarms, tourists, and the Christ-child. Hydrobiologia 451: 131–144.

Genzano, G., H. Mianzan, L. Diaz-Briz & C. Rodriguez, 2008. On the occurrence of *Obelia* medusa blooms and empirical evidence of unusual massive accumulations of *Obelia* and *Amphisbetia* hydroids on the Argentina shoreline. Latin American Journal of Aquatic Research 36: 301–307.

Gibbons, M. J. & A. J. Richardson, 2009. Patterns of jellyfish abundance in the North Atlantic. Hydrobiologia 616: 51–65.

Graham, W. M., F. Pagès & W. M. Hamner, 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451: 199–212.

Gwilliam, G. F., 1956. Studies on west coast stauromedusae. PhD Dissertation, University of California, Berkeley: 192 pp

Hamner, W. M. & M. N. Dawson, 2009. A review and synthesis on the systematics and evolution of jellyfish blooms: advantageous aggregations and adaptive assemblages. Hydrobiologia 616: 161–191.

Hanaoka, K.-I., 1934. Notes on the early development of a stalked medusa. Proceedings of the Imperial Academy (Tokyo) 10: 117–120.

Hirano, Y. M., 1986. Species of Stauromedusae from Hokkaido, with notes on their metamorphosis. Journal of the Faculty of Science, Hokkaido University, Series IV, Zoology 24: 182–201.

Holst, S., 2012. Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. Hydrobiologia. doi:10.1007/s10750-012-1043-y.

Hong, J., C. He-Qin, X. Hai-Gen, F. Arreguín-Sánchez, M. J. Zetina-Rejón, P. D. M. Luna & W. J. F. L. Quesne, 2008. Trophic controls of jellyfish blooms and links with fisheries in the East China Sea. Ecological Modelling 212: 492–503.

Hoover, R. A. & J. E. Purcell, 2009. Substrate preferences of scyphozoan *Aurelia labiata* polyps among common dock-building materials. Hydrobiologia 616: 259–267.

Houghton, J. D. R., T. K. Doyle, J. Davenport & G. C. Hays, 2006. Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. Marine Ecology Progress Series 314: 159–170.

Htun, T., H. Ikeda & S. I. Uye, 2012. The potential role of podocysts in perpetuation of the common jellyfish *Aurelia aurita* s.l. (Cnidaria: Scyphozoa) in anthropogenically perturbed coastal waters. Hydrobiologia. doi:10.1007/s10750-012-1045-9.

Hyman, L. H., 1940. Observations and experiments on the physiology of medusae. Biological Bulletin 79: 282–296.

Jarms, G. & H. Tiemann, 1996. On a new hydropolyp without tentacles, *Microhydrula limopsicola* n. sp., epibiotic on bivalve shells from the Antarctic. Scientia Marina 60: 109–115.

Kikinger, R. & L. von Salvini-Plawen, 1995. Development from polyp to stauromedusa in *Stylocoronella* (Cnidaria: Scyphozoa). Journal of the Marine Biological Association of the United Kingdom 75: 899–912.

Kogovšek, T., B. Bogunović & A. Malej, 2010. Recurrence of bloom-forming scyphomedusae: wavelet analysis of a 200-year time series. Hydrobiologia 645: 81–96.

Kowalevsky, A. O., 1884. Zur Entwicklungsgeschichte der Lucernaria. Zoologische Anzeiger 7: 712–719.

Kramp, P. L., 1961. Synopsis of the medusae of the world. Journal of the Marine Biological Association of the United Kingdom 40: 7–469.

Larson, J. L. & D. G. Fautin, 1989. Stauromedusae of the genus *Manania* (=*Thaumatoscyphus*) (Cnidaria, Scyphozoa) in the northeast Pacific, including descriptions of new species *Manania gwilliami* and *Manania handi*. Canadian Journal of Zoology 67: 1543–1549.

Licandro, P., D. V. P. Conway, M. N. Daly Yahia, M. L. Fernandez de Puelles, S. Gasparini, J. H. Hecq, P. Tranter & R. R. Kirby, 2010. A blooming jellyfish in the northeast Atlantic and Mediterranean. Biology Letters 6: 688–691.

Lilley, M. K. S., J. D. R. Houghton & G. C. Hays, 2009. Distribution, extent of inter-annual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. Journal of the Marine Biological Association of the United Kingdom 89: 39–48.

Ling, S. W., 1937. Studies on Chinese stauromedusae. I. Stauromedusae from Tsingtao. Amoy Marine Biology Bulletin 3: 1–35.

Mariottini, G. L., E. Giacco & L. Pane, 2008. The mauve stinger *Pelagia noctiluca* (Forsskål [SIC], 1775). Distribution, ecology, toxicity and epidemiology of stings. A review. Marine Drugs 6: 496–513.

Marques, A. C., 2001. Simplifying hydrozoan classification: inappropriateness of the group Hydroidomedusae in a phylogenetic context. Contributions to Zoology 70: 175–179.

Marques, A. C. & A. G. Collins, 2004. Cladistic analysis of Medusozoa and cnidarian evolution. Invertebrate Biology 123: 23–42.

Mayer, A. G., 1910. The Medusae of the World, Vol. III. The Scyphomedusae. Publication No. 109. Carnegie Institution of Washington, Washington, DC: 499–735

Mianzan, H., D. Sorarrain, J. W. Burnett & L. L. Lutz, 2000. Mucocutaneous junctional and flexural paresthesias caused by the holoplanktonic Trachymedusa *Liriope tetraphylla*. Dermatology 201: 46–48.

Mills, C. E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451: 55–68.

Mills, C. E., 2011. Stauromedusae: list of all valid species names. http://faculty.washington.edu/cemills/Staurolist.html. Accessed 05 Nov 2011

Mills, C. E. & Y. M. Hirano, 2007. Stauromedusae. In Denny, M. W. & S. D. Gaines (eds), Encyclopedia of Tidepools and Rocky Shores. University of California Press, Berkeley: 541–543.

Miranda, L. S., A. C. Morandini & A. C. Marques, 2009. Taxonomic review of *Haliclystus antarcticus* Pfeffer, 1889 (Stauromedusae, Staurozoa, Cnidaria), with remarks on the genus *Haliclystus* Clark, 1863. Polar Biology 32: 1507–1519.

Miranda, L. S., A. G. Collins & A. C. Marques, 2010. Molecules clarify a cnidarian life cycle—the ''hydrozoan''

Microhydrula limopsicola is an early life stage of the staurozoan *Haliclystus antarcticus*. Public Library of Science ONE 5: e10182.

Morandini, A. C. & A. C. Marques, 2010. Revision of the genus *Chrysaora* Péron & Lesueur, 1810 (Cnidaria, Scyphozoa). Zootaxa 2464: 1–97.

Nival, P. & G. Gorsky, 2001. Conditions for blooming of pelagic species. CIESM Workshop Series 14: 23–27.

Otto, J. J., 1976. Early development and planula movement in *Haliclystus* (Scyphozoa, Stauromedusae). In Mackie, G. O. (ed.), Coelenterate Ecology and Behavior. Plenum Press, New York: 319–329.

Otto, J. J., 1978. The settlement of *Haliclystus* planulae. In Chia, F. S. & M. E. Rice (eds), Settlement and Metamorphosis of Marine Invertebrate Larvae. Elsevier/North-Holland Biomedical Press, New York: 13–22.

Parsons, T. R. & C. M. Lalli, 2002. Jellyfish population explosions: revisiting a hypothesis of possible causes. La Mer 40: 111–121.

Pitt, K. A., D. T. Welsh & R. H. Condon, 2009. Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. Hydrobiologia 616: 133–149.

Purcell, J. E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. Journal of the Marine Biological Association of the United Kingdom 85: 461–476.

Purcell, J. E., 2007. Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata*. Marine Ecology Progress Series 348: 183–196.

Purcell, J. E., 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annual Review of Marine Science 4: 209–235.

Purcell, J. E. & J. J. Grover, 1990. Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. Marine Ecology Progress Series 59: 55–67.

Purcell, J. E., S. Uye & W.-T. Lo, 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Marine Ecology Progress Series 350: 153–174.

Purcell, J. E., R. A. Hoover & N. T. Schwarck, 2009. Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions in situ. Marine Ecology Progress Series 375: 139–149.

Purcell, J. E., D. Atienza, V. Fuentes, A. Olariaga, U. Tilves, C. Colahan & J.-M. Gili, 2012. Temperature effects on asexual reproduction rates of scyphozoan polyps from the NW Mediterranean Sea. Hydrobiologia. doi:10.1007/s10750-012-1047-7.

Raskoff, K. A., 2001. The impact of El Niño events on populations of mesopelagic hydromedusae. Hydrobiologia 451: 121–129.

Richardson, A. J., A. Bakun, G. C. Hays & M. J. Gibbons, 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends in Ecology & Evolution 24: 312–322.

Sars, M., 1846. Fauna littoralis Norvegiae. Hefte 1: 1–94.

Smayda, T., 1997. What is a bloom? A commentary. Limnology and Oceanography 42: 1132–1136.

Stangl, K., L. von Salvini-Plawen & T. W. Holstein, 2002. Staging and induction of medusa metamorphosis in *Carybdea marsupialis* (Cnidaria, Cubozoa). Vie Milieu 52: 131–140.

Stefani, F., B. Leoni, A. Marieni & L. Garibaldi, 2010. A new record of *Craspedacusta sowerbii*, Lankester 1880 (Cnidaria, Limnomedusae) in Northern Italy. Journal of Limnology 69: 189–192.

Straehler-Pohl, I. & G. Jarms, 2010. Identification key for young ephyrae: a first step for early detection of jellyfish blooms. Hydrobiologia 645: 3–21.

Uchida, T., 1927. Report of the biological survey of Mutsu Bay. 2. Medusae of Mutsu Bay. Science Reports of the Tohoku University 2: 215–238.

Uye, S., 2008. Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian Marginal Seas. Plankton & Benthos Research 3: 125–131.

Van Iten, H., J. M. Leme, M. G. Simões, A. C. Marques & A. G. Collins, 2006. Reassessment of the phylogenetic position of conulariids (?Ediacaran-Triassic) within the subphylum Medusozoa (phylum Cnidaria). Journal of Systematic Palaeontology 4: 109–118.

von Salvini-Plawen, L., 1987. Mesopsammic Cnidaria from Plymouth (with systematic notes). Journal of the Marine Biological Association of the United Kingdom 67: 623–637.

Werner, B., C. Cutress & J. P. Studebaker, 1971. Life cycle of *Tripedalia cystophora* Conant (Cubomedusae). Nature 232: 582–583.

Wietrzykowski, W., 1912. Recherches sur le développement des Lucernaires. Archives de Zoologie Expérimentale et Générale 5^{e} Série 10: 1–95

Willcox, S., N. A. Moltschaniwskyj & C. M. Crawford, 2008. Population dynamics of natural colonies of *Aurelia* sp. scyphistomae in Tasmania. Australia. Marine Biology 154: 661–670.

Yamaguchi, M. & R. Hartwick, 1980. Early life history of the sea wasp, *Chironex fleckeri* (class Cubozoa). In Tardent, P. & R. Tardent (eds), Developmental and Cellular Biology of Coelenterates. Elsevier/North-Holland Biomedical Press, Amsterdam: 11–16.

Zagal, C. J., 2004a. Diet of the stauromedusa *Haliclystus auricula* from southern Chile. Journal of the Marine Biological Association of the United Kingdom 84: 337–340.

Zagal, C. J., 2004b. Population biology and habitat of the stauromedusa *Haliclystus auricula* in southern Chile. Journal of the Marine Biological Association of the United Kingdom 84: 331–336.