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RECEIVED 05 December 2023  
ACCEPTED 15 January 2024  
PUBLISHED 02 February 2024

CITATION  
Fernández-Alías A, Marcos C  
and Pérez-Ruzafa A (2024) The  
unpredictability of scyphozoan  
jellyfish blooms.  
*Front. Mar. Sci.* 11:1349956.  
doi: 10.3389/fmars.2024.1349956

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# The unpredictability of scyphozoan jellyfish blooms

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The study of jellyfish blooms has gained attention in the recent decades because of the importance of forecasting and anticipating them and avoiding their interference with human activities. However, after thirty years of scientific effort (monitoring systems, empirical laboratory and field studies, modeling, etc.), the occurrence of blooms remains unpredictable, and their consequences unavoidable. Climate change, eutrophication, overfishing, coastal construction, and species translocation have been suggested as stressors that increase them, but robust evidence to support these claims is limited. The widespread belief that jellyfish blooms are "increasing in number" has been challenged in recent years. Among the gelatinous zooplankton, the bloom forming species are concentrated in the class Scyphozoa, and the number of species with at least one recorded bloom has increased during the last decade. The analyses of long-term time series show seasonality in the dynamic of each blooming jellyfish species population, but the blooms vary in intensity and there are years of an unexplained absence of jellyfish. In this review, we focus on the current state of knowledge, uncertainties and gaps in the critical points that can strongly influence the intensity of the bloom or even lead to the absence of the medusa population. These points include ephyrae, planulae and scyphistoma natural, predatory or fishing mortality, the molecular pathway of strobilation, benthic population dynamics, planula settlement and ephyra to medusa transition success. Some of these points account for certain empirical laboratory evidence under controlled conditions, and are difficult to be studied on the field, but the different sources of non-typically recorded variability need to be addressed to improve our understanding of jellyfish population dynamics.

## KEYWORDS

jellyfish proliferation, life cycle, modeling, predictability, Scyphozoa

## 1 Introduction

The massive proliferations of jellyfishes, commonly referred to as jellyfish blooms, are usually described in negative terms because of the interference with human activities that results from their appearance. Those interferences include competing with commercial fish species both through predation on fish larvae and through the direct competition for food,

clogging fishing nets, damaging catches, stinging fishermen and swimmers or clogging water intake systems in coastal power plants, among others (Purcell et al., 2007; Richardson et al., 2009; Purcell et al., 2013). The socio-economic impacts of the jellyfish blooms are often neglected in scientific studies (Bosch-Belmar et al., 2020), but some examples can be found. In the case of fisheries, catches can be reduced by up to 25.3%, the catch value can be reduced by up to 33.7%, and the economic loss, in Korean fisheries alone, can exceed US\$ 200 million in a single jellyfish season (Kim et al., 2012). For the tourism sector in the United Kingdom, avoiding the areas where jellyfish are present can result in an economic loss of more than 12000 US\$ per day for a 10 km<sup>2</sup> tourist area (Kennerley et al., 2022), while in Spain, the average visitor is willing to pay an additional 3.20 € per beach visit if it guarantees a lower risk of encountering jellyfish (Nunes et al., 2015).

However, despite the socio-economic impacts derived from the appearance of jellyfish blooms, the ecosystem services they provide should not be ignored. In eutrophication processes, jellyfish have been linked to the maintenance of water quality through top-down control of the food web (Pérez-Ruzafa et al., 2002; Fernández-Álías et al., 2022; Fernández-Álías et al., 2023), and their use as food has led to the emergence of a fishing and aquaculture industry focused on these organisms (Hsieh et al., 2001; Omori and Nakano, 2001; Purcell et al., 2007; Nishikawa et al., 2015; Khong et al., 2016; Leone et al., 2019). In addition, jellyfish are being studied in search of biomolecules with potential applications in pharmacology and medicine (Zimmer, 2005; Sugahara et al., 2006; De Rinaldis et al., 2021; De Domenico et al., 2023; Sudirman et al., 2023), and as the most energetically efficient swimmers, jellyfish biomechanics are a subject of study in the development of remotely operated swimming vehicles (Gemmell et al., 2013; Gemmell et al., 2015; Costello et al., 2021; Gemmell et al., 2021).

The disturbances and ecological services provided by jellyfish blooms have attracted the attention of the scientific community with increasing interest since the last decade of the twentieth century (Pitt et al., 2018). Along with the scientific community, the general public have also been engaged to participate in the monitoring of jellyfish blooms through citizen science campaigns (Marambio et al., 2021; Dobson et al., 2023). During the years in which this topic has been studied, the perception of a general

increase in the frequency, intensity, and extent of jellyfish blooms has become established in the scientific community, and a whole conceptual framework of how ocean degradation favors the occurrence of jellyfish blooms has been developed (Arai, 2001; Purcell, 2005; Purcell et al., 2007; Richardson et al., 2009; Purcell, 2012). Among the ocean degradation factors cited as drivers of jellyfish blooms, overfishing, climate change, species translocation, eutrophication, and habitat modification are commonly highlighted as part of an eventual regression of the ocean state to Cambrian-like assemblages dominated by short-lived organisms such as jellyfish (Figure 1) (Pauly et al., 1998; Parsons and Lalli, 2002; Pauly et al., 2008; Richardson et al., 2009).

The same authors who contributed to the development of the conceptual framework also noted its limitations, highlighting the paucity of reliable baseline data and the short length of the time-series those assumptions were made on (Purcell et al., 2007; Pauly et al., 2008; Richardson et al., 2009). The low availability of data forced scientists attempting to analyze these assumptions to gather all the organisms referred to as jellyfish (Brotz et al., 2012) into a single and generic 'gelatinous zooplankton' group (Condon et al., 2013), despite their taxonomic, genetic and life cycle differences (Hamner and Dawson, 2009; Khalturin et al., 2019). In addition, research efforts have not been equally distributed among all components of the gelatinous zooplankton, with an overrepresentation of the scyphozoan *Aurelia* spp. Lamarck, 1816 and the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 (Pitt et al., 2018). It should also be noted that bloom-forming species are not evenly distributed throughout the gelatinous zooplankton but are concentrated in the class Scyphozoa (Hamner and Dawson, 2009), with special incidence in the larger species dwelling in temperate, shallow waters (Fernández-Álías et al., 2021). The importance of this class is not limited to a higher number of bloom forming species, as they are also responsible for most of the disturbances in fisheries and aquaculture (Bosch-Belmar et al., 2020), but also collect the highest number of edible species (Brotz et al., 2017).

Despite the controversies and limitations, the conceptual framework is generally accepted by the scientific community, and the number of published papers on the topic increases every year, contributing to the dissemination of the idea of an increase in jellyfish blooms in some areas (Sanz-Martín et al., 2016; Pitt et al.,

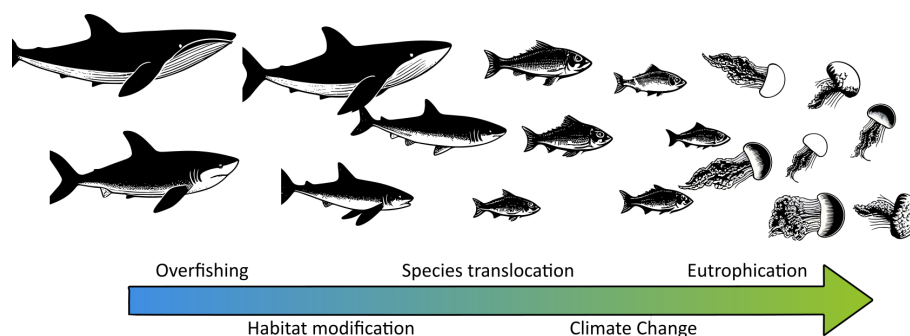


FIGURE 1

Conceptual framework of the change in the key-species controlling marine food webs in a regression to Cambrian-like assemblages because of ocean degradation (based on Pauly et al., 2008).

2018). Considering only the class Scyphozoa, where most of the blooms are concentrated, an increase in the percentage of bloom forming species has been detected in the last decade (Fernández-Álías et al., 2021). However, this increase does not necessarily mean that jellyfish populations are increasing worldwide (Brotz et al., 2012), as it is associated with a higher interest in the topic and more sampling efforts (Pitt et al., 2018).

Of all the variables analyzed within the conceptual framework, temperature is the one that stands out the most (Fernández-Álías et al., 2021), probably reflecting the seasonality that most species exhibit during their life cycle. In the class Scyphozoa, this variable has been shown to control the life cycle, modifying the asexual reproduction rate of the polyp stage, acting as a strobilation trigger and regulating the transition from ephyra to medusa (Prieto et al., 2010; Fuentes et al., 2011; Fuchs et al., 2014; Brekhman et al., 2015; Fernández-Álías et al., 2023). The effect of temperature can also be observed in short-term studies for most ecosystems and species (Fernández-Álías et al., 2020; Gueroun et al., 2020; Leoni et al., 2021a), but becomes blurred when longer time series are considered (van Walraven et al., 2015; Stone et al., 2019). This suggests that temperature is not an exclusive requirement for bloom development (Fernández-Álías et al., 2021). At the same time, the scyphozoan jellyfish species do not seem to have the thermal control on their phenology modified in the context of climate change (Fernández-Álías et al., 2023), but an increased period of suitable temperatures could extend the duration of the scyphozoan blooms (Ruiz et al., 2012; Edelist et al., 2020; Leoni et al., 2021b). In any case, both situations raise more questions and challenges about the interannual variability of bloom intensity in relation to thermal oscillations.

After more than 30 years of combined scientific research (monitoring systems, empirical laboratory and field studies, modeling, etc.), we are still unable to answer the main question asked by managers, tourists and other stakeholders: “Will there be jellyfish next season?”. There are several socio-economic implications of our inability to answer this demand, but one of the clearest examples is the cannonball jellyfish fishery in Mexico, where the national government promoted the activity and businesses developed in anticipation of a long-term productive industry, only to eventually experience a collapse in catches due to interannual variability or fisheries mismanagement (López-Martínez and Álvarez-Tello, 2013; Girón-Nava et al., 2015; Brotz et al., 2021). Improving the quality of jellyfish bloom predictions using traditional approaches, when not a single bloom has been correctly predicted in more than three decades of research, seems unlikely. Therefore, we have focused this review both on less commonly addressed sources of variability that affect the viability of scyphozoan blooms (e.g. predation on larval stages, parasitism, or interspecific competition), and on sources of variability that are commonly referred to as promoters of jellyfish blooms, but which can also induce physiological stress when they are not optimal (e.g. temperature, food availability or salinity).

This work builds on the systematic review by Fernández-Álías et al. (2021) in which all scyphozoan genera were individually used as keywords in the Web of Science and Scopus search engines to identify the bloom forming genera and species. The search

algorithm was modified in the genera *Cyanea*, *Chrysaora*, *Pelagia* to *Genus AND Jellyfish* to eliminate papers from unrelated scientific fields and further modified to *Genus AND Jellyfish AND (Bloom OR “Life cycle”)* in the case of *Aurelia* due to its use as a model species. The original search was replicated to include the publications on blooming genera from January 2021 to December 2023. Previously selected papers on blooming species were re-analyzed with the recent publications using the following selection criteria of i) reference to scyphozoan species, ii) analysis of aspects of the jellyfish ecology at any developmental stage, iii) description of possible facilitators or perturbations to the regular development of the life cycle. The review was supplemented by additional searches in Google Scholar under combinations of the term “Jellyfish” with “Predation”, “Disease”, “Parasitism”, “Fisheries”, “Mortality” and “Stress” to include thesis and other ‘gray literature’ items. No filter was applied in terms of number of citations or year of publication. Since the aim of the review was to construct a conceptual model of the factors that control the biological cycle of scyphozoans and to discuss the sources of variability that influence the difficulty of predicting the events of massive proliferations of these organisms, and not to perform meta-analyses, no attempt was made to quantify the retrieved publications, selected or excluded papers.

## 2 Control of the ‘never-ending jellyfish joyride’

The proposed conceptual framework for a jellyfish-dominated ocean depicted a series of interrelated mechanisms that further enhanced this jellyfish dominance over other marine species, based on how their own biological characteristics seemed to overcome any possible control over populations (Richardson et al., 2009). However, reports of long-term monitoring of jellyfish populations usually reveal the existence of years of unexplained absence of jellyfish. In the Mar Menor coastal lagoon (Spain), an ecosystem affected by eutrophication over the last 30 years, habitat modification, global warming, and fishing (Pérez-Ruzafa et al., 2019; Fernández-Álías et al., 2022), populations of *Cotylorhiza tuberculata* (Macri, 1778) and *Rhizostoma pulmo* (Macri, 1778) unexpectedly collapsed after two decades of benefiting from the factors described in the conceptual framework (Fernández-Álías et al., 2022; Fernández-Álías et al., 2023). In the Dutch Wadden Sea (Netherlands), another monitored eutrophic ecosystem, the different scyphozoan jellyfish species showed different patterns of abundance over the years, alternating between years of unexplained absence or sparse abundance of some individual species and bloom years (van Walraven et al., 2015).

Scyphozoan jellyfish species generally have a metagenic life cycle, alternating between benthic and pelagic phases (Hamner and Dawson, 2009). During the same, there are several stages where a numerical expansion of the population can occur: a single medusa can carry thousands to millions of planulae (Kikinger, 1992; Lucas, 1996), the polyp population can double to five times its initial number within a month under the appropriate food-temperature conditions (Lucas et al., 2012; Wang et al., 2015), and each strobila

can release from 1 to 30 ephyrae (Di Camillo et al., 2010; Fuentes et al., 2011; Lucas et al., 2012). Under the most optimal conditions without any kind of mortality, neither natural nor predatory, a single medusa can yield from a minimum of  $2 \times 10^3$  ( $\approx 1$  medusa  $\times$  1000 planulae/medusa  $\times$  2 polyps/planula  $\times$  1 ephyra/polyp) to a maximum of  $1.5 \times 10^8$  medusae ( $\approx 1$  medusa  $\times$   $10^6$  planulae/medusa  $\times$  5 polyps/planula  $\times$  30 ephyrae/polyp) within a single year (Figure 2, black arrows). Consequently, the large interannual variation in the abundance of the medusa phase of the scyphozoan jellyfish populations can only be explained by the existence of complex interactions that regulate, either as enhancers (Figure 2, green arrows) or inhibitors (Figure 2, red arrows), the dynamics of the different scyphozoan jellyfish populations during the different stages of the life cycle.

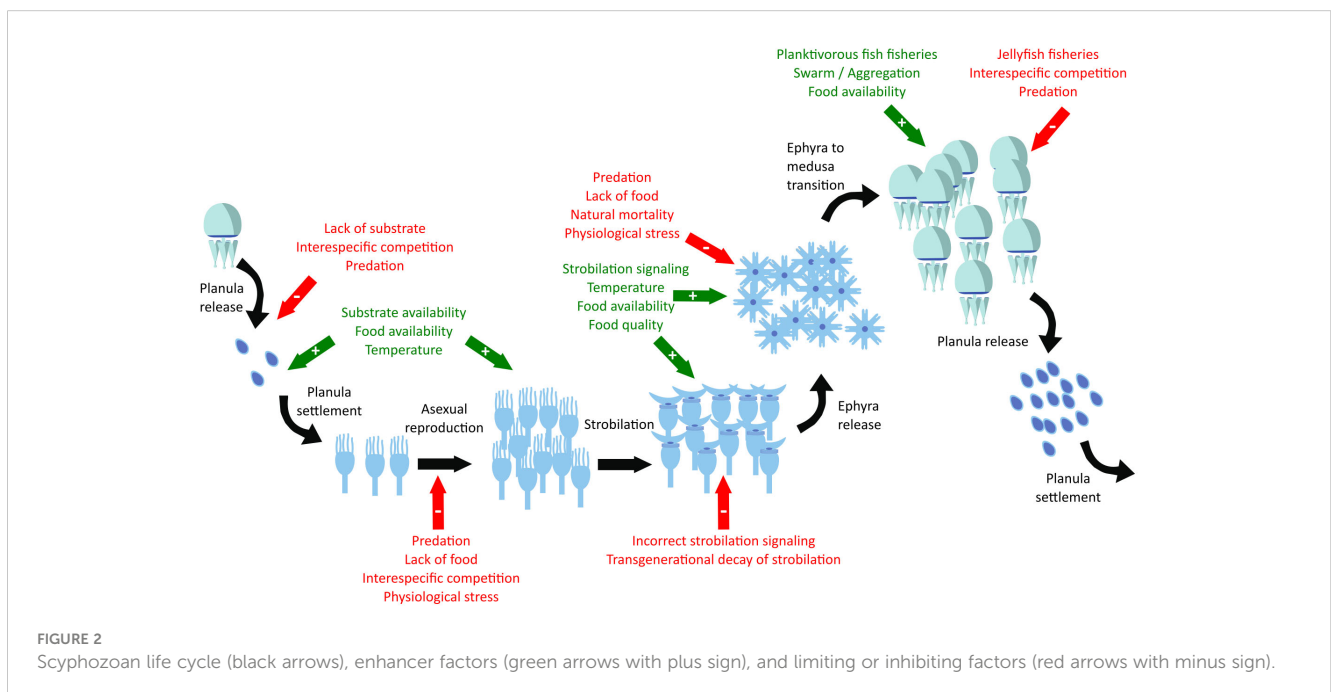
### 2.1 Planula stage

Scyphozoan planulae can settle on a variety of natural and artificial hard substrates, including shells, concrete, plastic, glass, wood, rope, seagrass, macroalgae, rocks, etc., with different efficiencies depending on the type and orientation of the substrate and the different scyphozoan species (Miyake et al., 2002; Holst and Jarms, 2007; Malej et al., 2012; Marques et al., 2015; Franco, 2016; Gambill et al., 2018; van Walraven et al., 2020). There is an environmental control by factors such as temperature, salinity or light on the settlement and excystment of the planulae, providing an efficiency of the process, with the absence of competition for the substrate or predation, which decreases from a maximum of  $\sim 60\%$  under the most suitable conditions to a minimum of 0% in a progression towards less suitable conditions (Prieto et al., 2010; Franco, 2016; Gambill et al., 2018; Feng et al., 2021; Gueroun et al., 2021; Holst et al., 2023). Even under the preferred environmental conditions and in the absence of competitors and predators, the

settlement needs to occur within the first few days after planula release to prevent a significant decline in its effectiveness (Gambill et al., 2018). However, spatial competition and predation cannot be ignored when attempting to build predictive models of jellyfish blooms, yet both topics remain largely understudied. Boughton et al. (2023) conducted an *in-situ* fouling settlement experiment on PVC panels testing the settlement efficiency of *Aurelia aurita* (Linnaeus, 1758) planulae against potential competitors, showing high competition for the space and a relative increase in planula settlement efficiency after removal of potential competitors. Predation on scyphozoan planulae, which is rarely addressed, can occur at least by ctenophores, ascidians, and bivalves at rates of 10 – 25, 20 and 40 planulae  $\times$  ind<sup>-1</sup>  $\times$  h<sup>-1</sup>, respectively (Javidpour et al., 2009; Kuplik et al., 2015), as well as by scyphozoan polyps (Gröndahl, 1988a; Gröndahl, 1988b). In this line, Franco (2016) linked the absence of planula settlement on live oyster shells to the filtering capacity of oysters. In contrast, Marques et al. (2015) linked the absence of polyps attached to oyster shells in the Thau lagoon (France) to the oyster farming method rather than to the oyster predation on planulae, while Malej et al. (2012) do provide images of polyps over oyster shells. However, in the latter example it is not certain whether the planulae have settled directly over the shell or whether the presence of polyps is due to a colonization by asexual reproduction and polyp motility (Feng et al., 2017; Zang et al., 2023).

### 2.2 Polyp stage

After the planula settlement, the polyps emerge in a process called excystment and develop tentacles to acquire their typical morphology in a process that can be negatively affected by inadequate temperature-salinity conditions or by the lack of food (Holst et al., 2023). Newly formed polyps can colonize the substrate through 7 different modes of asexual reproduction (Schiariti et al.,



2014; Wang F. et al., 2023). The different scyphozoan jellyfish species can exhibit a mono-mode asexual reproductive strategy (e.g. *Phyllorhiza punctata* von Lendenfeld, 1884; Schiariti et al., 2014), multi-mode asexual reproductive strategy (*Aurelia* spp.; Schiariti et al., 2014; Wang F. et al., 2023), or a preferential and a secondary strategy as it found in *R. pulmo* (Fuentes et al., 2011; Schiariti et al., 2014). Under the adequate food and temperature conditions, each polyp can produce 8 to 20 buds from which new polyps can develop (Purcell et al., 2012), but the overall efficiency in the absence of competitors or predators is typically limited to a two to fivefold increase in the initial number of polyps (Lucas et al., 2012; Wang et al., 2015). In general, species with multi-mode asexual reproductive strategies exhibit higher asexual reproduction rates (Schiariti et al., 2014).

Scyphozoan polyps generally exhibit a wide thermal and salinity tolerance, but the asexual reproduction rates can decline rapidly when the optimal conditions are not met and eventual mass mortality can occur when the upper or lower tolerance limits are exceeded (Purcell et al., 1999; Prieto et al., 2010; Purcell et al., 2012; Treible and Condon, 2019). As a result, the evolution of the different scyphozoan species has led to higher asexual reproduction rates of polyps at temperatures when their planulae are present in the water column (Prieto et al., 2010; Purcell et al., 2012; Schiariti et al., 2014; Treible and Condon, 2019). Scyphozoan polyps can also withstand starvation conditions, but surprisingly, when the food scarcity conditions are coupled with the optimal temperatures for the asexual reproduction, the survival is significantly reduced, likely due to increased metabolic demands (Zang et al., 2023).

In nature, the scyphozoan polyps face interspecific competition for food and space, predation, synergies with other organisms derived from the construction of their hard structures, and physiological stress associated with environmental conditions (Feng et al., 2017; Marques et al., 2019; Feng et al., 2021; Zang et al., 2023). The organisms that efficiently compete for the space and reduce substrate availability for scyphozoan polyps by killing and displacing them, have a slimy or soft surface that cannot be used as a substrate for polyp development (Zang et al., 2023). This first group mainly includes sponges and ascidians, but there are some exceptions, as *Aurelia* sp. has been shown to be able to grow on certain solitary ascidians (Miyake et al., 2002; Feng et al., 2017; Rekstad et al., 2021). A second group of organisms are those with a spiny or multibranched surface. This group includes species that never provide a suitable substrate for settlement and others that may eventually provide a suitable substrate, as happens when the mud tubes of amphipods become stiffer (Miyake et al., 2002). The third group includes bivalves, the calcareous tubes of polychaetes, balanoids, and, in general, organisms that build hard structures and increase the available substrate for polyps to attach to (Miyake et al., 2002; Rekstad et al., 2021; Zang et al., 2023). Scyphozoan polyp predators include crustaceans, nudibranchs, and gastropods with consumption rates greater than 300 polyps  $\times$  ind<sup>-1</sup>  $\times$  day<sup>-1</sup> (Arai, 2005; Takao et al., 2014; Feng et al., 2017; Tang et al., 2021). Intraguild predation among scyphozoan polyps has also been observed in laboratory studies co-culturing multiple species (Tang et al., 2020). The overall balance between polyp asexual

reproduction, competition, predation, and physiological stress may benefit the scyphozoan polyps during the initial stages of colonization of a bare substrate (Feng et al., 2021; Boughton et al., 2023), but it is reversed within months, leading to severe reductions in scyphozoan polyp densities or even the disappearance of polyp colonies of certain species (Hernroth and Gröndahl, 1983; Feng et al., 2017; Feng et al., 2021).

## 2.3 Strobila and post-strobila stages

The strobilation process involves the reabsorption of polyp tentacles and the differentiation of segments that will eventually produce ephyrae at the oral end of the scyphistoma (Schiariti et al., 2008; Fuentes et al., 2011). Triggering of the process occurs following physical or chemical signals (Holst, 2012; Lucas et al., 2012; Helm, 2018). The molecular mechanism of strobilation is not fully understood, but the candidate hormones that induce the process exhibit strong temperature regulation during the polyp stage (Fuchs et al., 2014; Brekhman et al., 2015; Ge et al., 2022) and show structural similarities to certain compounds used in aquaria to chemically trigger the process (Spangenberg, 1965; Helm, 2018). Temperature must act in concert with other factors to induce strobilation: in tropical ecosystems with low thermal oscillations, strobilation can be signaled by salinity shifts (Lucas et al., 2012; Helm, 2018), zooxanthellate bearing species must host their symbionts and be exposed to both light and temperature appropriate conditions (Kikinger, 1992; Prieto et al., 2010; Schiariti et al., 2014), and there is a food requirement for polyps to strobilate (Wang et al., 2015; Zang et al., 2023). In non-zooxanthellate species, where the light and symbionts are not required, the microbiota organisms still play a key role in the strobilation, as the process is inhibited by a downregulation of the genetic pathway in their absence (Jensen et al., 2023).

The seasonal appearance of the medusa phase in most of the scyphozoan species is indicative of a temperature regulated strobilation process (Holst, 2012; Fernández-Álías et al., 2021), but there are reports of ephyra appearing at temperatures unsuitable for their posterior development (Fernández-Álías et al., 2023). Incorrect strobilation signaling can be problematic for the completion of the life cycle as it is a stressful process for the scyphozoan polyps. In most species, the calix diameter of the polyp shrinks after ephyra release (Feng et al., 2017), and the remnant is not always able to recover. In *C. tuberculata*, the polyp population completely disappears shortly after the strobilation (Kikinger, 1992; Prieto et al., 2010), and the polyps of *Cyanea nozakii* Kishinouye, 1891, *Rhopilema esculentum* Kishinouye, 1891, and *Nemopilema nomurai* Kishinouye, 1922 were unable to recover their original size and eventually disappeared in the field experiment by Feng et al. (2017). In contrast, *R. pulmo* has been reported to regrow the tentacles within two weeks after strobilation (Fuentes et al., 2011), and *Rhopilema nomadica* Galil, Spanier and Ferguson, 1990 can undergo multiple strobilation events while reproducing asexually (Lotan et al., 1992). As a result, some scyphozoan polyp cultures can be maintained in an aquarium for years (Lucas et al., 2012), but

their ability to reproduce asexually may decline with successive generations (Chi et al., 2022). However, Holst (2012) observed that *Cyanea capillata* (Linnaeus, 1758) produced more ephyrae per polyp in older polyps, but the latter development to the medusa phase was not recorded and the overall effect on jellyfish population dynamics remains unknown.

## 2.4 Ephyra stage

The ephyra stage is not typically reported to limit the magnitude of the jellyfish blooms, but there is evidence that ephyra peaks followed by a massive mortality reduce the abundance of the medusa phase and even lead to an absolute absence of the same (Fernández-Álías et al., 2023). This occurs when a strobilation event occurs outside the appropriate temperature range for the development of the ephyrae, as there are upper and lower thresholds for the transition from ephyra to medusa (Astorga et al., 2012; Fernández-Álías et al., 2023).

The transition from ephyra to medusa involves a somatic growth, fusion of the rhopaliar lappets by the extension of the umbrella, the development of a gastric system, oral arms, and tentacles, and can last from 10 to 150 days, depending on the species and the environmental conditions (Holst et al., 2007; Fuentes et al., 2011; Astorga et al., 2012; Fernández-Álías et al., 2020; Gueroun et al., 2020; Fernández-Álías et al., 2023). During this period, ephyrae are exposed to natural mortality and intraguild predation by scyphozoan polyps, ephyrae, and medusae (Carrizo et al., 2016; Avian et al., 2021; Stoltenberg et al., 2021; Wang P. et al., 2023). To maintain the growth rate of the ephyra and increase the likelihood of completing the transition from ephyra to medusa, food requirements must be matched in quantity and quality (Chambel et al., 2016; Miranda et al., 2016; Ballesteros et al., 2022).

Mortality at this stage is rarely addressed, but it is likely to influence the development of the bloom. In the most conspicuous blooms of *C. tuberculata*, where ephyra abundance was also assessed, mortality at this stage was less than 5%, but the average mortality of *C. tuberculata* ephyra is around 70% and greatly affects the intensity of the bloom (Fernández-Álías et al., 2023). In the case of the moon jellyfish, *Aurelia* spp., the minimum recorded mortality at the ephyra stage is over 70%, the average mortality is over 90% and the maximum mortality is over 99% (Ishii et al., 2004; Fernández-Álías et al., 2023). The most likely factors involved in ephyrae mortality are physiological stress or predation (Carrizo et al., 2016; Stoltenberg et al., 2021; Fernández-Álías et al., 2023), but the absence of microbiota results in deformed ephyra after strobilation (Jensen et al., 2023), whose correct development is unlikely.

## 2.5 Medusa phase

The first observations in the water column of some individuals in their medusa phase can be a sign of an offshore bloom whose individuals have not yet been drifted ashore by winds or tides (Zavodnik, 1987; Keesing et al., 2016), an early bloom warning or an

unsuccessful inshore jellyfish bloom (Fernández-Álías et al., 2023). The importance of the medusa phase goes beyond the ecosystem services and disturbances resulting from the bloom that occurs, as they can carry from thousands to millions of planulae (Kikinger, 1992; Lucas, 1996). The underlying biological reason for the occurrence of swarms or aggregations of medusae during the bloom events is not fully understood, but it has been argued that the reproductive success and the protection from predators could be enhanced by these behaviors (Hamner and Dawson, 2009; Fernández-Álías et al., 2021).

In this line, the scyphozoan jellyfish have traditionally been considered as a trophic dead end, but their trophic role has probably been underestimated as their absence in stomach contents can be explained by their extremely high digestion rate (Ates, 1988; Arai et al., 2003; Hays et al., 2018). Recent analyses, including increased data collection of stomach contents, direct observations, stable isotope analyses, DNA metabarcoding, and animal-borne cameras have significantly increased our knowledge of gelatinous zooplankton predation (Hays et al., 2018). The wide variety of organisms that predate on scyphozoan medusae include sea anemones, corals, starfish, brittle stars, sea cucumbers, balanoids, amphipods, decapods, fishes, flying seabirds, penguins, turtles, and other scyphozoan jellyfish (Ates, 1988; Arai, 2005; Titelman et al., 2007; Heaslip et al., 2012; Thiebot et al., 2016; Ates, 2017; McInnes et al., 2017; Thiebot et al., 2017; Hays et al., 2018; Wang P. et al., 2023).

The interest in studying the link between scyphozoan jellyfish and predators is partly driven by the parasites that the scyphozoan medusae harbor as intermediate hosts before infecting commercially exploited fish (Browne, 2014; Kondo et al., 2016; Motta et al., 2023). This developmental stage can harbor parasites with single host life cycles, such as amphipods or anemones, and parasites with multiple host life cycles, such as digeneans and cestodes (Arai, 2005; D'Ambra and Graham, 2009; Diaz Briz et al., 2012; Browne, 2014). The high prevalence of parasites in scyphozoan medusae suggests that a fundamental part of the parasite life cycle may occur in jellyfish (Diaz Briz et al., 2012), providing benefits such as protection, feeding or transport (Sal Moyano et al., 2012; Gonçalves et al., 2022), but the effect of parasites on the scyphozoan life cycle is poorly understood (D'Ambra and Graham, 2009). This infection may be important for life cycle completion, as somatic growth, gonad size, and egg production of scyphozoan medusae may be reduced by parasitism (Chiaverano et al., 2015).

The final factor influencing the medusa phase of the scyphozoan jellyfish life cycle is fishing, which can promote or disrupt the biological strategies of scyphozoan species, depending on the species targeted by the fishery (Lynam et al., 2006; Brotz, 2016). Overfishing of filter-feeding fish has promoted a shift in the system toward jellyfish dominance in some locations (Lynam et al., 2006), but this has not occurred when an alternative stock of filter-feeding fish could replace the original species (Schwartzloze et al., 1999). Similarly, filter-feeding fishes may benefit from the collapse of a predatory fish fishery (Mullon et al., 2005). In these cases, there is no increase in jellyfish abundance (Richardson et al., 2009), but they are indicative of the complexity of the system. This can be further illustrated by the case of salmon fisheries on the Pacific coast

of North America, where the population of the sea nettle *Chrysaora fuscescens* Brandt, 1835 showed a complex pattern of zooplanktonic relationships that affected its abundance as well as the fisheries for the targeted salmon species (Ruzicka et al., 2016).

Scyphozoan jellyfish are also targeted species, and the impact of their fisheries on population dynamics must also be discussed. Indeed, jellyfish fisheries have become increasingly important worldwide, with more than 20 countries reporting their activity and average annual jellyfish landings exceeding  $7.5 \times 10^8$  kg (Brotz, 2016; Brotz et al., 2017), but the biological parameterization of the species necessary to develop sustainable fishing programs has only been carried out for certain species and locations (Palomares and Pauly, 2008; Brotz, 2016; Fernández-Álías et al., 2020; López-Martínez et al., 2020; Leoni et al., 2021a; Behera et al., 2022). Consequently, the overfishing has been identified as the main cause of the collapse of the jellyfish fisheries of *R. esculentum* in China (Dong et al., 2014) and of *Stomolophus meleagris* Agassiz, 1860 in Mexico (Brotz et al., 2021). However, it is important to consider that jellyfish populations fluctuate naturally, and this is one of the main challenges in establishing long-term, productive jellyfish fisheries. For example, to maintain the economic productivity of the *R. esculentum* fishery in China, a stock enhancement program was developed to maintain and increase the catches in anticipation of a population collapse due to overfishing (Dong et al., 2009). In contrast, the collapse of the *C. tuberculata* population in the Mar Menor coastal lagoon (Spain) occurred after the jellyfish removal program was suspended (Fernández-Álías et al., 2022; Fernández-Álías et al., 2023), suggesting that overfishing is not the only cause of population collapse.

## 2.6 Non-metagenic life cycle

The scyphozoan species do not require a metagenic life cycle to bloom (Hamner and Dawson, 2009). The most relevant holopelagic jellyfish of the class Scyphozoa capable massive proliferation *Pelagia noctiluca* (Forsskål, 1775) and *Periphylla periphylla* (Péron and Lesueur, 1810). The set of factors affecting their life cycle is likely to be similar to that described previously in this review, but their lack of a benthic stage justifies the inclusion of an additional section to discuss the transitions from planula to ephyra (*P. noctiluca*) and from fertilized egg to medusa (*P. periphylla*).

The mauve stinger, *P. noctiluca*, is one of the most conspicuous scyphozoan species in the western Mediterranean (Canepa et al., 2014). This species lacks a benthic phase, and the planula larva transforms directly into an ephyra (Canepa et al., 2014; Ramondenc et al., 2019; Ballesteros et al., 2021). The medusa stage can survive for more than one year (Lilley et al., 2014), shows different reproduction peaks during the same (Milisenda et al., 2018), and shows a heterogeneous bloom pattern and spatial variability across the Mediterranean Sea (Marambio et al., 2021; Pastor-Prieto et al., 2021; Bellido et al., 2020). The population dynamics seems to follow a regular seasonality (Benedetti-Cecchi et al., 2015) with the spawning period adapting to the most suitable temperature frame for the transition from planula to ephyra (Rosa et al., 2013; Milisenda et al., 2018). This seasonality is likely to be a product

of evolutionary selection, as the larval survival rate through the planula to ephyra transition decreases from 50% to approximately 12% when the temperature requirements are not met (Rosa et al., 2013). However, during the medusa spawning period, when the gonads of *P. noctiluca* reach their largest size (Milisenda et al., 2018), certain fish species have been reported to selectively feed on these organs, which are more nutritious than the somatic tissues (Milisenda et al., 2014), but the impact of this selective foraging over the species dynamics requires further exploration. Finally, during the ephyra stage, as is the case for the species with a metagenic life cycle, food requirements must to be matched in quantity and quality for its proper development to the medusa phase (Ballesteros et al., 2022).

*P. periphylla* is one of the scyphozoan blooming species that deviates the most from the metagenic life cycle and from the 'boom and boost' appearance of the medusae. In this species the medusae appear after direct transformation from the fertilized egg, thus, lacking not only the benthic phase, but also the planula and ephyra stages (Jarms et al., 1999). Moreover, the medusa stage has a low growth rate, and a lifespan of several years (Jarms et al., 1999; Båmstedt, 2023). The number of oocytes carried by a female *P. periphylla* increases with the medusa size and can be as high as 1000 oocytes per female in a 12 cm diameter, 9 year old female (Båmstedt et al., 2020; Båmstedt, 2023). This species has only been found in significant numbers in fjords, where there appears to be no predation or parasitism on the medusae, thus contributing to their longevity (Fosså, 1992). Within the fjords, *P. periphylla* medusae make vertical migrations to the surface during the night for reproductive purposes, allowing the fertilized eggs to sink to depths that prevent their predation by visual predators (Båmstedt et al., 2020), but leaving them vulnerable to the deep-water renewal (Båmstedt, 2023). Despite this strategy, and analogous to the planula settlement or the ephyra to medusa transition, the mortality in the fertilized egg to medusa transition exceeds 90% and can be almost complete in most cases (Båmstedt, 2023).

## 2.7 Combined effect of the control points over the life cycle

The predictability of jellyfish blooms is extremely limited because the "never-ending jellyfish joyride" is in fact strongly influenced by non-typically measured external conditions (Table 1). The magnitude of the link between planula settlement, polyp development, and medusae population size at any temporal and spatial scale is unexplored (Gibbons et al., 2016), but from our review it can be inferred that the blockage of the life cycle in any of the stages by any of the aforementioned factors can limit the occurrence of future blooms, while, on the other hand, the success of the different developmental stages may increase the number of individuals by orders of magnitude from tens, asexually in the benthic phase, to millions, sexually in the pelagic phase (Figure 2; Table 1). This means that the collapse of a scyphozoan population can be followed by a sudden explosive recovery of the same through the survival of sparse medusae from the previous season or through the reception of a few new individuals that restore

TABLE 1 Effect and magnitude of the different factors modulating the biological processes of the developmental stages during the scyphozoan life cycle.

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
Planula	Settlement	Maximum yield		60% of the released planulae	<i>Acromitus hardenbergi</i> , <i>Aurelia</i> spp., <i>Catostylus tagi</i> , <i>Chrysaora</i> spp., <i>Cotylorhiza tuberculata</i> , <i>Cyanea</i> spp., <i>Nemopilema nomurai</i> , <i>Rhizostoma octopus</i> , <i>Rhopilema esculentum</i>	Holst and Jarms, 2007; Javidpour et al., 2009; Prieto et al., 2010; Kuplik et al., 2015; Franco, 2016; Dong et al., 2018; Gambill et al., 2018; Takao and Uye, 2018; Feng et al., 2021; Gueroun et al., 2021; Miyake et al., 2021; Boughton et al., 2023; Holst et al., 2023
		Temperature (not optimal)	Longer settlement time	Up to 30 days of delayed settlement		
			Decreased settlement success	Up to 100% reduction of efficiency		
		Salinity (not optimal)	Decreased settlement success and mortality	Up to 100% reduction of efficiency and up to 100% mortality		
		Light (absence)	Decreased settlement success in zooxanthelated species	Up to 75% reduction of efficiency		
			Increased settlement success in non-zooxanthelated species	Up to 40% increase of efficiency from high light intensity to low intensity or absence of light		
		Substrate (type)	Better performance on artificial substrate	0 to 60% higher settlement on artificial substrate		
		Substrate (orientation)	Differential preferences between species	Generally better performance in substrate undersides		
		Predation	Removal of planulae	Removal of 10 to 40 planulae $\times ind^{-1} \times h^{-1}$		
		Fouling organisms	Reduction of available space	Negative, not quantified		
	Excystment	Maximum yield		45% of the settled planulae	<i>Catostylus tagi</i> , <i>Cyanea</i> spp., <i>Rhopilema esculentum</i>	Fu et al., 2019; Gueroun et al., 2021; Holst et al., 2023
		Temperature (not optimal)	Decreased excystment success	Up to 100% reduction of efficiency		
		Salinity (not optimal)	Decreased excystment success	Up to 60% reduction of efficiency		
		Salinity (oscillation)	Decreased excystment success	Up to 27% reduction of efficiency		
		Food	No effect	No effect		

(Continued)



TABLE 1 Continued

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
Polyp	Metamorphose from planulae	Temperature (not optimal)	Abnormal polyp development	Up to 60% reduction in the number of tentacles per polyp	<i>Catostylus tagi</i> , <i>Cyanea</i> spp.	Gueroun et al., 2020; Holst et al., 2023
		Salinity (not optimal)	Abnormal polyp development	Up to 20% reduction in the number of tentacles per polyp		
		Food (absence)	Abnormal polyp development	Up to 50% reduction in the number of tentacles per polyp		
	Asexual reproduction	Maximum yield		8-30 polyps derived from the original	<i>Aurelia</i> spp., <i>Cassiopea</i> sp., <i>Cephea cephea</i> , <i>Cotylorhiza tuberculata</i> , <i>Chrysaora</i> spp., <i>Lychnorhiza lucerna</i> , <i>Mastigias papua</i> , <i>Nemopilema nomurai</i> , <i>Phyllorhiza punctata</i> , <i>Rhizostoma</i> spp., <i>Rhopilema esculentum</i> , <i>Sanderia malayensis</i>	Hernroth and Gröndahl, 1983; Purcell et al., 1999; Holst et al., 2007; Purcell et al., 2007; Di Camillo et al., 2010; Prieto et al., 2010; Lucas et al., 2012; Pascual et al., 2015; Schiariti et al., 2014; Takao et al., 2014; Wang et al., 2015; Treible and Condon, 2019; Rato et al., 2021; Rekstad et al., 2021; Schäfer et al., 2021; Tang et al., 2021; Zang et al., 2023
	Asexual reproduction strategy	Better performance by multi-mode asexual reproduction species	0 to 95% asexual reproduction rate reduction from multi-mode to mono-mode strategy			
	Temperature (not optimal)	Decreased asexual reproduction rate	Up to 90% reduction of the asexual reproduction rate			
		Mortality of the polyps	Up to 100% in 30 days			
	Temperature (optimal)	Higher asexual reproduction rates at higher temperatures	2 to 5 times increase in the asexual reproduction rate			
	Salinity (not optimal)	Decreased asexual reproduction rate	Up to 90% reduction of the asexual reproduction rate			
		Decreased survival rate	Up to 60% decrease in survival rate			
	Food (absence)	Inhibition of asexual reproduction	Up to 100% reduction of the asexual reproduction rate			
	Food (absence) + Temperature (optimal)	Polyp mortality	Up to 100% polyp mortality			
	Light (absence)	No effect	No effect			

(Continued)

TABLE 1 Continued

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
		Long-term cultures	Transgenerational loss of asexual reproduction capacity	Up to 30% of asexual reproduction rate decay		
		Fouling organisms	Displacement and mass mortality by slimy surface organisms	Up to 100% of species replacement		
			Colonization of sessile organisms' hard structures	Positive, not quantified		
		Predation	Removal of polyps	Up to 300 polyps × ind <sup>-1</sup> × day <sup>-1</sup>		
Strobila	Strobilation	Maximum yield	Monodisc strobilation	1 ephyra/polyp	<i>Aurelia</i> spp., <i>Cassiopea</i> spp., <i>Catostylus mosaicus</i> , <i>Cephea cephea</i> , <i>Chrysaora hysoscella</i> , <i>Cotylorhiza tuberculata</i> , <i>Cyanea</i> spp., <i>Lychnorhiza lucerna</i> , <i>Mastigias papua</i> , <i>Nausithoe aurea</i> , <i>Nemopilema nomurai</i> , <i>Phyllorhiza punctata</i> , <i>Rhizostoma</i> spp., <i>Rhopilema</i> spp., <i>Stomolopus meleagris</i>	Kikinger, 1992; Purcell et al., 1999; Stampar et al., 2008; Prieto et al., 2010; Fuentes et al., 2011; Astorga et al., 2012; Holst, 2012; Lucas et al., 2012; Pascual et al., 2015; Feng et al., 2017; Treible and Condon, 2019; Feng et al., 2020; Enrique-Navarro et al., 2021; Schäfer et al., 2021; Jensen et al., 2023; Wang F. et al., 2023
			Polydisc strobilation	Up to 30 ephyrae/polyp		
		Temperature (oscillation)	Trigger strobilation	Up to 80% increase in total strobilating polyps		
		Temperature (not optimal)	Inhibition of strobilation	Up to 100% reduction in the strobilation rate		
			Polyp mortality	Up to 100% polyp mortality		
		Salinity (not optimal)	Inhibition of strobilation	Up to 100% reduction in the strobilation rate		
		Light (absence)	Inhibition of strobilation in some zooxanthelated species	100% reduction in the strobilation rate		
		Zooxanthellae (absence)	Inhibition of strobilation in some zooxanthelated species	100% reduction in the strobilation rate		
		Microbiome (absence)	Inhibition of strobilation	Up to 85% reduction in the strobilation rate		
		Food (absence)	Inhibition of strobilation	100% reduction in the strobilation rate		
			Polyp mortality	Up to 100% polyp mortality		

(Continued)

TABLE 1 Continued

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
		pH (future scenario)	Malformed ephyrae	Abnormal rhopalium development		
		Long-term cultures	Increased ephyra production per polyp	Up to double the number of ephyrae per polyp		
	Post-strobilation	Stress	Calyx diameter shrinkage	Up to 75% reduction of calyx diameter	<i>Aurelia</i> spp., <i>Cotylorhiza tuberculata</i> , <i>Cyanea nozakii</i> , <i>Nemopilema nomurai</i> , <i>Rhopilema</i> spp., <i>Rhizostoma pulmo</i>	Kikinger, 1992; Lotan et al., 1992; Prieto et al., 2010; Fuentes et al., 2011; Feng et al., 2017; Chi et al., 2022
			Polyp' residuum mortality	Up to 100% polyp mortality		
			Regrowth of the tentacles and survival	Up to 100% polyp recovery		
Ephyra	Ephyra to medusa transition	Maximum yield		1 medusa per ephyra	<i>Aurelia</i> spp., <i>Cassiopea xamachana</i> , <i>Cephea cephea</i> , <i>Chrysaora</i> spp., <i>Cotylorhiza tuberculata</i> , <i>Cyanea nozakii</i> , <i>Lychnorhiza lucerna</i> , <i>Pelagia noctiluca</i> , <i>Phyllorhiza punctata</i> , <i>Rhizostoma pulmo</i> , <i>Stomolophus meleagris</i>	Ishii et al., 2004; Astorga et al., 2012; Wang and Li, 2015; Wang and Sun, 2015; Carrizo et al., 2016; Chambel et al., 2016; Miranda et al., 2016; Schäfer et al., 2021; Ballesteros et al., 2022; Muffett et al., 2022; Fernández-Álias et al., 2023; Wang P. et al., 2023
		Temperature (optimal)	Reduced time in the ephyra to medusa transition	Not quantified		
		Temperature (not optimal)	Ephyrae mortality	Up to 100% ephyrae mortality		
		Salinity (not optimal)	Ephyrae mortality	Up to threefold increase in mortality risk		
		Food (quality and quantity)	Reduction in growth	Up to 45% reduction in growth under inadequate feeding regime		
			Ephyrae mortality	Up to 100% ephyrae mortality under inadequate feeding regime		
		Light (absence)	Reduced growth and bleaching in zooxanthelated species	Up to 4.5 times reduction in size in growth experiments		
		Predation	Removal of ephyrae	Removal of more than 7 ephyrae × ind-1 × h <sup>-1</sup>		
Medusa	Growth and sexual reproduction	Maximum yield		1.7×10 <sup>4</sup> to 2×10 <sup>6</sup> planulae per female	<i>Acromitus hardenbergi</i> , <i>Aurelia</i> spp., <i>Cassiopea</i> spp., <i>Catostylus</i> spp., <i>Cephea cephea</i> , <i>Chrysaora</i> spp., <i>Cotylorhiza tuberculata</i> , <i>Crambione</i> spp., <i>Crambionella</i> spp., <i>Cyanea</i> spp., <i>Dyrmonema</i> spp., <i>Linuche unguiculata</i> , <i>Lobonema smithi</i> , <i>Lobonemoides</i> spp., <i>Lychnorhiza</i>	Kremer et al., 1990; Kikinger, 1992; Lucas, 1996; Kawahara et al., 2006; Bayha et al., 2012; Heaslip et al., 2012; Chiaverano et al., 2015; Brotz, 2016; Båmstedt et al., 2020; Fernández-Álias et al., 2020; Ciriaco et al., 2021;
		Size of the individual	Increased gametes/planulae production with size	Positive		

(Continued)

TABLE 1 Continued

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
		Parasitism	Decreased medusa diameter	Up to 20% reduction in size	<i>Lucerna</i> , <i>Nemopilema nomurai</i> , <i>Periphylla periphylla</i> , <i>Phyllorhiza punctata</i> , <i>Rhizostoma</i> spp., <i>Rhopilema</i> spp., <i>Stomolophus meleagris</i>	Båmstedt, 2023; Mammone et al., 2023; Wang P. et al., 2023
			Lower egg production	Up to 50% reduction in egg production		
			Higher egg size	Up to 30% increase in egg sizes		
		Predation	Removal of medusae	Up to 330 kg of medusae × ind <sup>-1</sup> × day <sup>-1</sup>		
		Fisheries	Removal of medusae	7.5 × 10 <sup>8</sup> kg of medusae × year <sup>-1</sup>		

Studied species and references are indicated for each biological process. The rows were shaded differently for each biological process to ease the reading.

the population. Examples of the same are the recovery of the population of *Mastigias* sp. Agassiz, 1862 in the Jellyfish Lake (Palau) (Martin et al., 2006) or the recovery of the population of *C. tuberculata* in the Mar Menor (Spain) (Fernández-Álías and Pérez-Ruzafa, 2023). In the case of *Mastigias* sp., the collapse of the population was attributed to a warming of the waters beyond its tolerance limit, and the recovery of the same to a decrease in water temperature, both physical events driven by El Niño/Southern Oscillation (ENSO) (Dawson et al., 2001; Martin et al., 2006). For *C. tuberculata*, the control of the population is part of a complex top-down and bottom-up equilibrium in which phytoplankton could prevent the light from reaching the substrate, thus inhibiting the strobilation, while *C. tuberculata* predate on the phytoplankton and the symbiont zooxanthellae compete with the same for nutrient uptake (Pérez-Ruzafa et al., 2002; Fernández-Álías et al., 2020; Fernández-Álías et al., 2022; Fernández-Álías and Pérez-Ruzafa, 2023; Fernández-Álías et al., 2023).

### 3 Main challenges and future research directions

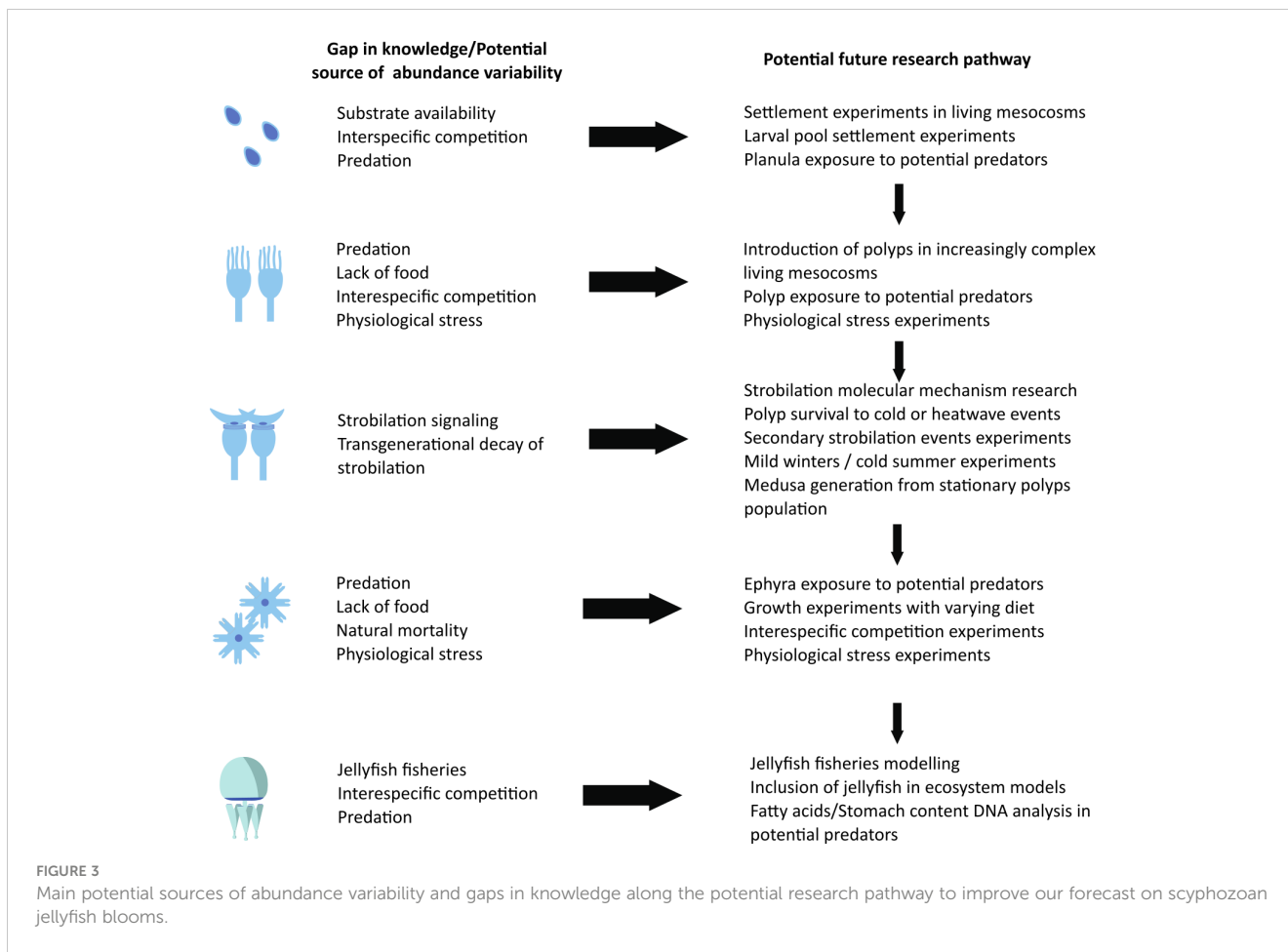
The small size and fragility of the larval stages (planula, polyp and ephyra) of scyphozoan species has limited the number of field studies on them, as it is difficult to find them and monitor their interactions with biotic and abiotic factors (Feng et al., 2017; Marques et al., 2019; Fernández-Álías et al., 2020; van Walraven et al., 2020; Leoni et al., 2021a; Boughton et al., 2023; Fernández-Álías et al., 2023; Zang et al., 2023). However, far from being discouraging, it should be noted that since the proposal of the conceptual framework for a general increase of jellyfish in the ocean (Arai, 2001; Purcell, 2005; Purcell et al., 2007; Richardson et al., 2009; Purcell, 2012), our knowledge of the factors that contribute to modulate the intensity of proliferations has greatly increased (Table 1).

Nevertheless, we are still far from developing truly useful predictive modeling tools, given the limited number of species for which each individual factor has been studied (Table 1) and the asymmetric response of different scyphozoan species to biotic and abiotic factors (Purcell et al., 1999; Schiariti et al., 2014; Feng et al., 2017; Fernández-Álías et al., 2021; Fernández-Álías et al., 2023). This likely limits the reliability of multispecies analyses across broad spatial and temporal scales (Brotz et al., 2012; Condon et al., 2013), but reinforces the need to build models that are site- and species-specific (Fernández-Álías et al., 2021). In this line, we propose a future research path that addresses the main knowledge gaps and sources of variability in jellyfish abundance to improve our understanding of the complex interactions (Figure 3).

#### 3.1 Planula stage

The planula stage is affected by physiological stress, interspecific competition for the substrate, and predation. However, even if suboptimal environmental conditions for planula settlement reduce the success of this biological process (Table 1), in nature planulae are typically released under optimal settlement conditions (Prieto et al., 2010; Rosa et al., 2013; Franco, 2016; Boughton et al., 2023). Therefore, we believe that planula settlement is more likely to be constrained by substrate availability and predation. We propose a potential research pathway to increase our knowledge of planula settlement efficiency in nature: testing the effects of substrate competition with both other potential settlers and previous colonizers, and calculating the effect of predation on planulae over the initial polyp population density.

Planulae are known to settle efficiently on bare substrate (Prieto et al., 2010; Franco, 2016; Boughton et al., 2023; Holst et al., 2023), but the competition for hard substrate in the ocean is one of the clearest examples of competition in nature (Dial and Roughgarden, 1998;



Connolly and Roughgarden, 1999). This substrate is typically dominated by species with an adult benthic phase, but the experimental designs of planula settlement have mostly been conducted on non-living substrates. The only examples we are aware of are a settlement experiment of *C. tuberculata*'s planulae on living oyster's shells with 0% settlement success (Franco, 2016), and a second in which *C. nozakii*'s planulae were incapable of settling on plates heavily colonized with biofouling organisms (Feng et al., 2021). Therefore, we suggest conducting planula settlement experiments in living mesocosms with bare and colonized substrate.

Marine species with a benthic adult phase have pulses of reproductive activity when the larvae are released into the water column before resettling to complete the life cycle (e.g. Gittings et al., 1992; Cárdenas and Aranda, 2000), and planulae compete with the larval pool present in the water column for the space in which to settle (Boughton et al., 2023). However, the observation of this competition is based on a single scyphozoan species and ecosystem (Boughton et al., 2023), and a quantification of the magnitude of the competition is lacking (Table 1). This highlights the need for settlement experiments with a larval pool of potential colonizers rather than just the scyphozoan planulae.

Finally, even though there is some evidence for the presence of planulae's predators (Javidpour et al., 2009; Kuplik et al., 2015), the

effect of planula removal by naturally present predators on population dynamics is unknown, indicating the need for further research on planula exposure to potential predators.

### 3.2 Polyp stage

The polyp stage faces a similar set of factors as the planula stage (Table 1), but contrary to what happened to the planulae, the perennial presence of polyps in most scyphozoan life cycle strategies (Fernández-Álías et al., 2021) implies that the role of physiological stress is higher in this stage. In fact, the further away the polyp population is from its optimal conditions, the lower the asexual reproduction rate and the higher the polyp mortality rate (Prieto et al., 2010; Wang F. et al., 2023). Therefore, when constructing polyp density models, it is important to consider where the thresholds of tolerance are and how long the benthic population is exposed to these inadequate conditions. Our information on these thresholds is limited to a few species, and yet it is sufficient to determine that they are species specific (Purcell et al., 1999; Schiariti et al., 2014). Thus, it is a prerequisite to know the thresholds, the decline in asexual reproduction, and the survival of the modeled species under inadequate conditions.

Most studies of polyp population dynamics have been conducted in the absence of competitors, synergistic organisms, or predators (Prieto et al., 2010; Purcell et al., 2012; Schiariti et al., 2014; Treible and Condon, 2019). These interactions should not be neglected, as their overall balance may be detrimental to the scyphozoan polyp populations (Feng et al., 2017; Zang et al., 2023). To fully understand polyp dynamics, it is necessary to increase the biological complexity of the mesocosms in which the physiological stress experiments are conducted.

### 3.3 Strobila and post-strobila stages

Strobilation is a stressful process for polyp populations (Feng et al., 2017), and their posterior recovery is not guaranteed in some species, while others have better chances (Prieto et al., 2010; Fuentes et al., 2011; Feng et al., 2017). In this context, it remains unclear why certain conditions, which could be cold or heat waves, trigger the strobilation process, when their return to normal water temperatures could affect the correct development of ephyrae into medusae (Fernández-Álías et al., 2023). It has also been shown that the strobilation process and the ephyra production are affected by the minimum sea temperature reached during the winter season, the length of the winter season, the water warming speed and the food regime (Feng et al., 2015a; Feng et al., 2015b; Loveridge et al., 2021; Zang et al., 2022), factors that should be further studied to increase our bloom predicting tools.

A better understanding of the process could be achieved with a complete description of the molecular mechanism of strobilation (Helm et al., 2018), but for now our knowledge of the molecular pathway is limited to certain aspects and to the genus *Aurelia* (Fuchs et al., 2014; Brekhman et al., 2015; Khalturin et al., 2019; Jensen et al., 2023). In fact, we are not aware of the presence of the gene CL390, the most overexpressed gene in the strobilation process (Fuchs et al., 2014; Brekhman et al., 2015), in any other scyphozoan species outside this genus. In the nucleotide database (GenBank) of the National Center for Biotechnology Information (<https://www.ncbi.nlm.nih.gov/>, accessed on 30 November 2023) there are only 4 DNA sequences of the gene translated into this protein, all of them belonging to *Aurelia*, and launching a Basic Local Alignment Search Tool (BLAST) with the most permissive parameters does not provide any additional sequence from a scyphozoan species (Fernández-Álías, A., unpublished result). Of the four available sequences, only two are supported by a publication, the one sequenced in Fuchs et al. (2014) and the one from Brekhman et al. (2015). Moreover, their transcribed proteins have only 68% identity (Brekhman et al., 2015), and their expression is induced by opposite temperature changes, a decrease in the case of the Fuchs et al. (2014) gene and an increase in the case of the Brekhman et al. (2015) gene. Therefore, there is a need for more transcriptomic analysis throughout the life cycle of the different scyphozoan species.

Finally, polyp populations have been reported to decrease their asexual reproduction rate within successive generations, but this may be associated with a higher ephyra production per polyp (Chi et al., 2022; Holst et al., 2023), and the overall balance of long-lived

polyp populations in ephyra production remains unclear. In addition, medusae developed from long-lived polyp cultures in the aquarium may show abnormal pulsation or even absence of pulsation (Fernández-Álías, pers. obs.), suggesting a need for refreshment of benthic populations.

### 3.4 Ephyra stage

It takes between 10 and 150 days for the ephyrae to reach the medusa stage, with an average success rate of less than 30% (Ishii et al., 2004; Kawahara et al., 2006; Fuentes et al., 2011; Astorga et al., 2012; Fernández-Álías et al., 2020; Gueroun et al., 2020; Fernández-Álías et al., 2023). Predation and physiological stress have been identified as the two most important factors affecting mortality at the ephyra stage (Table 1), but evidence is limited. The extremely fast digestion rate of the medusa phase has made it difficult to detect them as prey by stomach content analysis (Arai et al., 2003), and given their smaller size, the lack of detection of the ephyra phase in predator stomachs should be more acute. In fact, all the collected evidence on predation of ephyrae is based on their direct exposure to predators in aquarium experiments (Table 1), and the list of potential predators is likely to be much more extensive than those observed so far. The composition of the planktonic community available for the ephyrae to prey on is likely to influence proper development to the medusa stage (Chambel et al., 2016; Miranda et al., 2016; Ballesteros et al., 2022), suggesting the need to monitor the plankton assemblages along the ephyrae and medusae and conduct experiments to determine the most appropriate diet for the ephyrae. Finally, the disappearance of ephyrae when temperature conditions were inadequate has been observed in long-term studies (Fernández-Álías et al., 2023), but they did not discriminate whether temperature was the primary cause of mortality or whether it was starvation or the long-term exposure to potential predators without reaching the medusa phase. Thus, physiological stress experiments need to be conducted to determine the resilience of the ephyrae to inadequate conditions for their development.

### 3.5 Medusa phase

Once a bloom of a species occurs, interest usually shifts to the socioeconomic impacts of the massive proliferation and how to mitigate them (Bosch-Belmar et al., 2020), and less attention is paid to the implications of its development for subsequent seasons. In fact, attention to future blooms seems to have gained interest only since the development of jellyfish fisheries threatened by interannual variability in medusae abundance (Brotz et al., 2017), and yet not many efforts have been made to calculate the biological parameters required to implement sustainable fishing programs (Palomares and Pauly, 2008; Brotz, 2016; Fernández-Álías et al., 2020; López-Martínez et al., 2020; Leoni et al., 2021a; Behera et al., 2022). Traditionally considered a trophic “dead end” (Hays et al., 2018), medusae are not typically included in ecosystem management models (Pauly et al., 2008), and larval stages are

even less likely to be included in these models, despite their potential to influence adult abundance (Table 1). The inclusion of jellyfish in ecological models is particularly important in small, sheltered ecosystems, since the smaller the ecosystem, the greater the importance of jellyfish as keystone species (Pauly et al., 2008), to the point where they can act as top pelagic predators and as a buffer against dystrophic crises in eutrophicated coastal lagoons (Pérez-Ruzafa et al., 2002; Fernández-Álías et al., 2022; Fernández-Álías et al., 2023). In this line, it is also important to consider that the trophic role of scyphozoan jellyfish changes between species, within species between locations, and throughout their ontogeny (Holst et al., 2007; Marques et al., 2020; Wang et al., 2020; Leoni et al., 2022). For the correct implementation of these models, we need to put more effort in the parameterization of jellyfish growth and in the determination of trophic links with upper and lower levels.

## 4 Conclusions

The scyphozoan life cycle has the potential to numerically increase the number of individuals in the order of several million during a single generation, but the contour conditions can block the life cycle and cause a collapse of the population. The complex interactions between the different developmental stages of the life cycle and the set of biotic and abiotic factors are the main causes of the interannual variability in the abundance of the medusa phase, the most conspicuous stage of the life cycle. During the last decade we have increased our knowledge of the controlling factors that modulate the densities of the different developmental stages, but we are still far from being able to provide reliable predictions of the scyphozoan blooms. Therefore, it is important to distinguish between what it is known and what remains a gap in knowledge to effectively direct the future research on this topic.

Temperature seems to be the most important factor involved in the correct development of the life cycle, triggering processes and favoring the transition between phases when it is optimal, and causing mass mortality or abnormal development when it is not. The second important factor is the availability of food, the quality and quantity of which modulate the asexual reproduction, the strobilation process and the somatic growth. In general, the factors regulating the transition between the different stages of the life cycle would be what allows the species to anticipate adequate conditions for the development and growth of the individuals. In this context, food availability, productivity, and temperature act in concert with salinity, being it a key factor in many tropical and sheltered habitats, prone to host scyphozoan blooms, where salinity fluctuates due to storms, flash floods, and evapotranspiration, affecting the life cycle and the species distribution. In the same way, salinity may play a key role in the Mediterranean Sea under temperature rising scenarios. Despite their importance, these factors are reported to act asymmetrically between the different scyphozoan species, and here appears one of the most important limitations in our ability to predict massive proliferations: the knowledge we have generated is species-specific and cannot be extrapolated to the whole class. Moreover, for most of the species

the magnitude of the effect of these factors in some (or in all) of the biological processes that take place during the life cycle is unknown.

A second gap in our knowledge is the interspecific interactions between the scyphozoan species and the other faunistic groups. As a scientific community, we have reported the existence of numerous relationships between scyphozoan jellyfish and the other groups, including predator-prey interactions, both in the benthic and the pelagic stages, competition for the substrate in the planula settlement and polyp dynamics, symbiosis, commensalism, and parasitism. However, the description of the relationships is still in its infancy, not yet quantified and most likely we still underestimate the number of predators and competitors for the different stages.

To improve our forecasting ability, our research should focus on determining the parameters needed to implement ecosystem-based models. This includes determining the environmental tolerance limit for each species and stage, parameterizing how the growth, asexual reproduction, strobilation and mortality rates vary under inadequate conditions, and determining the interspecific and trophic relationships by progressively increasing the complexity of the design of the mesocosms in which the experiments are conducted.

## Author contributions

AF-A: Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. CM: Funding acquisition, Project administration, Writing – review & editing. APR: Conceptualization, Funding acquisition, Project administration, Supervision, Visualization, Writing – review & editing.

## Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This study has been supported by the project Monitoring the Ecological State of the Mar Menor funded by the General Directorate of the Mar Menor of the Community of the Region of Murcia. AF-A was supported by Fundación Séneca, Región de Murcia (Spain), grant number 21449/FPI/20. This work has also benefited from funding from the different projects on “Monitoring and predictive analysis of the ecological state evolution of the Mar Menor lagoon ecosystem and prevention of impacts (2016–2023)” financed by the General Directorate of the Mar Menor of the Autonomous Community of the Region of Murcia.

## Acknowledgments

This study was conducted as part of the Ph.D. dissertation of AF-A. We extend our gratitude to two reviewers whose comments improved the quality of the manuscript.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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