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# Life History Dynamics of the Schyphozoan Jellyfish *Aurelia* spp.: A Combined Meta-Analysis and Modelling Approach

September 2020

Master's thesis

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2020

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# Abstract

One of the most common jellyfish genera are the cnidarian scyphozoans *Aurelia* spp. They are spread across most of our oceans and seas, have a complex life cycle and are a bloom forming species. Jellyfish blooms are perceived by humans as a sign of degenerating oceans. They have been gaining public attention for the past couple of decades across the globe for disrupting major human activities and inflicting heavy economic costs. Still, very little is understood about their life history and solutions to blooms are still underdeveloped. An inevitable step to better manage such resources is the tracking of populations and the prediction of blooms. This study takes a closer look at the population dynamics of *Aurelia* spp.. By conducting a systematic literature review, I investigate the availability of demographic rates belonging to this genus and their distribution across different species of *Aurelia* and multiple geographic locations. I then use the captured demographic rates to develop predictive models, using ordinary differential equations, that simulate the life history of virtual *Aurelia* spp. populations. I discern a scarcity of publications dealing with *Aurelia* demography, unevenly spread across multiple variables. Nevertheless, meta-analyses showed little variability between estimates of the same demographic rates in the captured data. Model simulations of these demographic data highlighted trends and tendencies of increasing numbers of jellyfish. The gaps of knowledge were identified and improvements of the models to become management tools were suggested.

# Acknowledgments

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# Introduction

An increase in jellyfish occurrence reports has been recorded in the past several decades across the globe (Brodeur, Sugisaki, & Hunt, 2002; Brotz, Cheung, Kleisner, Pakhomov, & Pauly, 2012; Ceh, Gonzalez, Pacheco, & Riascos, 2015; Miller & Graham, 2012). Jellyfish have been gaining attention by appearing in high densities forming blooms. An increase in bloom intensity and frequency has been ascribed to different natural and anthropogenic causes. These include i.e. global warming, anthropogenic pollution, eutrophication, increased fishing activities and decreased predatory competition (Purcell, Uye, & Lo, 2007). Jellyfish are usually associated with threats to humans and are considered a nuisance in the environment (Brodeur et al., 2016). From disrupting large fishing activities to contaminating public beaches and clogging cooling systems of nuclear power plants (Purcell et al., 2007), jellyfish blooms have largely affected human activity and have rapidly gained global public attention (Richardson, Bakun, Hays, & Gibbons, 2009). Some even argue that public attention is the very reason behind a media-driven increase in jellyfish reports (Condon et al., 2012; Pitt, Lucas, Condon, Duarte, & Stewart-Koster, 2018; Sanz-Martín et al., 2016).

Nevertheless, the perception of jellyfish is starting to change. Today, they are becoming of increasing use to humans. In fact, some jellyfish species (e.g. *Rhopilema* spp.) has been part of a big market in east Asia, where they are sold as food. It is argued that jellyfish have great nutritional value and are considered as a delicacy and a traditional plate in some parts of China (Hsieh, Leong, & Rudloe, 2001). In addition, these collagen rich organisms are also used to produce cosmetic and nutraceutical products (Hsieh et al., 2001; Leone, Lecci, Durante, Meli, & Piraino, 2015). Some aquaculture feeds also rely partially on jellyfish diets (Liu et al., 2015). From an ecological aspect, perception of jellyfish is also witnessing a "paradigm shift" (Hays, Doyle, & Houghton, 2018). Until the end of the 20th century, they were considered as a trophic dead-end in marine ecosystems with very few predators (Verity & Smetacek, 1996). Yet, using technological advancements, new evidence suggests differently (Fossette, Gleiss, Casey, Lewis, & Hays, 2012; Marques et al., 2016). These studies put forward proof that many predators in the marine ecosystems (fish, sea turtles, seabirds, etc.) prey on jellyfish as a big part of their diets, making jellies an important level in the marine trophic web. Like any other aspect of nature, jellyfish can be considered as a natural resource, having both direct and indirect benefits and impacts on humanity. This implies that a comprehensive and sustainable management of this natural resource is needed. To enable a sustainable harvest, it is crucial to understand the ecology and reproductive

cycles of the resource itself. So far, knowledge on the different life stages of individual jellyfish species, their life spans, age of maturation, growth and natural reproduction cycles are still under-investigated (Duarte et al., 2013).

Here, I focused my study on the scyphozoan *Aurelia* spp. (Lamarck, 1816), one of the most common jellyfish genus (Lucas, 2001). Scyphozoans are considered to be one of the most ancient animals on our planet, dating back to the Cambrian period (Liu et al., 2017). They have been observed by humans for centuries, yet very little is known about most of the species. The *Aurelia* genus is cosmopolitan and can be found in most of the seas and oceans between 40°S and 70°N (Kramp, 1961; Russell, 1970). They can mostly be found in shallow waters, in enclosed bays, fjords and straits (Lucas, 2001). Having weak motility, they drift with the ocean currents. This also factors in their appearances along coastlines and tendencies to accumulate in small locations, forming blooms. The *Aurelia* genus is composed of several species (such as *A. aurita, A. coerulea, A. labiata, A. colpota,* etc.) with a wide distribution across multiple locations and remain having a rather cryptic phylogeny (Dawson, Gupta, & England, 2005; Dawson & Jacobs, 2001; Scorrano, Aglieri, Boero, Dawson, & Piraino, 2017). *Aurelia aurita* (Linnaeus, 1758) ("moon jellyfish") is one of the most studied species of jellyfish and has an exceptionally complex life cycle (Ceh et al., 2015), a common feature across the *Aurelia* genus (figure 1). From a fertilized egg, a planula larva hatches and is released in the water column. Released planulae sink in the water column until they settle on an adequate substrate. Once settled on the seafloor, they metamorphose into fixed scyphistomae (polyps). When conditions are adequate, a polyp begins strobilation, a transverse segmentation of its upper body into stacked discs-like ephyrae. Strobilation marks the start of the first reproductive stage, a benthic asexual reproduction. The strobilation of polyp releases small, upward swimming ephyrae, that will grow as they feed to become adult medusae. When conditions are no longer suitable for strobilation, a polyp can regress to its initial state (scyphistoma), in which it can survive for longer periods, often overwintering to the next season (Hernroth & Gröndahl, 1985; Makabe, Kurihara, & Uye, 2012). Adult medusae grow and develop to reach sexual maturity, marking the start of the second reproductive stage, a pelagic sexual reproduction. Once reproduction succeeds, fertilized eggs are attached to the oral arms of fecund female medusae, thus closing the life cycle. Several additional demographic processes have been observed taking place in *Aurelia* spp. life stages, adding more complexity to an already complex life cycle. A "secondary" asexual
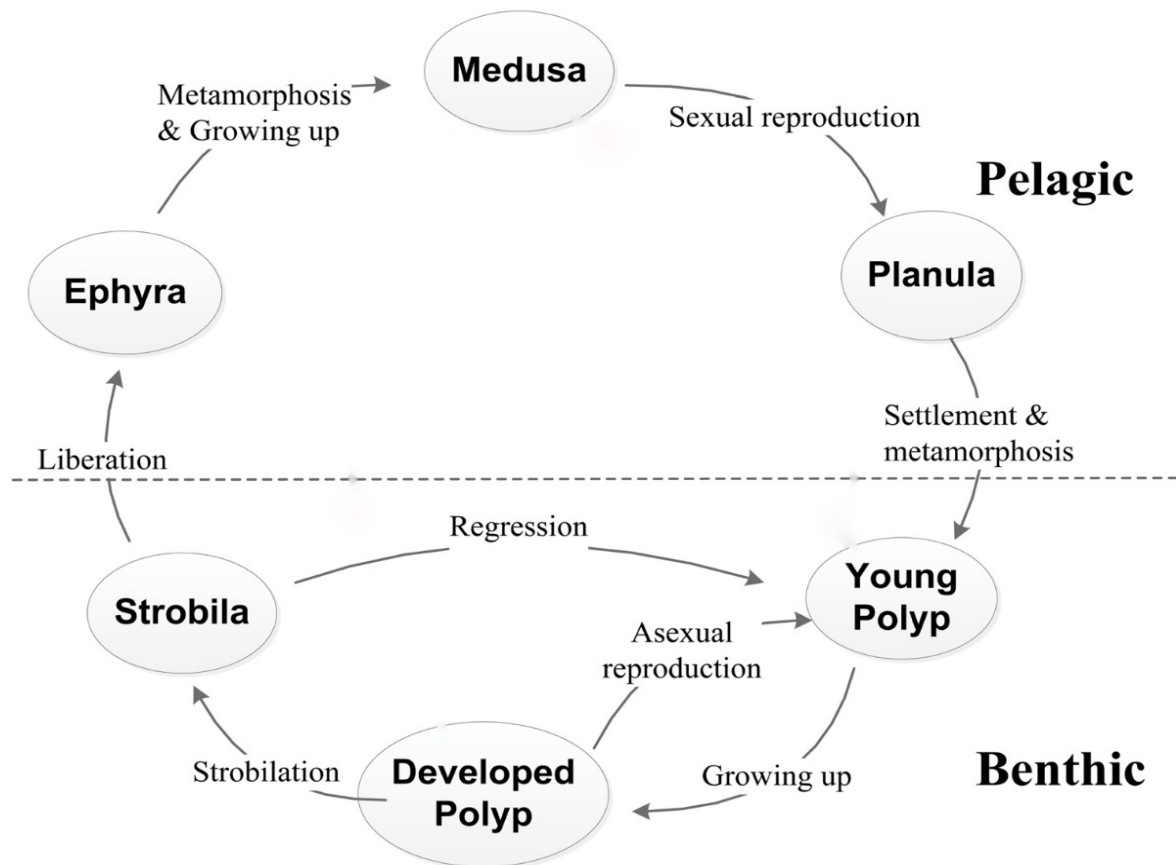
*Figure 1 Schematic diagram of the life cycle of scyphozoan jellyfish modified after Xie, Fan, Wang, & Chen, 2015. Grey arrows show the common natural life cycle.*

reproduction occurs at the scyphistoma stage, where new polyps bud form older polyps, a common asexual reproduction strategy in the Cnidaria phylum known as "asexual budding" (Arai, 1997). Other reproductive processes have also been observed, where planula-like cells are released from either the oral cavities or the exterior walls of polyps (Vagelli, 2007). In addition, it has been reported that planulae released from the medusae can metamorphose directly into ephyrae, skipping the benthic stages (Yasuda, 1975).

The timing of life history events varies greatly between and within jellyfish species. In fact, inter-population adaptations to environmental variation is well documented (Lucas, 2001; Pascual et al., 2015). This points out how environmental and demographic stochasticity shape *Aurelia* spp. dynamics and define their adaptations. Vital rates, such as the release rate of ephyrae by a polyp, are triggered and regulated by several physical and biological factors. Temperature (e.g. Pascual et al., 2015), salinity (e.g. Xing, Zhang, Zhen, & Mi, 2019), pH (e.g. Dong & Sun, 2018), dissolved oxygen concentration (e.g. Ishii, Ohba, & Kobayashi, 2008), food quality and food quantity (e.g. Fu, Shibata, Makabe, Ikeda, & Uye, 2014) are some of many factors that have evidence of controlling demographic dynamics in *Aurelia*

spp.. Polyp colonies have also been identified to be density dependent (Schiariti, Melica, Kogovšek, & Malej, 2015). This versatile life history makes scyphozoans in general, and *Aurelia spp.* specifically, adapted to the variations in biotic and abiotic conditions in the marine environment (Goldstein, Augustin, Bleich, & Holst, 2017). The sessile benthic stage offers an immediate and continuous supply of ephyrae as long as the conditions are favourable (Fuchs et al., 2014). In fact, the unpredictability of this rapid, seasonal fluctuation of medusae (e.g. blooms) is one of the reasons jellyfish are gaining global attention (Schnedler-Meyer, Kiørboe, & Mariani, 2018).

*Aurelia* spp. populations are, as yet, virtually impossible to track across every life stage, especially in their natural environment. Since medusa is the life stage that is most interacted with, it has been the main focus of demographic studies. Growth of medusae is considered by serveral studies as the most important meausure of jellyfish population dynamics (Olesen, Frandsen, & Riisgård, 1994; Van Der Veer & Oorthuysen, 1985). Nevertheless, growth measurements have also been made by a variety of methods, such as using the increase in dry weight (Haruto Ishii & Båmstedt, 1998; Lucas, 1996), wet weight (Aoki, Yamada, Toyokawa, Yasuda, & Kikuchi, 2012; Uye & Shimauchi, 2005) and bell diameter (Lucas & Williams, 1994; Möller, 1980; Palomares & Pauly, 2008) as a proxy for growth. This diversity can be an obstacle for further comparison (Marques et al., 2015). Studies on the other life stages becomes much more challenging due to their smaller size, difficult taxonomy and unclear locality (Haruto Ishii & Watanabe, 2003; van Walraven et al., 2016).

Very few attempts of modelling *Aurelia* populations has been made (e.g.: Goldstein & Steiner, 2020; Henschke, Stock, & Sarmiento, 2018). Goldstein & Steiner (2020) constructed a stage-based matrix *Aurelia aurita* population model, with monthly, individual-based, demographic rates. Vital rates fed to this model were captured in experiments done within the same study, a safer approach to tackle a generally heterogenous availability of data. It included the same four life stages chosen in this study (planula, polyp, ephyra and medusa). Henschke, Stock & Sarmiento (2018) developed an age-based, discrete-time model for the *Aurelia* spp. population of the Gulf of Mexico. This model tracked multiple cohorts of polyps, ephyrae and medusae of the same generation. Both studies confirmed the importance of the benthic stages in determining the size of the adult medusae population. Another study (Xie, Fan, Wang, & Chen, 2015) developed a two-state, polyp-medusa model based on ordinary differential equations (ODEs). This model was first to incorporate predation as a limiting factor, alongside with temperature and substrate. The two latter studies used a broad

range of demographic rates to parameterise their models, thus introducing bias to their results.

This study is part of GoJelly, an EU Horizon 2020 funded project. I worked under work package 2 (WP2) of this project focused at driving mechanisms and predictions of jellyfish blooms. I started on this project with the aim of building a modelling framework for predicting jellyfish blooms. Yet, it became evident that with the scarcity of literature, a solid understanding of the available information had first to be established.

My goals for this thesis were to build a comprehensive demographic rates dataset and use it to build and run population models of jellyfish. I therefore conducted a systematic literature review to make sure I cover as much as possible of the published data. I approached my review from a population dynamic standpoint to be able to pave way for my fundamental goal, by looking at five specific demographic rates of the life history of *Aurelia* spp.. I then proceeded to construct theoretical models that could simulate the life history of *Aurelia* spp. allowing me to visualize future population dynamics in multiple scenarios. This helped in developing preliminary tools from managers and decision maker to help address the increasing interest in jellyfish demography.

# Material and Methods

In the framework of this MSc project, there were two phases of work, (1) a systematic literature review supported by meta-analyses and (2) a population modelling approach. The two phases are complementary. The systematic literature review was aimed to gather the information needed to parameterise the models. But first, the complexity of the *Aurelia* spp. life cycle was tackled by introducing some simplifying assumptions.

## Simplification of the life cycle

I simplified the complex metagenetic life cycle to a four-stage (planula, polyp, ephyra and, medusa) life cycle (figure 2). Polyps are assumed to be the only stage to overwinter and all other survival rates represented in figure 2 are usually equal to zero across years (Goldstein et al., 2017). The benthic stages and asexual reproduction processes were merged into one step, the polyp stage. The pelagic sexual reproduction was also simplified down to the release of planulae by medusae.
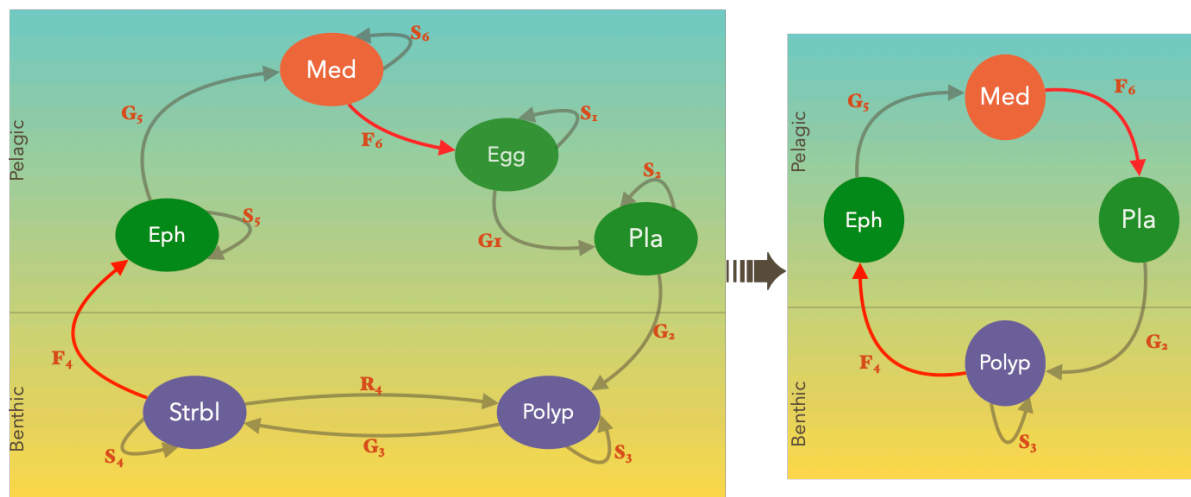


*Figure 2 Scheme of the metagenetic life cycle of Aurelia spp. (left) and a scheme of the simplified life cycle adapted in this study (right).* ***S*** *represents survival rates,* ***G*** *represents transition/growth rates,* ***F*** *represents reproduction rates and* ***R*** *represents the regression rate.*

## 1. Systematic literature review

In this section, I undertook a systematic literature review (SLR). It allows me to gain an unbiased and comprehensive understanding of the available data by performing a structured investigation of all related published material. I then retrieved the data from resulting articles and analysed it by performing meta-analyses.

## Search strategy

To search the literature, I constructed five search strings. I started with the term "Aurelia" to limit my results to the genus *Aurelia*. Second, each search string contained one of the life stages. Third, the strings contained a demographic vital rate. The five resulting search strings were:

- "*Aurelia* polyp settlement"
- "*Aurelia* polyp survival"
- "*Aurelia* ephyra release"
- "*Aurelia* ephyra growth"
- "*Aurelia* planula reproduction"

Each search string was then used in three different databases: Scopus, ScienceDirect and Web of Science (WoS). The resulting hits were then exported and combined to form one bibliographic dataset, representing potentially useful articles.



*Figure 3 Systematic literature review protocol.*

## Article screening

Once the bibliographic dataset was completed, the articles were screened for useful data. I used the online tool EPPI-Reviewer Web (Beta) (Thomas et al., 2020), developed for systematic reviews to help with the curation of bibliographic data and article screening. The screening protocol was adapted from Laverick et al. (2018) (figure 3). My protocol was executed in the following order:

1. Excluding duplicates
2. Screening on type
3. Screening on title
4. Screening on abstract
5. Retrieving full texts
6. Screening on full text
7. Data extraction

Duplicates were manually identified and excluded. Indexes, bibliographies, conference information or any other type of non-peer-reviewed article formats were excluded within the "screening on type" step. The screening on title excluded articles stating off-topic titles and publication sources (Medical, Molecular biology, Chemistry, etc.). Criteria for the relevance of topics included mentions of:

- *Aurelia* species
- vital functions or processes (e.g. settlement, survival, recruitment, bloom)
- at least one life stage name (e.g. polyp, planula, medusa)

The screening on abstract excluded articles stating in their abstracts off-topic studies. Criteria for the relevance of topics included:

- observational or experimental study designs of vital rate changes
- population dynamics of *Aurelia* spp.

The full-text articles were then retrieved for more detailed screening. Full texts of articles that could not be found were marked as "Unavailable data" and excluded.

The screening on full text evaluated articles on their methodology and results sections. Criteria for full text screening included mentions of:

- estimates of the vital rates
- measures of variability of these estimates
- vital rates reported must belong to the list of rates of interest

Articles satisfying the above criteria were chosen for data extraction. Remaining articles were excluded.

## Data extraction

Data available in text, tables, or supplementary materials were retrieved manually. Data represented in graphs could not be retrieved accurately. Corresponding authors were contacted by email for the data used in figures of interest. A one-month period was given to authors to respond. Only authors of articles with unavailable data displayed in figures were contacted. It is important to note that the emails were sent on the 25th of March 2020, coinciding with the outbreak of the COVID-19 pandemic. This unusual event could have affected the process of correspondence. Failure to contact many authors lead me to adapt alternative methods to acquire the data. I used Engauge Digitizer© (Version 12.1) to retrieve estimates of the data from graphs of interest (Mitchell et al., 2020). This method was only used for articles where correspondence with the authors failed. With Engauge Digitizer, the data could be extracted by digitizing a picture of the graph, designating the axes and selecting

the points that should be recorded. Some articles displayed data such as in heat maps or in low-resolution graphs, making it challenging to retrieve the data manually. Such articles were excluded from the study and were added to the category of "Unavailable data". To assess the availability of condition parameters throughout my data, multiple variables were extracted from each article as shown in table 1. Variables that were not available for certain articles were marked as NAs.

## Data synthesis

Once the data was extracted, I used Microsoft Excel and the R programming language (Version 3.6.2) (R. Team, 2013) for data handling. Each publication was given an individual ID (Paper_ID; appendix I). All studies were first separated into five categories, each category represented one of the five vital rates. The five categories were:

→ Planula settlement

→ Polyp survival

→ Ephyra release

→ Ephyra transition to medusa

→ Planula release

| Parameters | Units |
|---|---|
| Effect size | ratio |
| Error | ratio |
| Number of individuals | count |
| Number of Replicates | |
| Species | |
| Duration of experiment | days |
| Geographical origin | |
| Study type | |
| Temperature | °C |
| Salinity | |
| pH | |
| Oxygen concentration | mg/L |
| Copper concentration | µg/L |
| Prey concentration | mg.C/L |
| Prey type (species) | |
| Sexual mature medusa* | ratio |

*Table 1. Extracted parameters from articles. *Sexual Mature Medusa was only retrieved for the Planula release category, composed only of one publication (Goldstein & Riisgård, 2016).*

Some articles contained data for more than one vital rate, these were duplicated and divided into their corresponding categories under the same paper ID. Measurement units of each parameter were standardized to the units seen in table 1. Vital rates that were displayed as percentages were transformed to ratios along with their corresponding variance values (SD/SE) for analyses. Standard deviations of the mean were used to calculate standard errors of the means and vice versa, using the number of replicates and individuals from corresponding studies. This allowed me to have both parameters available for evaluation for every study. For the four other categories, the estimates were standardised by scaling them to daily rates. All error values (SD/SE) were scaled in the same manner as their corresponding estimate values in all the studies.

## Meta-analyses

After the extraction of data, meta-analyses were conducted to get consensus estimates. I used the package {*metafor*} (Viechtbauer, 2010) in R to perform the analyses. I fitted meta-analyses with random effects for each vital rate as the effect size and used the restricted maximum likelihood (REML) estimator for between-study heterogeneity (Patterson & Thompson, 1971). Fitting a model with random effects assumes that the used effect sizes are drawn from a population of vital rates which could be observed in the environment. I fitted my models using the *rma.mv* function to my data. Cochran's $Q$ (Cochran, 1950) was used as a between-study heterogeneity measure, to quantify the variability between the estimates I retrieved. Paper ID, species and geographic origins were set as independent random effects to control for the extra variance they may introduce between studies. I did not include any interaction terms between the random effects in my models, the three factors were not crossed, and this would have risked overfitting. I used funnel plots (Light & Pillemer, 1984) to evaluate the fit of my models and visually assess for bias and extreme estimates from studies. The R code for these models is available in Appendix II.

## 2. Modelling *Aurelia* life history

Here, I set out to build models that could depict the life history of *Aurelia* spp., and help to better understand the importance of each vital rate to the continuity of the population. I built the models in the R programming language using the {*tidyverse*} (Wickham et al., 2019). I constructed two different models. The first, a medusa-to-medusa model, representative of the full life cycle of *Aurelia* spp. that aims to simulate future generations. The second, a polyp-to-medusa model, is representative of the mechanism that directly influences the medusa population, and consequently bloom dynamics.

### Building the medusa-to-medusa model

The medusa-to-medusa model contains all of the five vital rates retrieved in section 1, in four periods, chained as a life cycle. I model the process of polyp survival at every period in the model since it is documented that polyps are the only stage that can survive for multiple years (Lucas, 2001). This resulted in a four-period cycle for a one-year generation. The four functions based on ordinary differential equations (ODEs) were:

1. Period one:

   Polyp to Ephyra: (1) $N_{Ephyra} = n_{Polyp} \cdot R_{Polyp} \cdot d_1$

   Polyp survival: (2) $N_{Polyp1} = n_{Polyp} \cdot S_{Polyp}{}^{dp}$

   Where $N_{Ephyra}$ is the number of ephyrae resulting from the first period; $n_{Polyp}$ is the initial number of polyps fed to the model; $R_{Polyp}$ is the daily release rate of ephyrae by polyps. $N_{Polyp1}$ is the new number of polyps resulting from the first period after the release of ephyra and $S_{Polyp}$ is the daily survival rate of polyps. $d_1$ is the duration in days of the first period and $d_p$ is the duration of survival of polyps.

2. Period two:

   Ephyra to Medusa: (3) $N_{Medusa} = N_{Ephyra} \cdot S_{Ephyra}{}^{d2}$

   Polyp survival: (4) $N_{Polyp2} = N_{Polyp1} \cdot S_{Polyp}{}^{dp}$

   Where $N_{Medusa}$ is the number of medusae resulting from the second period; $S_{Ephyra}$ is the daily proportion of ephyrae which survive and successfully metamorphose into medusae. $N_{Polyp2}$ is the new number of polyps still alive after the second period. $d_2$ is the duration in days of the second period.

3. Period three:

   Medusa to Planula: (5) $N_{Planula} = N_{Medusa} \cdot R_{Medusa}$

   Polyp survival: (6) $N_{Polyp3} = N_{Polyp2} \cdot S_{Polyp}{}^{dp}$

   Where $N_{Planula}$ is the number of planulae resulting from the third period; $R_{Medusa}$ is the average number of planulae released from medusae and $N_{Polyp3}$ is the new number of polyps still alive after the third period. $d_3$ is the duration in days of the third period.

4. Period four:

   Planula to Polyp: (7) $N_{Polyp4} = ( N_{Polyp3} \cdot S_{polyp}{}^{dp} ) + ( N_{Planula} \cdot T_{Planula} \cdot d_4)$

   Where $N_{Polyp4}$ is the new number of polyps at the end the fourth period (cycle) and $T_{Planula}$ is the daily rate of settlement of planula to become polyps. $d_4$ is the duration in days of the fourth period.

These four functions (periods) were linked into a single function (year) which receives a starting polyp population and estimates of vital rates. As defined in the above formulae, the model also includes a time span component through period-specific durations ($d_x$). These components were used as an exponent with survival rates ($S_{Ephyra}$ & $S_{Polyp}$), since survival is a multiplicative probability over a time span. With the input of daily vital rates, this allowed me to tailor location-specific simulations. The full year function could then be iterated to simulate multiple consecutive generations. With that, I was able to plot and visualize the population dynamics of *Aurelia* spp. and monitor how the different life stages affect each other's development. The R code for this model is available in Appendix III.

## Building the polyp-to-medusa model

The annual model is unnecessarily complex for addressing jellyfish blooms. Since polyps are the only overwintering stage, medusa levels will arise directly from polyps within a given year. This means that to address bloom formation, the polyp-to-medusa part of the lifecycle is where the answers lie. Here, I proceed to use the first model, to create a one-generation polyp-to-medusa model, that allows me to evaluate how fluctuating vital rates in this part of the lifecycle can influence the medusa population (Figure 4).

Since the focus of the polyp-to-medusa model is to gauge the medusa population, I needed a model that returns the number of medusas produced from a defined number of polyps.
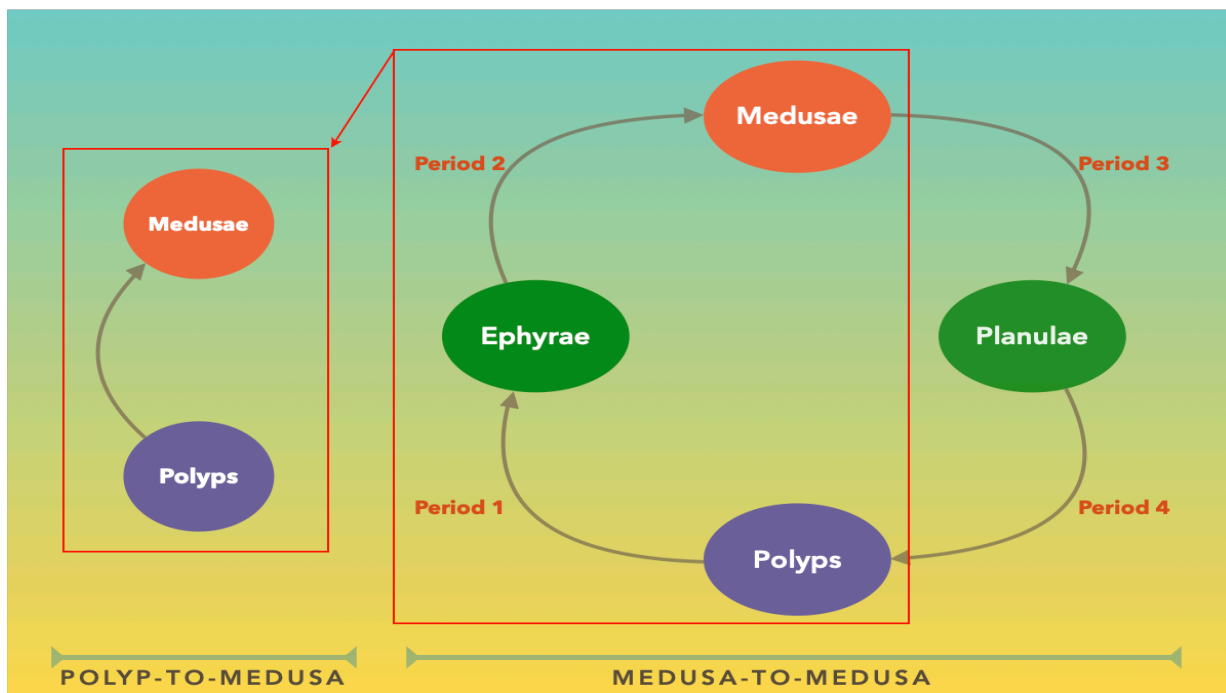


*Figure 4 Schemes of the models. The initial medusa-to-medusa model (left) and the simplified polyp-to-medusa model (right).*

Assuming that polyp numbers are stable from one year to the next, I can remove the sexual reproductive stage at the medusa level and consequently the successive stage of planula settlement from this model. I therefore end up with two consecutive steps, from polyp to ephyra and from ephyra to medusa. I used the first and second periods from the previous model and excluded the polyp survival formulae. The two remaining formulae were combined under one function that takes an initial number of polyps and vital rates as inputs and returns an estimate of the medusa population size. The formulae as defined above, were:

$$(8)\ N_{Ephyra}\ =\ \mathbf{n}_{Polyp}\ \textbf{.}\ \mathbf{R}_{Polyp}$$

$$\mathbf{R}_{Polyp} \sim tN(\ \mathbf{R}_{Meta\text{-}polyp}\ ,\ \boldsymbol{\sigma}_{Meta\text{-}polyp}{}^2,\ [0,1]\ )$$

$$(9)\ N_{Medusa}\ =\ N_{Ephyra}\ \textbf{.}\ \mathbf{S}_{Ephyra}$$

$$\mathbf{S}_{Ephyra} \sim tN(\ \mathbf{S}_{Meta\text{-}ephyra}\ ,\ \boldsymbol{\sigma}_{Meta\text{-}ephyra}{}^2,\ [0,1]\ )$$

Where $\mathbf{n}_{Polyp}$ is the initial number of polyps fed to the model. I introduced stochasticity into the model by sampling from a truncated normal distribution (bounded by 0 and 1) of vital rates for each of $\mathbf{R}_{Polyp}$ and $\mathbf{S}_{Ephyra}$. The distributions were parameterised with the means and variances ($\sigma^2$) returned by the meta-analyses in the first section. I then iterated this function to simulate a distribution of possible medusae blooms for a given set of conditions. The R code for this model is available in Appendix IV.

For the polyp-to-medusa model, I used estimates from the meta-analyses as vital rates along with their variance values. Using the {*rtruncnorm*} function in R, I generated random estimates for the different simulations as described above. I simulate a population size of 10 000 polyps and iterate this simulation 1000 times. I then calculated the population growths rate (PGR) by dividing the number of medusae produced by an initial number of polyps in each simulation. Here, PGR represents how many medusae can be produced by one polyp.

# Results

## 1. Systematic literature review

### Search, screening and synthesis

The search strategy captured in total 648 hits out of the three databases; Scopus (97), WoS (150) and ScienceDirect (401). These hits were processed using the screening protocol as described in the methodology section and in figure 3. The numbers of included articles decreased substantially with every screening step (figure 5). Almost half of the hits were discarded as duplicates. 86 hits were discarded on type screening. After a thorough evaluation of titles and sources, 118 articles were discarded. Less than 6% made it to the final full text screening, whereof half of the articles (n = 21) made it



*Figure 5 Schematic of the literature review protocol results. n represents the number of publications.*

to the final stage of data extraction. Under "Data unavailability", three out of five articles (Ishii & Ogawa, 2005; Sun et al., 2017; Xing, Zhang, Zhen, & Mi, 2019) were excluded because their full texts were unavailable. I contacted 12 corresponding authors to acquire the meta-data from 20 articles. Only three authors answered, two of which provided me with the needed material. The data for two articles could neither be retrieved (using Engauge Digitizer), nor were provided by the authors. This was due to the way the data was displayed as heatmaps (Amorim et al., 2018) or in low data resolution (Watanabe & Ishii, 2001) making it challenging to designate plotted points. These were also discarded under "Data Unavailability". The final count of publications from which I retrieved data was 19 articles. The data from these articles were then processed and standardized according to the procedure described in the methodology section.

The planula release category included only one publication (Goldstein & Riisgård, 2016). In this paper, the authors did not report the vital rate needed, but enough information to calculate it. Therefore, the percentage of sexually mature medusa ($N_{Mm}$) and the number of

planula larvae per female medusa ($N_L$) were the two parameters that had to be retrieved from the supplementary material to be able to calculate the estimates of planulae released per mature medusa. $N_{Mm}$ was transformed into ratio and multiplied by $N_L$ resulting in the estimate of planula released per mature medusa.

Across my data, three articles did not provide variance measures of the estimates measured and were therefore excluded from meta-analyses. One study (Goldstein et al., 2017) displayed the range of values (max/min) as error bars; therefore, I was not able to calculate the standard deviation of the means of estimates from this publication and consequently the standard error of the means. The two other studies (Ishii, Ohba, & Kobayashi, 2008; Purcell, 2007) did not mention the type of errors displayed in the graphs making their values unusable.

## Data distribution

From 19 articles, I was able to retrieve 264 estimates spread across multiple locations, species and other parameters. These parameters were not equally available for all estimates as seen in figure 6. The distribution of captured publications across multiple locations from which the studied jellyfishes originated are depicted in figure 7. It is important to note that some of
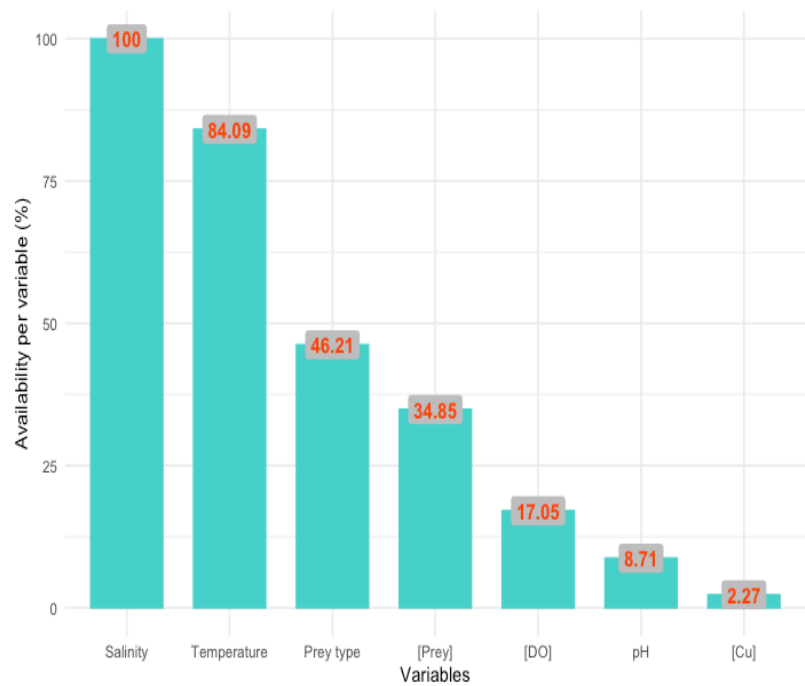


*Figure 6. Additional variables availability across estimates of vital rates.*

the captured publications reported data from several geographic origins in the same paper. This results in a total number of publications greater than n=19 displayed in the figures. The same applies to species and vital rates in cases where studies reported on more than one species of *Aurelia* in the same paper or estimated more than one vital rate.

A high proportion of publications was found for East Asia, especially within Chinese waters (e.g. Yellow Sea) and Tokyo Bay in Japan, and Northern Europe with a higher number of
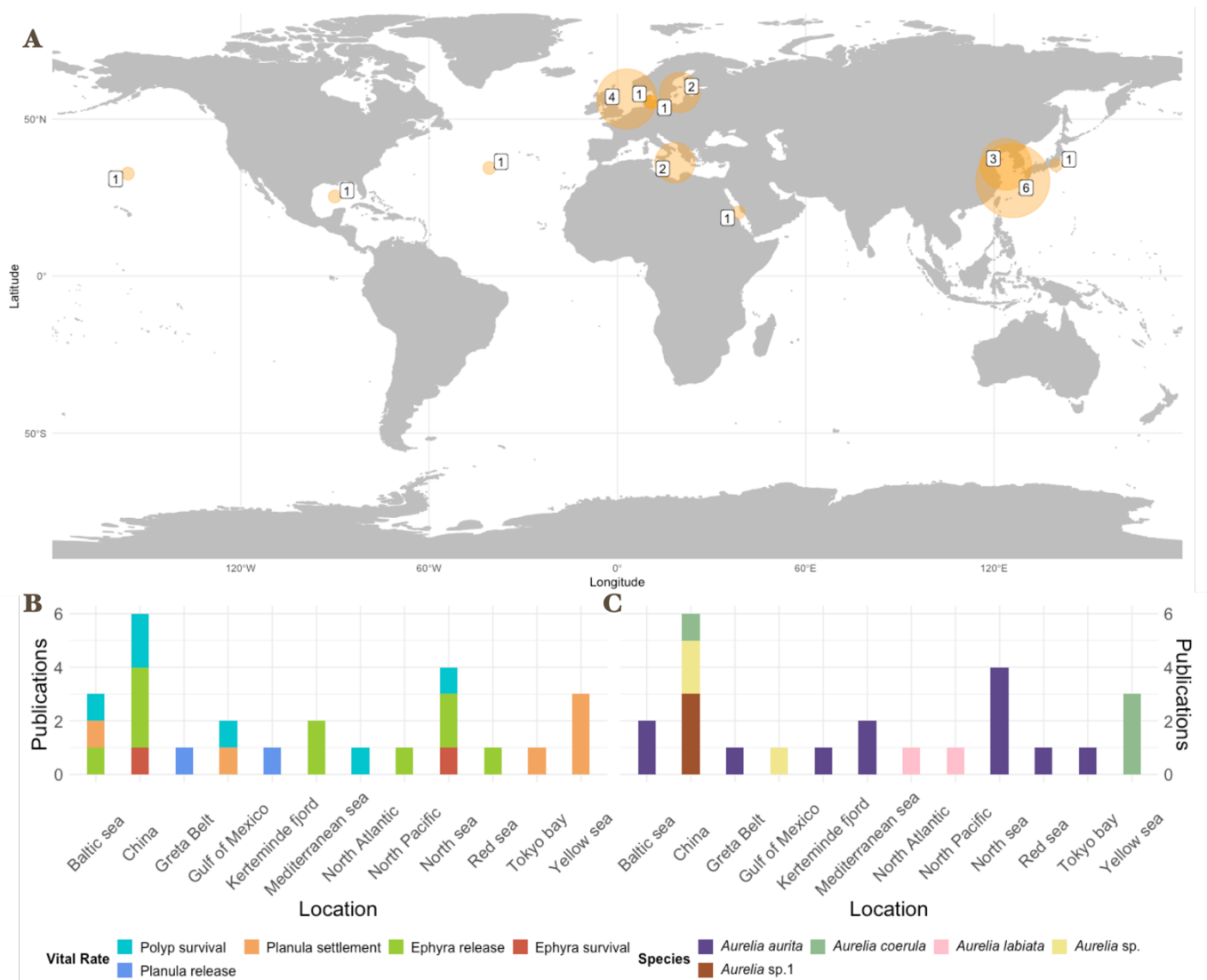
Figure 7. Summary of the systematic literature review results. **A**. The geographical distribution of the origin of jellyfish studied across the captured bibliography. The labels represent the numbers of publication per location. **B**. The distribution of vital rates across the geographical locations. **C**. The distribution of Aurelia species (as mentioned in studies) across the geographical locations.

publications from the North Sea, the Baltic Sea, the Danish strait (Great Belt) and Kerteminde fjord (Figure 7A). The remaining studies were scattered across the Red Sea, the Mediterranean Sea, the North Atlantic, the Gulf of Mexico and the North Pacific. These regions can be considered as understudied in terms of *Aurelia* spp. when compared to the regions mentioned above.

Studies on jellyfish originating from East Asia and labelled "China" were either collected from the Jiaozhou Bay or obtained from cultured jellyfish at the Chinese Academy of Science, Institute of Oceanology in Qindao, China. Studies from East Asia show not only the largest number of publications but cover also a higher diversity in terms of *Aurelia* spp. and in vital rates (Figure 7B & C). Nevertheless, this review did not capture studies covering the process of planula release in Chinese or Japanese waters. The only locations where *Aurelia*

*coerulea* was studied was in Chinese waters (Figure 7C). Diverse studies are also reported from Northern Europe, where all five vital rates were covered (Figure 7B). Publications in this region discuss a single species, *Aurelia aurita*, across all their studies (Figure 7C).

In this review it became clear that *Aurelia aurita* is the most studied species, while on the other hand *Aurelia labiata* is the least studied one (Figure 7C). *Aurelia* sp. and *Aurelia* sp.1 are two taxonomic nomenctlaures mentioned in the literature as the studied species (Figure 3C). *Aurelia* sp. is a broad definition of the *Aurelia* genus, pointing out that the authors did not have enough evidence to identify the jellyfish to the species level. *Aurelia* sp.1 is a name for taxa belonging to the *Aurelia* genus but has not been officially described, in my data belonging to a cohort in Chinese waters.

## Meta-analyses

Four out of the five categories of vital rates were included in the meta-analyses. Planula release data were excluded since all the data were extracted from a single publication. In addition, the three publications missing variance measures were excluded from these analyses. I also excluded all effect sizes with variance equal to zero to meet the requirements of the *rma.mv* function, used to build the meta-analyses models. All four models returned estimates of random effects equal to zero, meaning that the selected random effects (Paper ID, species and geographical location) do not influence the resulting estimates of the model. I therefore proceeded with simpler models, by omitting the random effects. Heterogeneity between studies within each category were measured using Cochran's $Q$, where higher $Q$ indicates more variability. Results presented in funnel plots (Appendix V) showed no outlier studies, and symmetry to the plotted indicates no notable bias.

### Planula settlement

The planula settlement category included four articles and a total of 20 estimates. This category scored the highest heterogeneity measure of all categories (Q = 0.3094; df = 19; p-val = 1.0). The planula settlement model resulted in an estimate of 0.7785 ± 0.2428 (SE) planulae settled per day.

### Polyp survival

The polyp survival category included five articles and a total of 28 estimates. It scored a relatively low heterogeneity measure (Q = 0.0984; df = 18; p-val = 1.0). The polyp survival model resulted in an estimate of 0.9561 ± 0.2512 (SE) polyps survived per day.

The ephyra release category included eight articles and a total of 77 estimates. It scored a relatively low heterogeneity measure (Q = 0.0222; df = 63; p-val = 1.0). The ephyra release model resulted in an estimate of 1.0151 ± 0.1375 (SE) ephyrae released per day.

Ephyra survival

The ephyra survival category included two articles and a total of 30 estimates. It scored the lowest heterogeneity measure (Q = 0.0061; df = 29; p-val = 1.0). The ephyra survival model resulted in an estimate of 0.9800 ± 0.1724 (SE) ephyrae survived per day.

| Vital rate category | Estimate (ratio/day) | SE | SD | n | df | Q |
|---|---|---|---|---|---|---|
| Planula settlement | 0.7785 | 0.2428 | 1.08583461 | 20 | 19 | 0.3094 |
| Polyp survival | 0.9561 | 0.2512 | 1.32922546 | 28 | 18 | 0.0984 |
| Ephyra release | 1.0151 | 0.1375 | 1.2065576 | 77 | 63 | 0.0222 |
| Ephyra survival | 0.98 | 0.1724 | 0.94427369 | 30 | 29 | 0.0061 |

*Table 2. Results from meta-analyses displaying each of the models' resulting estimates, standard error (**SE**) and standard deviation (**SD**) of the mean, the total number of studies analyzed (**n**), the degree of freedom (**df**) and Cochran's **Q** test.*

## 2. Modelling *Aurelia* life history

Medusa-to-medusa model

*Model behaviour*

I started by running a test simulation to assess the behaviour and performance of the medusa-to-medusa model. I fed the model with a population of 100 polyps and a set of five arbitrary vital rates. Each vital rate did not change through the years simulated. I simulated 5 years for this test. The four period-specific-duration components ($d_x$) were set as 90 days each, adding up to 360 days in total (≈1 year). The four polyp-survival-duration components ($d_p$) were also set as 90 days each, adding up to 360 days (≈1 year). The random vital rates for the test simulations were as follows:

- → Polyp survival = 100%

- → Planula settlement = 10%

- → Ephyra released per polyp = 200

- → Ephyra survival = 5%

- → Planula release per mature medusa = 180

The model simulates four different populations of the four life stages, simultaneously for a length of the simulated years (5 years) (Figure 8). This model is designed by assuming that the populations of planula, ephyra and medusa collapse after one period. As a result, I could see that in the planula, ephyra and medusa life stages exhibit a seasonal cycle (Figure 8A-C). In contrast, I could observe that the polyp population never collapses but accumulates from year to year and is comparatively stable within a year (Figure 8D). This is not a pre-set condition like the latter but is completely dependent on the values of the vital rates fed into the model.
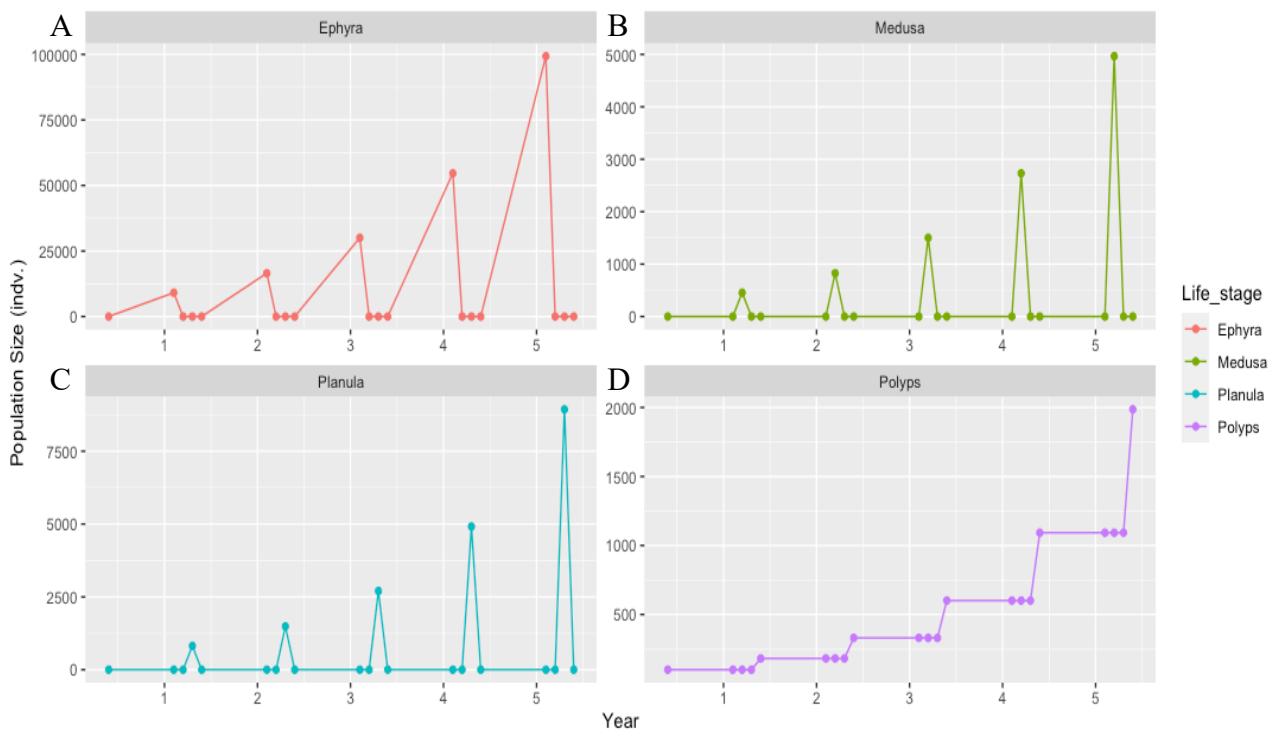


*Figure 8. Results of the test simulation of the medusa-to-medusa model for the four different jellyfish life-stages A) ephyra, B) medusa, C) planula and D) polyps.*

*Simulations*

After assessing the model's behaviour, I ran it with data from the meta-analyses conducted previously (Table 2). From these values, I generated multiple estimates of vital rates via the{*rtruncnorm*} function in R. Since the meta-analyses did not cover planula release rates, I calculated the mean of the estimates of these rates retrieved by the SLR (531.21). I then used this value, with a standard deviation equal to one, to iterate multiple random estimates for the model. I ran simulations for five, seven and twenty years to try and observe the development for various fluctuations levels in the population's stages. The initial polyp population was set to 100 individuals. The populations of all four stages increases considerably with the years, noting that in figure 9, values higher than 1e+204 (A/B), 1e+206 (C) and 1e+246 (D) are not correctly scaled due to their extremely high values. Even though ephyra, medusa and planula populations collapse every year, they recovered and showed an increase in population size the following year. The polyp population displayed a steep increase in population size in the first two years (Figure 9D). A notable drop in the number of polyps is recorded after the third year. This is due to a randomly selected low survival rate of polyps for these two consecutive years combined with a low settlement rate of planula. Nevertheless, the polyp population recovered within the same year and continued to grow. After seven years, the model yields in all the four periods extremely big populations of each stage respectively.
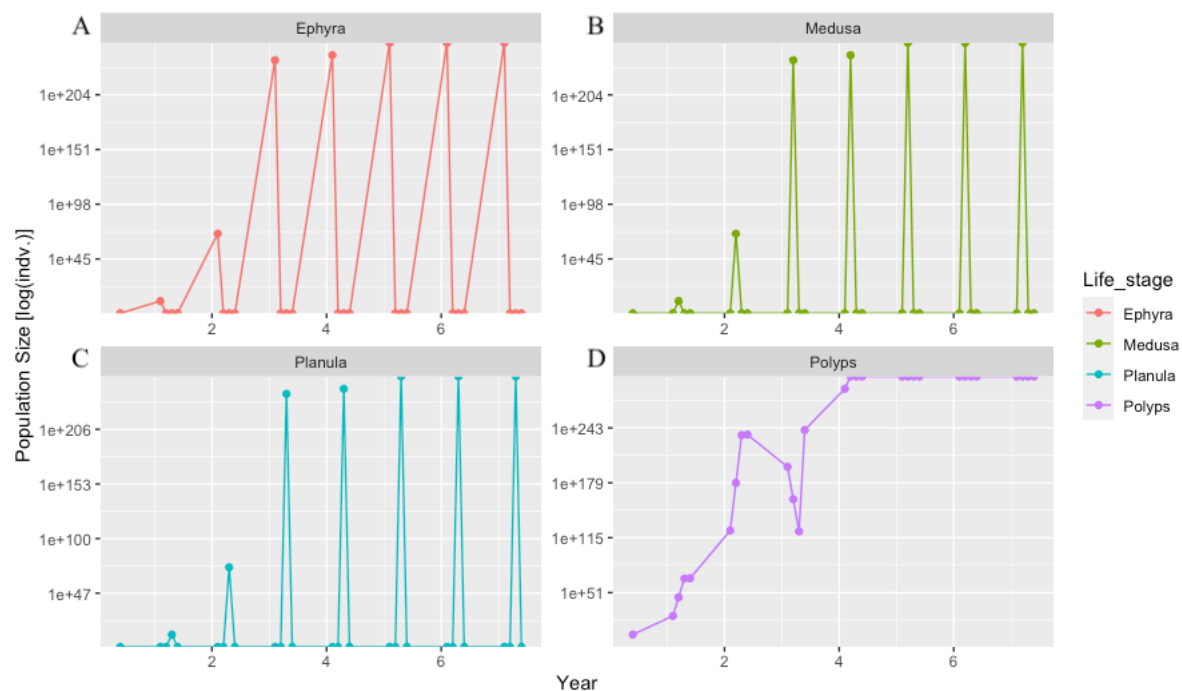


*Figure 9. Results of a seven-years simulation using the meta-analyses results for the four different jellyfish life-stages A) ephyra, B) medusa, C) planula and D) polyps.*

Polyp-to-medusa model

*Simulations*

The distribution of PGRs is represented in figure 10. In this figure, the distribution is skewed towards zero. This means that according to my data, it is more probable for the population to have a low growth rate. The largest frequency of the results also lies bellow the red line (PGR<1), while the median is above the red line (PGR>1). This further indicates that, using this data, the medusa populations might often be smaller than the polyp populations. Nevertheless, figure 10 also points out that population growth can, less probably, reach high rates (up to 10 times). The 95% confidence interval lies between rates of 0 and 5.5. The 50% quantile lies between rates of 0.5 and 2.6.
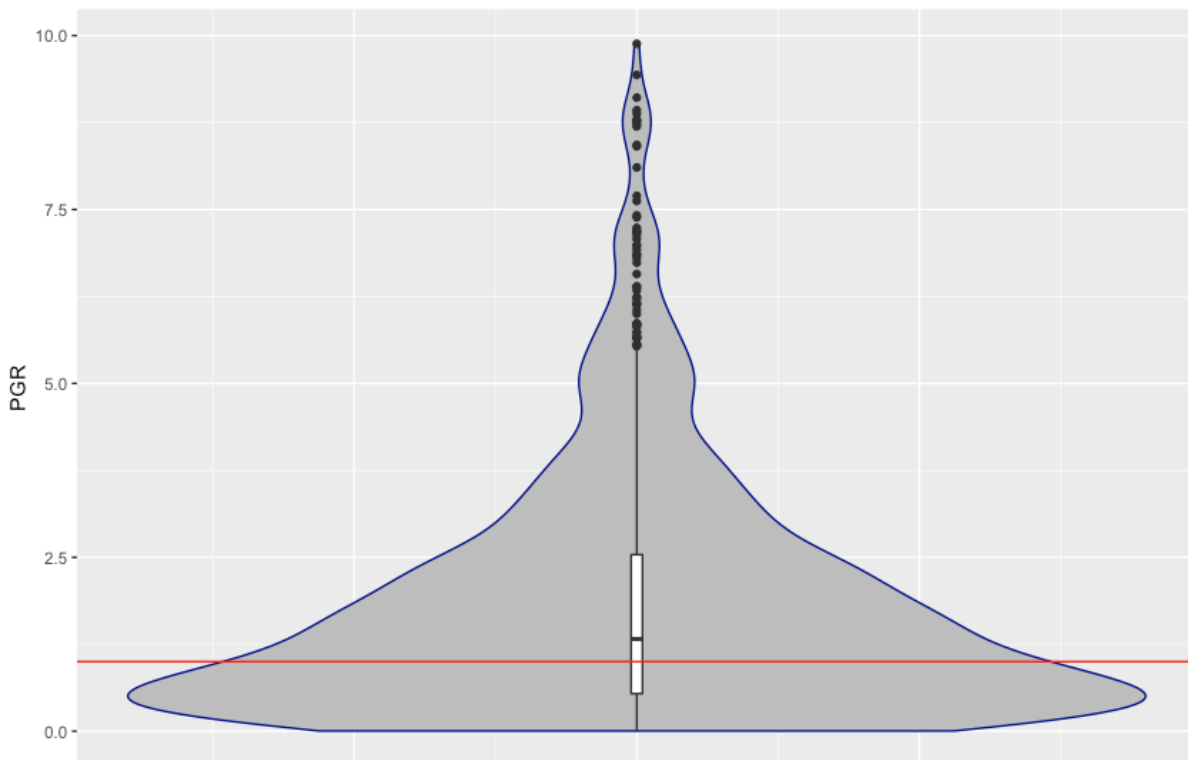


*Figure 10. Violin plot representing the distribution of the population growth rates (PGR) simulated using the meta-analyses results in the polyp-to-medusa model. The boxplot in the center of the violin plot represents the same data. The white box represents the 50% quartile range of results with the black horizontal strip marking the median. The black vertical line represents the 95% confidence interval. The red line represents a PGR value of one.*

# Discussion

This study sought an evaluation of the availability of demographic rates and their distribution, and their use to model and simulate virtual populations of *Aurelia* spp.. The results of this study highlighted the scarcity and inconsistency of data describing the demography of *Aurelia* spp. and the need for additional studies focusing on the different components of jellyfish life-cycles.

## Demographic rates & data resolution

A small number of articles was captured during the systematic literature review. The total number of hits resulting from the initial search strategy (350 hits – excluding duplicates) is small despite following good practices and searching multiple databases (Konno & Pullin, 2020). This pointed out early in my study, how the *Aurelia* genus is understudied and consequently why there are fewer studies on its population dynamics. The data extracted at the end of the screening protocol shows an uneven distribution across the captured variables. Seen in the results is a clear concentration of articles about *Aurelia* population dynamics originating from northern European and East Asian waters. Usually, research increases with the increase of funding opportunity, while research funding is often only invested when it is considered to solve anthropocentric challenges. The impact of jellyfish blooms on human infrastructure can be extremely costly (Brodeur et al., 2016). Therefore, areas impacted by blooms will have a tendency to invest in jellyfish research. When comparing my data to the distribution of time-series data of jellyfish abundance (figure 12) (Condon et al., 2013), the locations match. Almost all locations picked up by the SLR are areas that generally show an increasing abundance of jellyfish over time in the Condon et al. (2013) study. This suggests that one of the reasons that these areas have a higher number of publications, is that they are impacted by *Aurelia* blooms. This further supports claims of a media-driven increases in jellyfish occurrence studies (Condon et al., 2012). Other locations are also known to be affected by jellyfish blooms such as the Mediterranean Sea, the Red Sea, and the Gulf of Mexico. When overlapped with figure 12, these locations have either no or a decreasing trend of time-series data about jellyfish, which can considerably influence research preferences. This underlines the importance of time-series in demographic studies and how their absence can hinder prospects of research. They might also be affected by different species of jellyfish and therefore would not be picked up by my review. Such broader variations could be covered by a similar study, by taking into consideration a multitude of blooming species, and

identifying the patterns of distribution of studies interpreting the different species. On the other hand, another study (Brotz et al., 2012) pointed out that not all areas have an equal certainty of measurements. For instance, Brotz et al. (2012) demonstrated how East Asian studies scored a high certainty degree, by having more reliable data, while the northern European studies scored a low certainty degree. Differences like these can occur due to the quality of data collection and can have repercussions on the reliability of area specific-trends.

Retrieved publications were also unevenly spread across vital rates and species. As expected, the species that is most reported in various locations is *Aurelia aurita*. *A. aurita* is known to be the most common species of the *Aurelia* genus, as well as one of the most common jellyfishes (Arai, 1997). In my data, it also is the only species that has been covered by all five vital rates. The least reported vital rate was the release of planulae. During the SLR, two publications mentioned counts of planulae produced by adult female medusa, yet only one of them made it to the final stage of data extraction (Goldstein & Riisgård, 2016). Goldstein & Riisgård (2016) captured wild, ripe (planulae-carrying) medusae from different locations and accounted for the numbers of planulae released within containment. The other paper (Lucas, 1996) was excluded from this study as it did not provide the number of planulae released by a medusa, but an averaged number of planulae counted on several medusae oral arms, which is
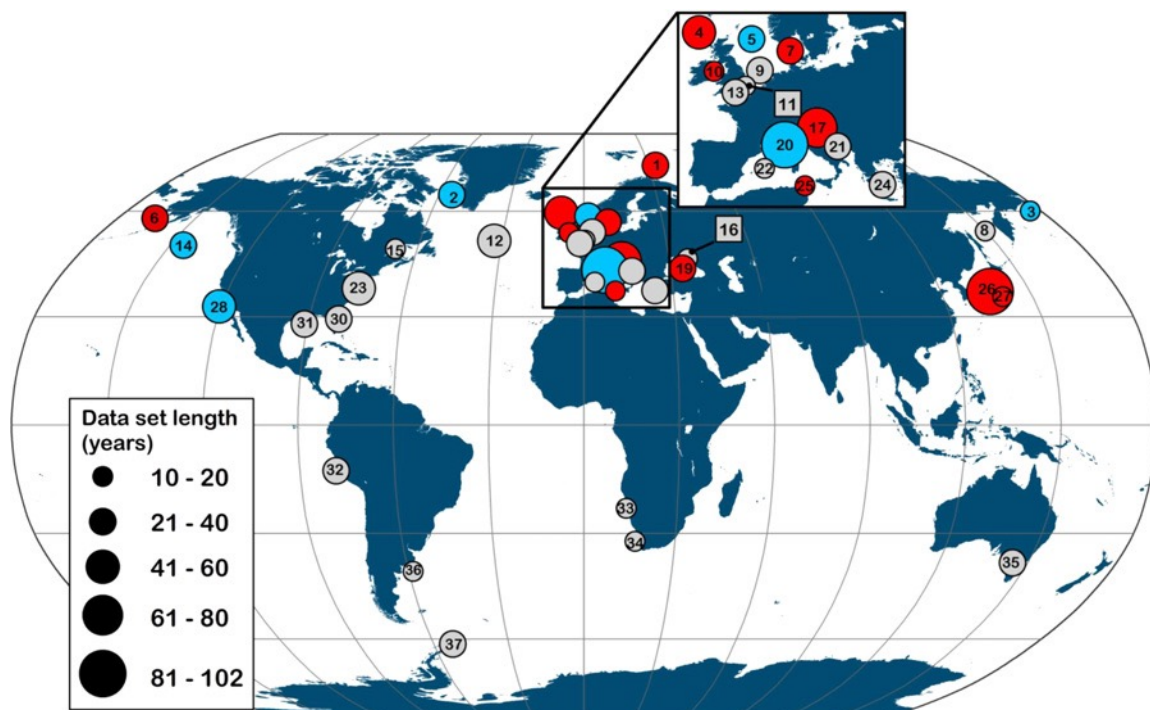


*Figure 11. Retrieved from Condon et al., 2013. "Distribution of jellyfish time-series. Time-series of observations on jellyfish abundance >10 y in length from 1874 to 2011. The diameter of the symbols is proportional to the duration of the dataset, colors indicate trends (linear regressions, P < 0.05): significant decrease (blue), significant increase (red), or no trend (grey) in jellyfish abundance over time for the duration of the study. Most datasets were from the northern hemisphere (87%), in particular the Atlantic Ocean (17%) and the Mediterranean region (17%), and comprised medusae (89%)."*

not representative of the process of release, but rather the production of planulae. It is unsurprising to find a scarcity of studies dealing with planulae release rates, since the nature of the work needed to gauge these microorganisms is very demanding (Haddock, 2004). As seen in several publications, universal and efficient methodologies have been developed so far to count and assess the planulae larvae attached to medusa, rather than released by the medusae (Goldstein & Riisgård, 2016; Lucas, 1996; Suzuki et al., 2019). In addition, it is possible that a lack of demand for such data is the reason behind such vital rates still being under-investigated. In the light of future predictions of jellyfish population dynamics, this aspect is now considered as a crucial part (Gibbons & Richardson, 2013). It's becoming clearer in the literature that a trend towards understanding the driving mechanisms of the blooming process, rather than the entire life history, is happening (Ceh, Pacheco, & Riascos, 2017). This trend is embodied in my data, where more studies discuss polyp and ephyra related demography, then medusa and planula.

## Methodological constraints of the SLR

It is important to note that in this study I limited my search to three databases. Despite being the world's leading citation databases, assuming that these three directories cover all jellyfish related publications is unrealistic. One should consider the possibility of finding more published articles discussing the subject matter only available in foreign languages (national publications) or in grey literature. Moreover, Scopus and ScienceDirect databases usually overlap heavily (Elsevier, 2018), since they both contain all published articles by Elsevier, which can explain the high number of duplicates excluded during the screening protocol. In addition, WoS can also possibly contain duplicates of publications present in the other two databases. Including more databases in such a study would certainly provide a more comprehensive answer yet it remains only possible when more time and resources are affordable. During the screening protocol, I was also the only reviewer conducting the review. This provides room for subjectivity and thus bias in the results obtained. Involving more reviewers during the screening protocol would increase the reliability of the results.

## Meta-analyses

The meta-analyses provided a comprehensive, unbiased (Appendix V), yet diverse set of demographic estimates. Each of the four meta-analysis models resulted in an estimate that summarised all the effect sizes of its category, which were later used in the population models. These estimates condensed effect sizes of experiments controlling for a wide

spectrum of variables. In addition, all the retrieved demographic rates belonged to experimental studies. Experimental studies, even though widely used, do not usually have a comprehensive representation of a stochastic environment since they are based on the isolation of specific physical or biological factors. One would expect such data with a wide range of variables to be fairly heterogeneous. Nevertheless, all four categories expressed a relatively low heterogeneity measure (Cochran's $Q \leq 0.3094$), with the highest value belonging to the planula settlement rates. Since Cochran's $Q$ is known to be less powerful for smaller number of studies (Gavaghan, Moore, & McQuay, 2000) and the planula settlement category has the least number of effect sizes (n = 20), one can conclude that its $Q$ is the least accurate. Yet, this last category is composed of four articles, covering three different species (*A. aurita, A. coerulea* & *A.* sp.) across four different locations (Baltic Sea, Gulf of Mexico, Tokyo Bay & Yellow Sea), which can be its source of heterogeneity. Moreover, all four categories showed no outliers in the funnel plots (Appendix V) confirming the consistency of my data. I therefore proceeded to use these estimates in my population models, assuming they carry enough variability to express environmental stochasticity.

## Medusa-to-medusa model and *Aurelia* life history

The four-periods-model based on ordinary differential equations was used instead of the conventional population matrix model for simplicity. In matrix models, all vital processes happen spontaneously in a single timestep, yielding a population of all life stages at the end of each cycle. This is not biologically accurate in the case of *Aurelia* spp., since theoretically, not all stages can exist at the same time, and therefore specific stages will collapse (e.g. planula) before the others are observed (e.g. ephyra). Consequently, several stage-specific matrices must be developed when adapting the population matrix method (Goldstein & Steiner, 2020; Henschke et al., 2018). To avoid this, I expressed this asynchrony in life stages through the year as five ordinary differential equations in four temporal periods.

The design of the medusa-to-medusa model has a wide applicability. A researcher could use this model to investigate the importance of demographic processes by changing vital rates in a sensitivity analysis. This can be done to express changes in environmental or biological conditions, using data from an experiment or from multiple studies. For example, to evaluate the effect of increasing temperatures on future generations, vital rates from experiments with high temperature treatments can be retrieved and this information can in turn be fed into the model. This helps to customize scenarios for specific events like sea temperature rise, eutrophication, pollution or overfishing. Yet consequently, further development of the

applicability of my model solely depends on the availability of data. The main challenge faced to run realistic simulations using the medusa-to-medusa model was the absence of a homogenous dataset representative of a specific *Aurelia* population. It is known that the *Aurelia* genus possesses a highly plastic life cycle (Lucas, 2001; Marques et al., 2015). Therefore, to run a realistic simulation, it is essential that the vital rates fed to the model belonged at least to the same population of jellyfishes and the same species. Such data was not captured during the SLR. I nevertheless proceeded to use the outcome of the meta-analyses, which included vital rates from various locations and species, after they showed very little variability in the assessments conducted (low Cochranes' Q values), as discussed previously. Another aspect of applicability in this model lies in its duration coefficient components. Since demographic processes are triggered/blocked by biotic and abiotic factors, the availability of these factors would determine the time span of each of these processes.

This model, with no constraints on population growth, is bound to produce projections of exploding or collapsing populations, especially when projected on longer time spans. The test simulation was used to assess the behaviour of my model and insure its functioning. That was accomplished by identifying inter-annual and intra-annual (between periods of the same year) patterns in population change. Once identified, I could move on to simulate more realistic data, such as the estimates calculated in the meta-analyses.

Density-dependence of *Aurelia* spp. can be challenging to account for because of the multiple life stages in its life history, their nature and consequently their different habitats, diets and trophic role. It is until recently that the academic community is showing interest in polyps (Marques et al., 2019; Sun et al., 2017), locating their habitats (Feng, Lin, Sun, & Zhang, 2017; van Walraven et al., 2016) and starting to look into the processes which regulate their population dynamics (Fuchs et al., 2014; Schiariti et al., 2015). On the other hand, one can also argue that the meta-analyses estimates are representative of the stochasticity of the environment. First, the data used to calculate these estimates have been retrieved from a multitude of studies and covers a wide variety of physical and biological variables. Second, the meta-analyses showed high homogeneity of results of each category which can be seen in the funnel plot (Appendix V), implying no bias within each category. Third, the generation of random estimates within the ranges presented by the meta-analyses can also be considered an unmonitored source of stochasticity to the model. After considering the three latter facts, it can be proposed that, even though my model is missing density-dependence components or other growth limiting factors, it expresses this stochasticity through sampling the vital rates

provided to it from a distribution. In this context, the comprehensiveness of my data describes general behavioural trends of population dynamic of *Aurelia* spp. and its evolutionary adaptations (e.g. meta-genetic life cycle), rather than a specific population´s case. Nevertheless, no strict conclusion can be made from a specific simulation of the medusa-to-medusa model (e.g. Figure 9) since every simulation will be sampling new estimates from the distribution of demographic rates provided. One could iterated the simulations multiple times, as done in the polyp-to-medusa model, which would result in a distribution of population predictions.

## Polyp-to-medusa model and bloom dynamics

The polyp-to-medusa model approaches more closely the bloom dynamics. It only accounts for the demographic processes directly involved in the production of medusae. The results of this model showed a distribution of population growth rates within the same generation, using the demographic estimates provided by the meta-analyses. These results are very representative of the data, since the simulations were iterated multiple times (x1000) thus generating numerically a probability density field. The skewed distribution indicates that a polyp population tends to culminate in a larger number of medusae than its own (figure 10: median > 1). This increase in numbers, when considerably higher (e.g. 10x), can possibly describe a blooming behaviour. Nevertheless, the challenge, when addressing bloom formations, is not only in understanding its demographic dynamics, but more importantly in defining what it is in the first place.

Jellyfish blooms are widely discussed in scientific literature yet remain extremely hard to define from a demographic point of view. A bloom is a high concentration of individuals (not necessarily belonging to the same population) appearing in a distinct area abruptly. Consequently, understanding jellyfish blooms is also a question of geography, bathymetry and hydrography. Having weak motility, jellyfish dispersal is almost completely dependent on winds, ocean currents and coastal topography. Yet, even before investigating the effect of the latter factors on the dispersal of jellyfish, one needs to track the origin of seed populations and the location of polyps. Locating polyps alone is a big technical challenge (van Walraven et al., 2016). When polyps are located, biotic and abiotic factors are forecasted, demographic rates are assessed and geographic factors are studied, only then would scientists be able to make more reliable jellyfish bloom predictions. Nevertheless, unpredictable biotic factors, such as reproduction and predation, can always play a crucial role in regulating demographic dynamics and introduce uncertainties to forecasts.

## Assumptions and constraints of the models

Multiple assumptions introduced constraints to achieve realistic predictions. It is important to note that the models assume that all life stages, except polyps, die after one period. This function ensures that planulae, ephyrae and medusae of one generation either develop or grow into its next stage or die (Ceh et al., 2015; J Goldstein et al., 2017; Van Der Veer & Oorthuysen, 1985). None the less, some reports indicate that it is possible for *Aurelia* medusae to overwinter and stay sexually active during the next year (Han, Kawahara, & Uye, 2009; Hernroth & Gröndahl, 1985; Makabe et al., 2012), yet determining the longevity is challenging because of the possibility of a continuous recruitment (Lucas, 1996). My models did not include a specific rate for the asexual budding processes as I did not focus the systematic review on finding rates for this process specifically. Nevertheless, polyp survival rates could take it into consideration by incorporating in their estimates the effects of asexual budding. In fact, two of the extracted articles providing polyp survival rates included asexual budding in their rates (Miller & Graham, 2012; Y.-T. Wang, Zheng, Sun, & Zhang, 2015). Therefore, I could simply express this process in my model by using the estimates from these articles.

Ephyra growth rates used in the models are in fact ephyra survival rates. They were retrieved from the only two articles (Algueró-Muñiz, Meunier, Holst, Alvarez-Fernandez, & Boersma, 2016; Y.-T. Wang & Sun, 2015) that discussed the dynamics of ephyra in the SLR. These articles provided me with experimental, long time-span survival rates of ephyrae tested across a variety of limiting factors. Even though there is a good understanding of some *Aurelia* species' ephyrae bioenergetics (Båmstedt, Lane, & Martinussen, 1999; Wang & Li, 2015), no articles in the SLR mentioned a specific rate of transition from the ephyra to medusa. Consequently, an assumption had to be made, that when ephyrae survive a certain period of time they transition into medusa. This assumption implied that enough prey is available, at the right abiotic condition, for the ephyra to grow into a medusa. I carried on with this assumption, knowing that it is the only one available so far.

## Developing tools for managers & prospects for future research

Room for improvements of the medusa-to-medusa model remains open. In this study, the model was fed with estimates summarizing effect sizes spread across a spectrum of variables. This data can be organized into combinations of specific variables with corresponding estimates of vital rates. The model can then be structured to read environmental forecasts

such as water temperature, freshwater influx, etc. Knowing that demographic events are triggered by environmental factors, one can determine the time span of each period using forecasts. In addition, the vital rates can be set to be selected simultaneously depending on the forecast, hence, the model would choose the adequate vital rate depending on the environmental forecast given to it. This could then be developed into a tool to be used by managers. It could help simulate projections of specific population in specific areas and possibly predict major demographic events such as blooms. Yet, such an advanced model would only be functional once comprehensive datasets are made available. As seen in the previous part of this thesis, the captured data lacks homogeneity within each vital rate category and is scattered across multiple locations and species. Before attempting to build a more complex model these gaps need to be filled.

# Conclusion

This study investigated the availability and distribution of five types of demographic rates of *Aurelia* species that outlines its complex life cycle. The systematic literature review allowed for a thorough and accurate examination of the available published data and the identification of several knowledge gaps. The main gaps identified by this study were the need for more release rates of planulae by fecund female medusae and the lack of growth and transition rates of ephyrae to become mature medusae.

Building the population models played an important role in this study by highlighting the importance of comprehensive demographic datasets, the essential building blocks for a population prediction framework. A comprehensive demographic dataset of a specific population is defined by having a species-specific and location-specific set of demographic rates for each and every life-stage of the metagenetic life-cycle with their distribution across the multiple fluctuating variables (biotic & abiotic) affecting them. Such a dataset would allow researchers to better address specific populations, and use prediction models, such as the models developed in this study. The models developed here can further be used as tools for management and decision making. Such tools would not only be used for predicting jellyfish population blooms, but once realistic enough, could also help understand the complex demography of these animals. Better understanding jellyfish demography would help develop pest control strategies to tackle their nuisance and create a sustainable approach to harvest them as a resource. Finally, it became evident that the demographic importance and ecological effect of jellyfish blooms is largely undermined, while published studies convey their interest solely towards there anthropogenic impact. To be able to address jellyfish blooms, there needs to be a clear demographic definition of what a bloom is.

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# Appendixes

## Appendix I – List of articles chosen for data extraction.

| ID | Authors | Year | Title | DOI | Data location | Category | Retrieved |
|---|---|---|---|---|---|---|---|
| Wang_2015(1) | Wang Y-T; Sun S | 2015 | Population dynamics of *Aurelia* sp.1 ephyra and medusae in Jiaozhou Bay, China | https://doi.org/10.1007/s10750-014-2021-3 | Fig 7 | Survival of Ephyra | Yes |
| Alguero-Muniz _2016 | Alguero-Muniz M; Meunier, CL; Holst, S; Alvarez-Fernandez, S | 2016 | Withstanding multiple stressors: ephyrae of the moon jellyfish (*Aurelia aurita* , Scyphozoa) in a high-temperature, high-CO2 and low-oxygen environment | https://doi.org/10.1007/s00227-016-2958-z | Fig 1 (g-h-i) | Survival of Ephyra | Yes |
| Xing_2020 | Xing Y ; Liu Q ; Zhang M ; Zhen Y ; Mi T ; Yu Z ; | 2020 | Effects of temperature and salinity on the asexual reproduction of *Aurelia coerulea* polyps | https://doi.org/10.1007/s00343-019-8337-0 | Fig 3 | Release of Ephyra | Yes |
| Watanabe_2001 | Watanabe T Ishii, H; | 2001 | In situ estimation of ephyrae liberated from polyps of *Aurelia aurita* using settling plates in Tokyo Bay, Japan* | - | Fig 5 & 6 | Release of Ephyra | No |
| Holst_2012 | Holst S | 2012 | Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish | https://doi.org/10.1007/978-94-007-5316-7_10 | Fig 2 (right) | Release of Ephyra | Yes |
| WangN_2015(1) | Wang N ; Li C ; Liang Y ; Shi Y ; Lu J ; | 2015 | Prey concentration and temperature effect on budding and strobilation of *Aurelia* sp. 1 polyps | https://doi.org/10.1007/s10750-014-1978-2 | Fig 5 | Release of Ephyra | Yes |
| Holst_2010 | Holst S; Jarms, G | 2010 | Effects of low salinity on settlement and strobilation of scyphozoa (Cnidaria): Is the lion's mane *Cyanea capillata* (L.) able to reproduce in the brackish Baltic Sea? | https://doi.org/10.1007/978-90-481-9541-1_5 | Table 6 | Release of Ephyra | Yes |
| Pascual_2015 | Pascual M; Fuentes, V; Canepa, A; Atienza, D; Gili, JM; Purcell J E | 2015 | Temperature effects on asexual reproduction of the scyphozoan *Aurelia aurita* s.l.: differences between exotic (Baltic and Red seas) and native (Mediterranean Sea) populations | https://doi.org/10.1111/maec.12196 | Ephyrae . Scyphistoma + (Fig4?) | Release of Ephyra | Yes |
| Purcell_2007 | Purcell J E; | 2007 | Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata* * | https://doi.org/10.3354/meps07056 | Table 1 & 2 & 6 | Release of Ephyra | Yes |
| Purcell_2012 | Purcell J E; Atienza D ; Fuentes V ; Olariaga A ; Tilves U ; Colahan C ; Gili J M; | 2012 | Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea | https://doi.org/10.1007/978-94-007-5316-7_13 | Table 1 & 2 | Release of Ephyra | Yes |
| WangN_2015(2) | Wang N ; Li C ; | 2015 | The effect of temperature and food supply on the growth and ontogeny of *Aurelia* sp. 1 ephyrae | https://doi.org/10.1007/s10750-014-1981-7 | Table 1 & 3 | Release of Ephyra | Yes |
| Goldstein_2016 | Goldstein J ; Riisgård H U | 2016 | Population dynamics and factors controlling somatic degrowth of the common jellyfish, *Aurelia aurita* , in a temperate semi-enclosed cove (Kertinge Nor, Denmark) | https://doi.org/10.1007/s00227-015-2802-x | Supplementary material Online resource 1 | Release of Planula | Yes |
| Dong_2018(1) | Dong ZJ; Sun, TT | 2018 | Combined effects of ocean acidification and temperature on planula larvae of the moon jellyfish *Aurelia coerulea* | https://doi.org/10.1016/j.marenvres.2018.05.015 | Fig 4 | Settlement of Planula | Yes |
| Dong_2018(2) | Dong ZJ; Wang, L; Liu, QQ; Sun, TT | 2018 | Effects of salinity and temperature on the recruitment of *Aurelia coerulea* planulae | https://doi.org/10.1080/17451000.2018.1459725 | Fig 2 | Settlement of Planula | Yes |
| Dong_2019 | Dong ZJ; Wang, FH; Peng, SJ; Chen, GF; Sun, S | 2019 | Effects of copper and reduced salinity on the early life stages of the moon jellyfish *Aurelia coerulea* | https://doi.org/10.1016/j.jembe.2019.02.005 | Fig 2 | Settlement of Planula | Yes |
| Miller_2012 | Miller Mary-Elizabeth C; Graham William M; | 2012 | Environmental evidence that seasonal hypoxia enhances survival and success of jellyfish polyps in the northern Gulf of Mexico* | https://doi.org/10.1016/j.jembe.2012.07.015 | Fig 2 | Settlement of Planula | Yes |
| Ishii_2008 | Ishii H ; Ohba T ; Kobayashi T ; | 2008 | Effects of low dissolved oxygen on planula settlement, polyp growth and asexual reproduction of *Aurelia aurita* | https://doi.org/10.3800/pbr.3.107 | Fig 3 | Settlement of Planula | Yes |
| Goldstein_2017 | Goldstein J; Augustin, CB; Bleich, S; Holst, S | 2017 | A matter of tolerance: Distribution potential of scyphozoan polyps in a changing environment* | https://doi.org/10.1111/maec.12457 | Fig 1 | Settlement of Planula | Yes |
| Wang_2015(2) | Wang Y-T; Zheng S; Sun S; Zhang F | 2015 | Effect of temperature and food type on asexual reproduction in *Aurelia* sp,1 polyps | https://doi.org/10.1007/s10750-014-2020-4 | Fig 1 | Survival of Polyps | Yes |
| Miller_2012 | Miller Mary-Elizabeth C; Graham William M; | 2012 | Environmental evidence that seasonal hypoxia enhances survival and success of jellyfish polyps in the northern Gulf of Mexico* | https://doi.org/10.1016/j.jembe.2012.07.015 | Fig 3 | Survival of Polyps | Yes |
| Amorim_2018 | Amorim K; Mattmuller, RM; Alguero-Muniz, M; Meunier, CL | 2018 | Winter river discharge may affect summer estuarine jellyfish blooms | https://doi.org/10.3354/meps12356 | Fig 4 - B | Survival of Polyps | No |
| Xupeng_2019 | Chi Xupeng ; Mueller-Navarra Doerthe C; Hylander Samuel ; Sommer Ulrich ; Javidpour Jamileh ; | 2019 | Food quality matters: Interplay among food quality, food quantity and temperature affecting life history traits of *Aurelia aurita* (Cnidaria: Scyphozoa) polyps | https://doi.org/10.1016/j.scitotenv.2018.11.469 | Fig 1 | Survival of Polyps | Yes |
| Goldstein_2017 | Goldstein J; Augustin, CB; Bleich, S; Holst, S | 2017 | A matter of tolerance: Distribution potential of scyphozoan polyps in a changing environment* | https://doi.org/10.1111/maec.12457 | Fig 3 | Survival of Polyps | Yes |
| Huang_2015 | Huang XG; Huang, BQ; Zeng, Y; Li, SX | 2015 | Effect of dinoflagellates and diatoms on the feeding response and survival of *Aurelia* sp polyps | https://doi.org/10.1007/s10750-014-2023-1 | Fig 4 | Survival of Polyps | Yes |
| Purcell_2007 | Purcell J E; | 2007 | Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata* * | https://doi.org/10.3354/meps07056 | Table 1 | Survival of Polyps | Yes |

*Table listing the articles chosen for data retrieval, after making it through the screening process. A Paper ID (column 1) was designated for each article. Articles with "*" provide more than one category of vital rate and therefore if present more than once in this table. Two of these articles' data were not retrieved.*

```r
### Meta-analysis models


    library(metafor)


# Meta-analysis model for the planula settlement data


    planula_set.ma <-  rma.mv(yi = `Normalized Estimate`,
                              V = `Normalized Variance`,
                              random = list(~1 | Paper_ID , ~1 | Species , ~1 | Origin),
                              data = Planula_Settlement_Data,
                              slab = Paper_ID,
                              method = "REML",
                              control=list(optimizer = "optim", optmethod = "Nelder-Mead"))


# Meta-analysis model for the polyp survival data


    polyp_sur.ma <- rma.mv(yi = `Normalized Estimate`,
                           V = `Normalized Variance`,
                           random = list(~1 | Paper_ID , ~1 | Species , ~1 | Origin),
                           data = Polyp_Survival_Data,
                           slab = Paper_ID,
                           method = "REML")


# Meta-analysis model for the ephyra release data


    ephyra_rel.ma <- rma.mv(yi = `Normalized Estimate`,
                            V = `Normalized Variance`,
                            random = list(~1 | Paper_ID , ~1 | Species , ~1 | Origin),
                            data = Ephyra_Release_Data,
                            slab = Paper_ID,
                            method = "REML")


# Meta-analysis model for the ephyra survival data


    ephyra_sur.ma <- rma.mv(yi = `Normalized Estimate`,
                            V = `Normalized Variance`,
                            random = list(~1 | Paper_ID , ~1 | Species , ~1 | Origin),
                            data = Ephyra_Survival_Data,
                            slab = Paper_ID,
                            method = "REML")
```

*R Code of meta-analysis models using the {metafor} package. Four different models of four different data-sets (vital rates).*

# Appendix III – R Code: Medusa-to-medusa model

```r
### Base Functions for the Medusa – to – Medusa Model ###

#### 4 time periods ####

# Period 4 Transition formula - Planula to Polyp #

Period1 <- function(Planula_currentyr, Polyps_currentyr, survival_Polyps, transitionto_Polyps) {

  Polyps_currentyr <- (Polyps_currentyr * survival_Polyps ^90) + (Planula_currentyr * transitionto_Polyps *90)

  Life_stages <- data.frame("Polyps" = Polyps_currentyr,
                            "Ephyra" = 0,
                             "Medusa" = 0,
                            "Planula" = 0,
                            "Period" = 4)

  return(Life_stages)
}

# Period 1 Transition formula - Polyp to Ephyra #

Period2 <- function(Polyps_previousyr, reproductionto_Ephyra, survival_Polyps) {

  Ephyrae_currentyr <- Polyps_previousyr * reproductionto_Ephyra *90

  Polyps_currentyr <-  Polyps_previousyr * survival_Polyps ^90

  Life_stages <- data.frame("Polyps" = Polyps_currentyr,
                            "Ephyra" = Ephyrae_currentyr,
                            "Medusa" = 0,
                            "Planula" = 0,
                            "Period" = 1)

  return(Life_stages)
}

# Period 2 Transition formula - Ephyra to Medusa #

Period3 <- function(Ephyrae_currentyr, transitionto_Medusa, Polyps_currentyr, survival_Polyps) {

  Medusa_currentyr <- Ephyrae_currentyr * transitionto_Medusa ^90

  Polyps_currentyr <-  Polyps_currentyr * survival_Polyps ^90

  Life_stages <- data.frame("Polyps" = Polyps_currentyr,
                            "Ephyra" = 0,
                            "Medusa" = Medusa_currentyr,
                            "Planula" = 0,
                            "Period" = 2)

  return(Life_stages)
}

# Period 3 Transition formula - Medusa to Planula #

Period4 <- function(Medusa_currentyr, reproductionto_Planula, Polyps_currentyr, survival_Polyps) {

  Planula_currentyr <- Medusa_currentyr * reproductionto_Planula

  Polyps_currentyr <-  Polyps_currentyr * survival_Polyps ^90

  Life_stages <- data.frame("Polyps" = Polyps_currentyr,
                            "Ephyra" = 0,
                            "Medusa" = 0,
                            "Planula" = Planula_currentyr,
                            "Period" = 3)

  return(Life_stages)
}

# Link as a year #

year <- function( Polyps_previousyr , survival_Polyps ,  transitionto_Polyps ,
                  reproductionto_Ephyra , transitionto_Medusa , reproductionto_Planula, Year) {

  Second_result <- Period2(Polyps_previousyr, reproductionto_Ephyra, survival_Polyps )

  Third_result <- Period3(Ephyrae_currentyr = Second_result$Ephyra, transitionto_Medusa , Polyps_currentyr =
                  Second_result$Polyps , survival_Polyps)

  Fourth_result <- Period4(Medusa_currentyr = Third_result$Medusa, reproductionto_Planula , Polyps_currentyr =
                  Third_result$Polyps , survival_Polyps)

  First_result <- Period1(Planula_currentyr = Fourth_result$Planula, Polyps_currentyr = Fourth_result$Polyps ,
                  survival_Polyps , transitionto_Polyps )

  year <- bind_rows(Second_result , Third_result , Fourth_result , First_result ) %>%
          mutate(Year)

  return(year)
}
```

```r
library(tidyverse)
#### Setting initial conditions ####
Population <- data.frame("Polyps" = 10,
                         "Ephyra" = 0,
                         "Medusa" = 0,
                         "Planula" = 0,
                         Period = 4,
                         Year = 0)
# Years to simulate
Years <- 15
# TEST - building vital rate data frame #
Vital_rate <- data.frame(survival_Polyps = rep(1, length.out = Years),
                         transitionto_Polyps = rep(0.1, length.out = Years),
                         reproductionto_Ephyra = rep(2, length.out = Years),
                         transitionto_Medusa = rep(0.05, length.out = Years),
                         reproductionto_Planula = rep(1.8, length.out = Years))


# META - building vital rate data frame #
library(truncnorm)
Vital_rate <- data.frame(survival_Polyps = rtruncnorm(mean= meta_results$Estimate[[2]],
                                              sd= meta_results$SD[[2]], n=Years, a=0),
                    transitionto_Polyps = rtruncnorm(mean= meta_results$Estimate[[1]],
                                                sd= meta_results$SD[[1]], n=Years, a=0),
                    reproductionto_Ephyra = rtruncnorm(mean= meta_results$Estimate[[3]],
                                                  sd= meta_results$SD[[3]], n=Years, a=0),
                    transitionto_Medusa =  rtruncnorm(mean= meta_results$Estimate[[4]],
                                                  sd= meta_results$SD[[4]], n=Years, a=0),
                    reproductionto_Planula =  rtruncnorm(mean= Averages$Mean[[5]], n=Years))


### Simulate a future ###
    Life.cycle <-  for (i in 1:Years) {

        cycle <- year(Polyps_previousyr = Population$Polyps[ i * 4 - 3 ],
                    survival_Polyps = Vital_rate$survival_Polyps[i],
                    transitionto_Polyps = Vital_rate$transitionto_Polyps[i],
                    reproductionto_Ephyra = Vital_rate$reproductionto_Ephyra[i],
                    transitionto_Medusa = Vital_rate$transitionto_Medusa[i],
                    reproductionto_Planula = Vital_rate$reproductionto_Planula[i],
                    Year = i)

        Population <- bind_rows(Population, cycle)
         }


Population <- Population %>%
  pivot_longer(Polyps:Planula, names_to = "Life_stage", values_to = "Population_size") %>%
  mutate(time_step = as.numeric(paste0(Year, ".", Period)))

print(Population)
```

*R code of the medusa-to-medusa model. First box contains the base functions of the model which is composed of the four functions for four periods and one function binding all four periods into one cycle. The second box contains settings for initial condition, the two simulation ran in this model (Test and meta-analysis) and a loop function, to simulate consecutive years.*

## Appendix IV – R Code: Polyp-to-medusa model

```r
### Polyp.to.Medusa Model ###


 Polyp.to.Medusa <- function(Polyps_pop, releaseof_Ephyra, transitionto_Medusa){


     Ephyrae_pop <- Polyps_pop * releaseof_Ephyra


     Medusa_pop <- Ephyrae_pop * transitionto_Medusa


     PM.Population <-  tibble("Polyps" = Polyps_pop,

                             "Medusa" = Medusa_pop,

                             "Ephyra Release rate" = releaseof_Ephyra,

                             "Ephyra Growth rate" = transitionto_Medusa)


  return(PM.Population)
 }




g <- rerun(.n = 1000,
 Polyp.to.Medusa(
   Polyps_pop = 10000,
   releaseof_Ephyra = rtruncnorm(mean = meta_results$Estimate[[3]],
                                 sd = meta_results$SD[[3]], n = 1, a = 0),
   transitionto_Medusa = rtruncnorm(mean= meta_results$Estimate[[4]],
                                 sd= meta_results$SD[[4]], n = 1, a = 0)))
 %>% bind_rows() %>% mutate(PGR = Medusa / Polyps )
```
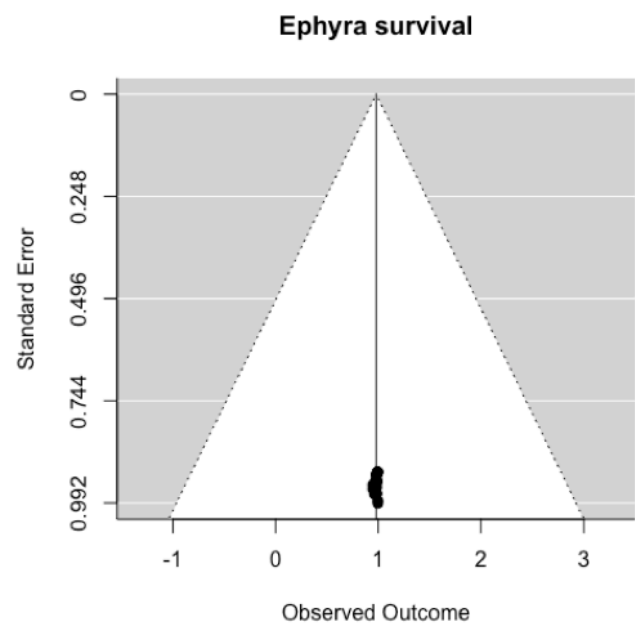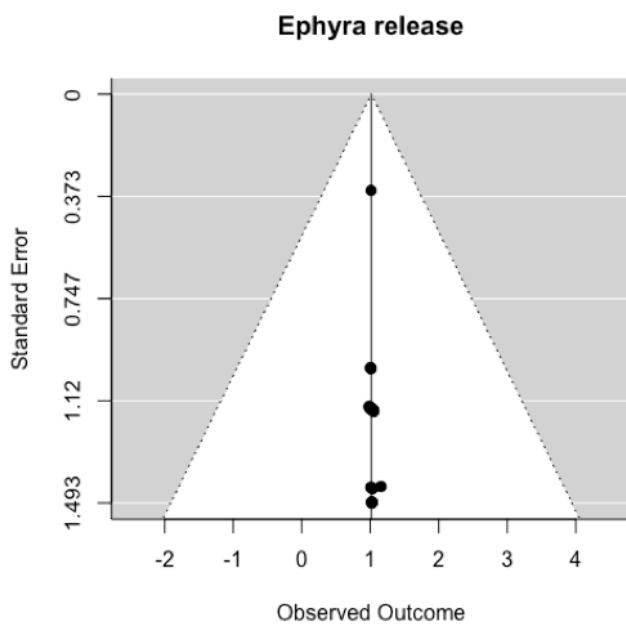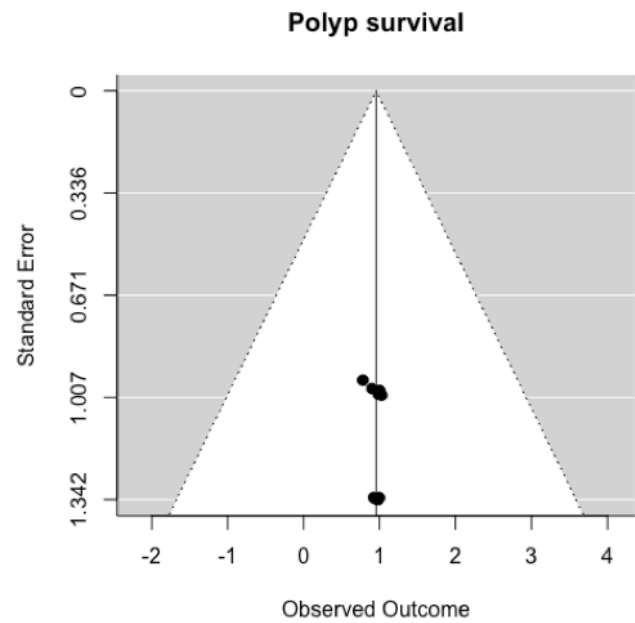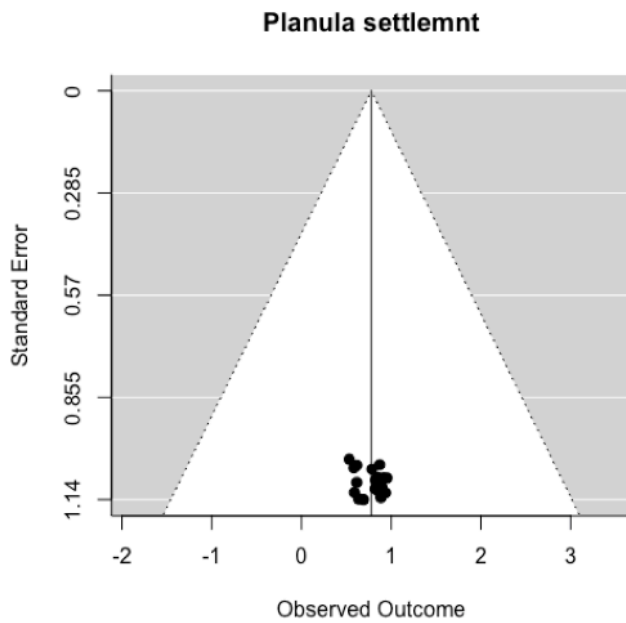
*R Code of the polyp-to-medusa model. This code is composed of one function representation the vital transition*

*Four funnel plots, representing the results of the four meta-analyses of their corresponding vital rates.*