



# Ecologie de *Rhizostoma pulmo* dans les mers du sud de l'Europe : De la biogéographie à la dynamique des populations

Valentina Leoni Silva

## ► To cite this version:

Valentina Leoni Silva. Ecologie de *Rhizostoma pulmo* dans les mers du sud de l'Europe : De la biogéographie à la dynamique des populations. Agricultural sciences. Université de Montpellier, 2022. English. NNT : 2022UMONG024 . tel-04131200

**HAL Id: tel-04131200**

**<https://theses.hal.science/tel-04131200v1>**

Submitted on 16 Jun 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Sciences de la Mer

École doctorale GAIA

Unité de recherche MARBEC (MARine Biodiversity, Exploitation and Conservation)

## Ecology of *Rhizostoma pulmo* in the southern European seas: From biogeography to population dynamics

Présentée par Valentina LEONI SILVA

Le 28 Juin 2022

Sous la direction de  
Juan Carlos MOLINERO et Delphine BONNET

Devant le jury composé de

Olivier MAURY, Directeur de recherche, IRD, Sète, France

Laura PRIETO, Chercheuse, CSIC, Cadiz, Espagne

Alenka MALEJ, Professeure, NIB, Ljubljana, Slovenia

Priscilla LICANDRO, Chercheuse, SZN, Naples, Italie

Juan Carlos MOLINERO, Directeur de recherche, IRD, Sète, France

Delphine BONNET, Maître de conférences, UM, Montpellier, France

Président du jury

Rapportrice

Rapportrice

Examinatrice

Directeur de thèse

Co-encadrante de thèse



UNIVERSITÉ  
DE MONTPELLIER











## ABSTRACT

Global changes have altered biogeography, phenology and abundance of marine populations, thereby promoting a reconfiguration of marine ecosystems' functioning. Increasing jellyfish blooms warn of major changes not only in ecosystem structure but also in their services and ultimately in human welfare. *Rhizostoma pulmo* is a large native scyphomedusa of the southern European seas, and in the last decade has gained notoriety due to massive bloom events. Underlying factors driving this phenomenon remain so far elusive, mainly due to the lack of knowledge on the species' ecology. The aim of this Ph.D. was to uncover drivers of the population dynamics and trophic ecology of *R. pulmo* through a multi-scale approach. To achieve it, three nested and complementary approaches were employed. The first one assessed, by means of data mining, environmental drivers shaping geographical patterns of bloom events on a long-term scale along the Mediterranean and Black Seas (7,359 records from 1875 to 2019). Secondly, the effect of biotic and abiotic factors on the dynamics of a *R. pulmo* population, and its trophic role along ontogeny were studied. To do so, an *in-situ* monitoring was performed during one year (2019) in Bages Sigean, a northwestern French Mediterranean lagoon. It is a natural mesocosm that offers the possibility to track the species on time, as all its life cycle occurs in the lagoon. For a deeper understanding of the processes behind the observed patterns, as a final step, these results were incorporated into a food web model. The 0D plankton food web model coupled low trophic level dynamics, based on a classical Nutrient Phytoplankton Zooplankton Detritus (NPZD) model, to copepods and a jellyfish model based on the pelagic life stages from ephyrae to large medusae.

The study showed that *R. pulmo* blooms exhibited an enhanced magnitude and frequency in recent decades, concurrently with positive temperature anomalies. The biogeographical patterns of the species appear also to be shaped by latitudinal temperature gradients, as northern locations with colder waters showed less intense blooms than southern warmer locations, where the most intense bloom events were recorded. Results uncovered a significant effect of warmer springs on phenological changes, which boosted an earlier start and a longer duration of the medusae season. An intersite comparison revealed different environmental niches in three Mediterranean lagoons, suggesting the existence of a metapopulation. At a local scale, three cohorts were identified during one year, and mesozooplankton abundance appeared to drive the population dynamics in the lagoon, evidencing a bottom-up control. Results showed that the diet composition differs from the availability of prey in the environment with contrasting preferences along ontogeny. Calanoid and harpacticoid copepods were the most frequent prey and the major carbon contributors for young medusae (bell diameter < 15 cm), whilst ciliates were the most frequent prey for large organisms (> 15 cm). Model simulations emphasized a leading effect of temperature on the bloom timing, while bloom development was promoted by food availability. These results bring an integrated overview of how multiscale environmental signals shape the ecology and population dynamics of *R. pulmo*. With jellyfish's broad diversity of forms, life strategies and trophic roles, we encourage future research to apply similar strategies in other species, that will allow identifying which species will increase in the future, and where.

## Keywords

Jellyfish • Scyphozoa • Mediterranean Sea • Climate change • Phenology • Trophic ecology

## RESUME

Les changements climatiques impactent la biogéographie, la phénologie et l'abondance des populations marines, favorisant une reconfiguration du fonctionnement des écosystèmes marins. L'augmentation des proliférations de méduses révèle des changements de la structure des écosystèmes, ainsi que de leurs services et par conséquent du bien-être des populations humaines. *Rhizostoma pulmo* est une scyphoméduse des mers du sud de l'Europe qui au cours des dernières années a montré des proliférations massives. Les facteurs sous-jacents à l'origine de ce phénomène restent jusqu'à présent inconnus en raison d'un manque de connaissances sur l'écologie de l'espèce. Le but de cette thèse a été de déterminer les facteurs écologiques contrôlant la dynamique de populations et l'écologie trophique de *R. pulmo*. Cela a été accompli en utilisant trois approches complémentaires à différentes échelles. Premièrement, les facteurs environnementaux qui façonnent les tendances géographiques des proliférations à long terme dans la Méditerranée et la mer Noire ont été évalués. Deuxièmement, les effets des facteurs biotiques et abiotiques sur la dynamique d'une population de *R. pulmo* et son rôle trophique tout au long de l'ontogenèse ont été étudiés. Pour ce faire, un suivi *in situ* a été réalisé pendant un an sur l'étang de Bages Sigeon, un écosystème semi-fermé qui offre la possibilité de suivre l'espèce pendant tout son cycle de vie. Finalement, ces résultats ont été intégrés dans un modèle dynamique de réseau trophique.

Les résultats obtenus ont montré que les proliférations de *R. pulmo* ont augmenté en intensité et fréquence au cours des dernières décennies, parallèlement à des anomalies de température positives. La biogéographie de l'espèce semble également être façonnée par les gradients de température latitudinaux, car les zones les plus au nord où les eaux sont plus froides ont montré des proliférations moins intenses que les zones les plus au sud où la température est nettement supérieure. Les résultats ont aussi révélé un effet significatif de la température printanière sur les changements phénologiques, favorisant un début plus précoce et une plus longue saison des méduses. Les différentes niches environnementales déterminées pour les populations de trois lagunes méditerranéennes suggèrent l'existence d'une métapopulation. À l'échelle locale, trois cohortes ont été identifiées au cours d'une année, et la disponibilité en nourriture semble être le facteur contrôlant la dynamique de la population. Les résultats ont montré que la composition du régime alimentaire diffère de la disponibilité des proies dans l'environnement, avec des préférences contrastées tout au long de l'ontogenèse. Les copépodes étaient les proies les plus fréquentes pour les jeunes méduses (diamètre de l'ombrelle < 15 cm), et les ciliés étaient préférés par les grandes méduses (> 15 cm). Les simulations du modèle ont souligné que la température influence le début de la prolifération et que son développement est contrôlé par la disponibilité de la nourriture. Ces résultats apportent une approche intégrée des effets de la variabilité environnementale sur l'écologie et la dynamique des populations de *R. pulmo* à de multiples échelles temporelles et spatiales. Face à l'extraordinaire diversité de formes, de stratégies de vie et de rôles trophiques des méduses, nous encourageons les recherches futures à appliquer des méthodes similaires sur d'autres espèces, ce qui permettra d'identifier les zones du globe et les espèces susceptibles de voir leur abondance augmenter à l'avenir.

## Mots clés

Méduse · Scyphozoaire · Méditerranée · Changement climatique · Phénologie · Ecologie trophique

## ACKNOWLEDGMENTS

Multiple organizations and people contributed to this research, and made it possible.

This research was funded by the National Agency of Research and Innovation from the Government of Uruguay (ANII), the Embassy of France in Uruguay and Campus France. I also acknowledge the funding support of the CIGOEF project.

Foremost, I would like to express my gratitude to my supervisors Juan Carlos and Delphine for their assistance at every stage of the research project. Thank you for welcoming me into your laboratory, for the work done together and for pushing me to improve in every aspect of my career.

Besides my supervisors, I would like to thank to my thesis supervision committee, François Bonhomme, Olivier Maury, Verónica Fuentes, and Agustín Schiariti, for their advice and their visible interest in improving this thesis.

I would like to extend my sincere thanks to all members of the Unité Mixte de Recherche ‘MARBEC’, the University of Montpellier (UM) and the École Doctorale GAIA for providing me a good working environment.

*Merci* to the nice MARBEC gang at the UM, for your welcome to the laboratory and the lovely and necessary work breaks: Juliette, Sunny, Raquel, Thibaut, Criscely, Tanguy, Laure, Fabien, Nico, Theo, Claire, Bea, Nacho, Cécile, Virginie, Marie-Charlotte, Justine, Elsa, Mariam, Thomas, Olga...Special thanks to Raquel, Thibaut, Criscely and Sunny for your friendship and support. Justine, thank you for the wonderful illustrations you designed for my thesis. Tanguy, it was a pleasure to share the office with you and to have interesting discussions in three-languages at the same time! Thanks to the admin staff, to Solange, Sandrine and Yann, and to the technician team from Montpellier and Sète, Fabien, Herve, Cécile, Nicolas, Elise and Sandrine, thank you for kind support.

Un grand merci à toi Sandrine, pour ta patience avec mon français, ton soutien en laboratoire et sur le terrain, ta belle curiosité pour la culture de mon pays et de partager la tienne avec moi. Merci pour ton amitié et pour partager le *mate* !

Special thanks to the jelly-hunters who help me at field, this study will not be possible without your support. I am also very thankful for the support of fishermen at the Bages Sigean lagoon, in particular to Stephane Marin for your readiness and for sharing your valuable knowledge on the lagoon in every ride. Thanks also to the staff from the École de Voile and from the Parc Naturel PNM.

I am deeply grateful to all students I worked with during these three years: Rubén, Marie, Lila, Noémie, Fanny, Johanna and Nathan. It was a pleasure to work and learn with you. Special thanks to Marie, for your enthusiasm and hard work during the long hours at field and in the lab.



My thanks also go to the lovely labmates at Laboratory of Oceanography of Villefranche sur Mer, to Amanda, Marc, Laëtitia and Katia, and to the staff in the Médusarium of Trocadero Aquarium in Paris, Anaïs and Guillaume.

Thanks to the beautiful international community of jelly-busters, in particular to Agustín Schiariti, André Morandini, Renato Nagata, Javier Quiñones and Vidal Haddad Junior, for sharing your valuable knowledge and passion for these fascinating organisms. Thanks Eduardo Ramírez-Romero for your support during my PhD and for invaluable modelling lessons.

Some may be surprised, but a brain can not work without a heart. Those who filled these years with encouragement, joy, friendship and love, also contributed to the successful performance of this thesis.

To my international family in France: Ixchel, Elvira, Criscely, Gastón, Anita, Agus, Natt, Carlos, Gus, Hans, Juli, Lucila (you all were my connection to Latin America!), Emma, Olivier, Lorinda, Dani, Davide, Manu, Ago, Nikos, Martin and Élise. Special thanks to Arnaud Bertrand and David Kaplan and his family. Thanks to all of you for your friendship and to provide me the necessary balance of life before, during and after the pandemic.

A mi familia española, a Tere y Gabriel, a mis cuñadas, cuñados, sobrinos y sobrinas, gracias por cuidarme como una más de su tribu. A Yera, Carla, Juancar, Rosalía, Hugo, Edi, Clara, Blanquita, gracias amigos por toda la alegría y el apoyo durante estos años.

A Uruguay y mi gente. Quiero agradecer a mis amigos que desde la distancia estuvieron siempre conmigo de diferentes maneras, PeCo, Mati, Eli, Nana, Javi, MaPi, Gabi, Gastón... A Fran, Romi, Vicky, Mai y Mei, por su amistad incondicional, expresada entre mates, charlas a distancias y días enteros de 'pomodoros'. También quiero agradecer a mi referente y amigo Fabrizio Scarabino, quien siempre impulsó las ciencias marinas en nuestro país y me motivó a estudiar el zooplancton gelatinoso.

A mi familia, mis padres, a Sofi, Andre, Pablo y Hernán, por ser mi puerto seguro a donde llegar siempre. Mamá, papá, gracias por darme la oportunidad de estudiar que ustedes no tuvieron. Sin todos ustedes no hubiera llegado hasta aquí. Gracias abuela, tíos, tías y 'postis', que siempre están allí acompañándome.

A los soles de mi vida, Joaquín y Thao, por llenar mis días de colores y sonrisas.

A mi compañero de vida, Alejandro Ariza. Sería demasiado largo nombrar todas las razones por las que quisiera agradecerte. Simplemente decirte que este trabajo fue posible gracias a tu apoyo, y a la serenidad que me transmites para hacer frente a todas las tormentas. Gracias por todo el amor, la comprensión, y, sobre todo, por confiar en mí.



*A mis padres, Fanny y Ricardo, por el amor, sacrificio y dedicación a nuestra familia, y  
nunca poner límites a nuestros sueños.*



## RESUME EN FRANÇAIS

### Chapitre 1. Introduction générale

Dans les écosystèmes marins, le réchauffement climatique, la surpêche et les modifications des habitats ont induit divers types de réponses biologiques (Sage 2020). Les plus fréquentes sont des changements biogéographiques, des variations phénologiques (Poloczanska et al. 2016) et de l'abondance des populations. Alors que 40% des populations d'animaux marins ont diminué entre 1970 et 2010, principalement à cause de la surpêche et de la perte d'habitat (WWF 2014), certaines espèces opportunistes ont été favorisées par les perturbations environnementales et ont vu leur abondance augmenter (Atkinson et al. 2004). Cette augmentation d'abondance est particulièrement évidente lorsque des populations impactant les activités humaines sont impliquées, comme pendant les proliférations d'algues toxiques (Fu et al. 2012) ou de certaines espèces de zooplancton gélatineux (Mills 2001).

Le zooplancton gélatineux comprend des espèces de divers phylums qui sont composées principalement d'eau. Parmi elles, les espèces de cnidaires présentent un stade pélagique au cours de leur cycle de vie (Phylum Cnidaria; Subphylum Medusozoa) — méduses— et représentent 92% de la biomasse gélatineuse mondiale (Lucas et al. 2014). Certaines espèces de méduses peuvent former de grandes accumulations de biomasse, un phénomène appelé 'proliférations'. Diverses activités économiques, comme la pêche, l'aquaculture, les installations de l'industrie côtière et les activités touristiques, sont gênées par ces proliférations qui entraînent des pertes économiques importantes (Kim et al. 2012). Cependant, ces événements peuvent aussi favoriser l'économie, à travers l'exploitation de cette ressource, soit comme nourriture (Youssef et al. 2019), soit pour le tourisme (Purcell et al. 2007 ; Dawson et al. 2001 ; Graham et al. 2014). Néanmoins, les impacts des méduses ne sont liés qu'à un petit nombre d'espèces (environ 10% de la diversité totale), puisque peu d'entre elles sont capables de former des densités de population aussi élevées (Hamner and Dawson 2009).

Des études récentes ont montré que certaines zones côtières sont davantage confrontées à une augmentation de ces populations que d'autres (Brotz et al. 2012 ; Condon et al. 2013). La mer Méditerranée est considérée comme un point chaud de la biodiversité non seulement par le nombre d'espèces qui y habitent, mais aussi parce qu'elle fait partie des régions les plus impactées par les activités anthropiques dans le monde (Coll et al. 2012). Sur ces côtes, l'augmentation de certaines populations de méduses est un vrai problème. Bien que les

pressions anthropogéniques soient probablement à l'origine de ces changements (Purcell 2012), il n'existe que très peu d'explications mécanistiques sur la façon dont l'environnement force la dynamique des populations de méduses durant leur cycle de vie (Pitt et al. 2018). Comme les proliférations sont des événements démographiques mono-spécifiques, plusieurs auteurs ont suggéré d'évaluer les réponses aux perturbations environnementales au niveau de l'espèce (Pitt et al. 2018), plutôt que de mener une approche plurispécifique.

*Rhizostoma pulmo* (Macri, 1778) est l'une des plus grandes (diamètre d'environ 40 cm) et communes méduses qui prolifère dans les mers du sud de l'Europe, et l'une des six espèces considérées comme une nuisance (Kokelj and Plozzer 2002). La grande taille, la consistance des ombrelles et les événements d'agrégation massive ont suscité l'intérêt pour cette méduse en tant que ressource alimentaire pour les humains (Youssef et al. 2019). Ces dernières années, la fréquence et l'intensité des proliférations de l'espèce ont augmenté dans de nombreuses zones côtières de la Méditerranée et de la mer Noire (Tinta et al. 2012 ; Stabili et al. 2018 ; Dönmez and Bat 2019 ; De Domenico et al. 2019 ; Basso et al. 2019), mais les origines de ce phénomène restent hypothétiques, à cause notamment d'un manque de connaissances sur ses traits d'histoire de vie et sur son écologie trophique.

Cette thèse propose une approche intégrale sur l'écologie des méduses, intégrant les réponses fonctionnelles telles que la croissance, les niches thermiques et la phénologie, ainsi que les interactions trophiques, pour quantifier le rôle de ces organismes dans les réseaux trophiques planctoniques. Une synthèse de données historiques et contemporaines sur l'abondance de *R. pulmo*, à partir de la littérature scientifique et de données de programmes de science participative, a permis de caractériser la biogéographie et la phénologie de l'espèce à l'échelle du bassin méditerranéen. Pour comprendre cette configuration spatio temporelle, une étude locale a été réalisée pendant une année (2019) sur la population de *R. pulmo* dans la lagune de Bages Sigeon (France) où l'espèce réalise l'ensemble de son cycle de développement. Enfin, ces résultats ont permis de développer un modèle trophique afin de comprendre les processus qui régulent ces populations et d'évaluer le possible devenir de la population dans le cadre de futurs scénarios de changement climatique. Ce faisant, nous avons tenté de décrypter les processus écologiques de l'espèce, dans le but de mieux comprendre le développement des blooms et leur impact dans la dynamique du réseau trophique.



## Chapitre 2. Biogéographie et phénologie de *R. pulmo* dans les mers du sud de l'Europe (Article 1)

Les observations à long terme des espèces et des populations naturelles sont essentielles pour comprendre comment elles s'adaptent à l'environnement et pour quantifier les effets possibles du changement climatique. De nos jours, grâce à des outils d'intelligence artificielle et à la modélisation, un grand nombre d'études à l'échelle mondiale sur la biogéographie (Deutsch et al. 2020), la phénologie (Harrison et al. 2018) et les prédictions de la distribution des espèces marines et des changements de biomasse (par exemple, Bryndum-Buchholz et al. 2019 ; Lotze et al. 2019) a été réalisé. Néanmoins, le manque de données historiques sur les méduses entrave la possibilité de déterminer si les abondances et la phénologie des espèces ont subi des changements dans le temps. De plus, les études d'une espèce de méduse en particulier sur toute son aire de répartition sont rares (Goy et al. 1989 ; Hardinge 2019).

Depuis 1970, de nombreuses régions de la mer Méditerranée ont montré une augmentation de l'abondance des méduses (Condon et al. 2013), modifiant fortement les activités humaines dans les zones côtières (Halpern et al. 2008). Pour cette raison, l'objectif de ce chapitre a été de tester, sur l'espèce *R. pulmo*, les hypothèses actuelles reliant la dynamique des méduses au réchauffement et à l'eutrophisation. Des données historiques et contemporaines de *R. pulmo* sur toute son aire de répartition -la mer Méditerranée et la mer Noire- au cours des deux derniers siècles ont été rassemblées, soit un total de 7359 données de 1875 à 2019. Des modèles statistiques généralisés ont été utilisés pour évaluer l'influence des gradients thermique (latitudinal) et de productivité (longitudinal) sur la biogéographie et la phénologie de l'espèce.

L'abondance et fréquence d'apparition de *R. pulmo* ont augmenté au cours des dernières décennies, parallèlement à une élévation significative de la température. Ces résultats suggèrent que cette espèce tire profit de températures plus chaudes. Les proliférations ont été observées entre 15 et 22°C, mais elles sont plus abondantes entre 20 et 21°C. Il a été démontré en conditions expérimentales chez *R. pulmo* et d'autres scyphoméduses, que des températures élevées induisaient une augmentation du taux de libération des éphyrules, ainsi qu'une augmentation du taux de croissance et de reproduction sexuée des méduses (Lucas et al. 2012 ; Purcell et al. 2012a ; Marques et al. 2019). Toutefois, l'hypothèse d'une phase ascendante d'une oscillation de la dynamique de populations de méduses a aussi été émise pour expliquer la perception actuelle d'une augmentation mondiale des méduses (Condon et al. 2013). Bien que nous n'écartions pas cette hypothèse, l'augmentation des proliférations observées, en lien avec une accélération des changements environnementaux dans les mers du sud de l'Europe

(c'est-à-dire la température, les événements climatiques extrêmes, la pollution, la disponibilité du substrat ; Lejeusne et al. 2010), pourrait laisser penser qu'une augmentation plus importante que prévue par cette oscillation pourrait avoir lieu pour *R. pulmo*. Nous avons aussi constaté que le gradient latitudinal de température, mais pas celui de la productivité, façonnait l'intensité des proliférations sur le long terme et la biogéographie de l'espèce.

En plus d'une augmentation de la fréquence et de l'intensité des proliférations, pendant une période de 10 ans (2008-2018), un effet significatif de la température printanière a été détecté sur la phénologie de l'espèce. Les printemps plus chauds favorisent une durée plus longue de la saison des méduses, passant de 5 à 7 mois. Cela pourrait résulter de plusieurs processus agissant sur les premiers stades de vie, avec une strobilation plus tôt dans l'année, tel que cela a été observé chez *Aurelia* spp. et chez *R. pulmo* dans des conditions expérimentales (la période avant la strobilation passe de 85,5 jours à 14°C à 9,5 jours à 28°C ; Purcell et al. 2012b). Des températures chaudes peuvent aussi accélérer le métabolisme des méduses, et par conséquent leur taux de croissance. Par exemple, pendant les années de printemps les plus chauds, les proliférations apparaissent plus tôt dans la colonne d'eau (5,9 jours/an). Ces résultats sont similaires aux observations faites chez d'autres méduses, pour lesquelles le principal changement phénologique observé est un démarrage plus tôt dans l'année, attribué à une augmentation de la température hivernale ou printanière (Van Walraven et al. 2015 ; D'Ambrosio et al. 2016). Ces changements phénologiques ont cependant montré des disparités entre les régions méditerranéennes : d'une part par un changement de température différent entre les régions, comme le réchauffement plus élevé dans le nord-ouest que dans le sud-est (Lejeusne et al. 2010 ; Salgado-Hernanz et al. 2019) et d'autre part, ces différences peuvent être liées à des populations isolées, adaptées à différentes conditions environnementales, c'est-à-dire, à une métapopulation (Ben Faleh et al. 2017 ; Mizrahi et al. 2021).

Parmi les hypothèses expliquant les variations d'abondance de méduses par les perturbations anthropiques, seule l'hypothèse basée sur le réchauffement a été confirmée sur de larges échelles spatio-temporelles pour *R. pulmo*, tandis que l'hypothèse du rôle de l'eutrophisation semble être validée principalement à des échelles locales. Cependant, même si ces dernières années des efforts substantiels ont été déployés pour déterminer l'effet de l'environnement sur le cycle de vie des méduses, la compréhension des forçages interagissant sur la dynamique des populations de *R. pulmo* n'a pas encore été suffisamment étudiée.

### **Chapitre 3. Variabilité des taux de croissance et des niches thermohalines de *R. pulmo* (Article 2)**

Comprendre la dynamique de populations des espèces est fondamental pour identifier les processus structurant les communautés. Cela inclut l'évaluation de leurs taux de croissance et des interactions interspécifiques, comme la compétition ou la prédation (Hastings 2013). En effet, ces informations de base sont nécessaires pour concevoir des plans de conservation, ou lorsqu'il s'agit d'espèces d'intérêt commercial, pour une bonne gestion de la ressource.

Chez les Medusozoaires, les éphyrules libérées et transformées en méduses, grandissent rapidement. L'estimation de la croissance des méduses est difficile en raison des limites techniques de leur collecte, de leur manipulation ou de leur fixation (Purcell 2009). Ainsi, la plupart des estimations de croissance ont été réalisées dans des conditions de laboratoire (par exemple, Astorga et al. 2012 ; Acevedo et al. 2013). De plus, l'une des caractéristiques de ce groupe est l'apparition imprévisible de ses populations (Ceh et al. 2015) et la présence de plusieurs cohortes pendant une année (Fernández-Alías et al. 2020). Ces deux paramètres soulignent l'importance des études de dynamique de population pour mieux comprendre la persistance des proliférations. Par ailleurs, dans un contexte de changement global, la détermination des niches environnementales et des taux de croissance est essentielle pour comprendre la plasticité des espèces dans des écosystèmes marins en évolution. Cependant, les facteurs favorisant ces populations et la façon dont les conditions environnementales affectent les taux de croissance et de mortalité ne sont toujours pas bien compris pour la plupart des espèces. L'objectif principal de ce chapitre a été de déterminer la dynamique d'une population de *R. pulmo*, et d'évaluer comment les taux de croissance et les niches environnementales varient dans le temps et entre des populations ou sous-populations méditerranéennes.

Nos résultats ont montré que les niches thermohalines varient au cours de l'ontogenèse, mais aussi entre les populations de trois lagunes côtières méditerranéennes: Bages Sigeon (France), Mar Menor (Espagne) et Bizerte (Tunisie). Ben Faleh et al. (2017) ont distingué trois lignées phylogénétiques, c'est-à-dire trois populations, dans le nord de l'Adriatique, l'ouest de la Méditerranée et la côte tunisienne. La différenciation génétique détectée pourrait être attribuée à des barrières intrinsèques et/ou extrinsèques à l'échange génétique entre des populations qui pourraient s'être adaptées à différentes conditions environnementales. Cette étude est la première à comparer des niches environnementales entre les populations de *R. pulmo*, suggérant l'existence possible d'une métapopulation.

La dynamique saisonnière de *R. pulmo* dans la lagune de Bages Sigean en 2019 a été caractérisée par un pic d'abondance ( $19,1 \text{ ind } 100\text{m}^{-3}$ ) des méduses au printemps (avril) et une disparition totale en hiver (novembre), tandis que la population a atteint une biomasse maximale ( $10,2 \text{ g m}^{-3}$ ) en été (juillet). Cette dynamique corrobore les observations antérieures dans la lagune de Mar Menor et sur la côte espagnole (Fuentes et al. 2011 ; Fernández-Alías et al. 2020). De multiples cohortes, sur une base annuelle, ont été identifiées, la première débutant en avril, la deuxième en mai et la troisième juin 2019. Des observations similaires signalant un recrutement multi-cohorte ont été faites pour cette espèce en Mar Menor en 1997, où quatre cohortes ont été déterminées (Fernández-Alías et al. 2020). Dans la lagune de Bages Sigean en 2019, nous avons observé un pic de juvéniles en début d'année sans avoir collecté d'éphyrules, ceci pourrait correspondre à l'initiation d'une cohorte supplémentaire, ce qui porterait à quatre le nombre de cohortes dans cette lagune.

Sur la base d'une analyse multinomiale et en utilisant le modèle de von Bertalanffy, nous avons déterminé le taux de croissance pour les deux premières cohortes, car nous n'avons pas assez de données pour la troisième. Dans les deux cas, le taux de croissance était plus élevé chez les juvéniles (individus sans gonades et de diamètre  $< 15 \text{ cm}$ ) (cohorte 1 :  $4,7$  et cohorte 2 :  $2,4 \text{ mm jour}^{-1}$ ) que chez les adultes (individus avec gonades et de diamètre  $> 15 \text{ cm}$ ) (cohorte 1 :  $1,8$  et cohorte 2 :  $0,9 \text{ mm jour}^{-1}$ ). En effet, chez les adultes, une partie de l'énergie est affectée à la reproduction. La première cohorte a montré un taux de croissance plus élevé que la seconde, et la taille maximale atteinte par les adultes de la deuxième cohorte a été inférieure ( $24 \text{ cm}$ ) à celle des adultes de la première ( $34 \text{ cm}$ ). La saisonnalité de la communauté zooplanctonique de la lagune pourrait ainsi expliquer cette différence entre les cohortes, mais aussi la taille maximale de ces adultes.

Pour *R. pulmo*, les processus de 'bottom-up' semblent être les principaux moteurs de la dynamique de population à Bages Sigean, comme suggéré par d'autres études sur les Rhizostomeae (Addad et al. 2008 ; Fernández-Alías et al. 2020 ; Xie et al. 2021). À Bages Sigean, les abondances de copépodes jouent un rôle clé dans la prolifération de *R. pulmo*. L'amélioration des connaissances sur le régime alimentaire de l'espèce est nécessaire pour évaluer non seulement le rôle de la communauté planctonique dans la dynamique de l'espèce, mais également la pression de prédation de *R. pulmo* sur le réseau trophique tout au long de son cycle de vie.

## Chapitre 4. Changements ontogénétiques alimentaires de la méduse *R. pulmo* (Article 3)

De plus en plus d'études mettent en évidence les processus de '*bottom-up*' comme moteurs centraux de la dynamique des populations de méduses, c'est-à-dire, que la nourriture est un facteur clé et limitant pour les stades benthiques et pélagiques (Rosa et al. 2013 ; Marques et al. 2015b). Divers travaux soutiennent l'idée que, dans de futures conditions eutrophes et plus chaudes, la communauté planctonique passera d'un écosystème dominé par les diatomées, les copépodes et les poissons à un état alternatif où les flagellés, le microzooplancton et les méduses domineront (Parsons and Lalli 2002 ; Richardson et al. 2009 ; Uye 2011). Cependant, la plupart des régimes alimentaires des méduses sont encore inconnus (Nagata 2015), et très peu d'études se sont intéressées aux relations trophiques des méduses durant leur croissance pour identifier une variabilité ontogénétique dans l'alimentation (Álvarez-Tello et al. 2016). La grande diversité morphologique des structures et des stratégies d'alimentation des méduses rend la prévision de la réponse trophique de ces populations encore plus complexe.

Ce chapitre a eu comme objectif d'étudier le régime alimentaire de *R. pulmo* tout au long d'une année à partir de contenus stomacaux, parallèlement à l'analyse des abondances des proies potentielles dans le milieu. Les objectifs spécifiques étaient de décrire la diversité et la taille des proies, d'identifier s'il y avait des changements ontogénétiques et des préférences alimentaires, et de quantifier leur impact sur le réseau trophique. Pour cela, le régime alimentaire de 127 méduses de tailles comprises entre 0,95 et 34,00 cm de diamètre a été évalué. Cette étude est la première à détailler le régime alimentaire de l'espèce pendant une année, sur différentes tailles de méduses.

Les résultats ont montré que l'espèce se nourrit sur différents niveaux du réseau trophique, notamment des ciliés (20,8%) et des copépodes (22,8%), en cohérence avec l'étude menée en mer Noire (Dönmez and Bat 2019). Malgré la large gamme de taille des proies (45 à 9000  $\mu\text{m}$ ) observée, 80% des proies avaient une taille comprise entre 165 et 240  $\mu\text{m}$ . La taille des proies varie significativement entre les méduses juvéniles et les adultes (Kruskal-Wallis,  $p < 0.001$ ), les juvéniles se nourrissant de plus grandes tailles ( $385 \pm 190 \mu\text{m}$ ) que les adultes ( $136 \pm 60 \mu\text{m}$ ). Dans l'ensemble, ces tailles de proies ne sont pas surprenantes compte tenu de la petite taille des orifices alimentaires ( $< 3000 \mu\text{m}$ ) des Rhizostomeae (Dawson and Hamner 2009).

Le régime alimentaire de l'espèce diffère en fonction de la disponibilité des proies dans le milieu naturel, avec des préférences contrastées durant l'ontogenèse. Les copépodes



calanoïdes (70%) et harpacticoïdes (45,8%) sont les proies les plus fréquentes et les principaux contributeurs en carbone pour les petites méduses (< 15 cm). En revanche, les ciliés (43,5%) sont les proies les plus fréquentes pour les grands spécimens (> 15 cm), qui, avec les œufs de poisson, ont constitué la majeure partie de la teneur en carbone du contenu stomacal. Nos résultats sont en accord avec ce qui a été observé précédemment chez d'autres espèces de méduses, pour lesquelles un certain degré de sélectivité a été détecté. Cependant, d'autres études, à une échelle plus fine, sont nécessaires pour comprendre les mécanismes sous-jacents de cette sélectivité (par exemple, la composition en nématocystes, la vitesse des micro-courants), ainsi que les processus qui conduisent à une diversification de l'alimentation entre les stades de développement.

Nous avons estimé que les petites méduses pouvaient consommer 5% du stock quotidien de copépodes, tandis que les grandes méduses consommaient 8% du stock quotidien de ciliés. Ces résultats sont proches des valeurs rapportées pour *Lychnorhiza lucerna*, pour laquelle une consommation de 6 à 12% du stock de copépodes par jour a été estimée (Nagata and Morandini 2018), mais restent inférieurs aux estimations faites pour *Nemopilema nomurai* (24% du stock de mésozooplancton consommé par jour ; Uye 2008). Les estimations sur les Semaestomeae présentent aussi une large variabilité, allant de moins de 3% (Purcell 2003) à 21% des stocks de crustacés consommés par jour (Gueroun et al. 2020). Malgré ces différences, nous avons observé que les adultes de *R. pulmo* consommaient des pourcentages plus faibles de copépodes que les juvéniles. Ces résultats soulignent que la pression de prédation de certaines espèces de méduses sur les copépodes pourrait n'être importante que pendant les premiers stades pélagiques. Nos résultats montrent que *R. pulmo* participe à différentes voies trophiques tout au long de son ontogénie ; la méduse interagit d'abord avec le réseau trophique classique, puis passe à une plus grande interaction avec la boucle microbienne.

Les observations sur (i) la température et la phénologie de l'espèce (Chapitre 2), et sur (ii) la dynamique de la population et la disponibilité de la nourriture (Chapitre 3) sont principalement des études corrélatives qui, bien qu'utiles pour générer des hypothèses, ne peuvent pas attribuer de causalité. D'autre part, la compréhension détaillée de l'écologie trophique de l'espèce (Chapitre 4) nous a permis de mieux décrire comment l'espèce interagit avec son environnement au cours de sa vie pélagique. Les corrélations entre les variables environnementales et la dynamique des populations peuvent être testées avec une approche de modélisation du réseau trophique afin d'obtenir une compréhension mécanistique de ces observations.

## Chapitre 5. Modélisation d'un réseau trophique planctonique incluant la dynamique de populations de *R. pulmo* dans des conditions de réchauffement (Article 4)

De grands efforts ont été faits pour comprendre comment l'environnement affecte les proliférations de méduses, en particulier à partir d'expériences de laboratoire *in vivo* (Prieto et al. 2010 ; Purcell et al. 2012 ; Treible and Condon 2019 ; Enrique-Navarro et al. 2021) ou de simulations de modèles. Cependant, les modèles de dynamique de populations sont souvent limités à quelques espèces emblématiques (Malej and Malej 1992 ; Henschke et al. 2018 ; Alekseenko et al. 2019). A notre connaissance, seuls deux modèles de dynamique de population ont été développés pour des espèces de Rhizostomeae ; chez *Cotylorhiza tuberculata* et *N. nomurai* (Ruiz et al. 2012 ; Xie et al. 2021). Au cours des dernières décennies, le réchauffement en Méditerranée a favorisé une augmentation de l'abondance de la méduse *R. pulmo* (Leoni et al. 2021a). Leur impact négatif sur la pêche et les activités touristiques alarme sur la réponse potentielle de cette espèce dans les scénarios de réchauffement prévus.

En utilisant des données collectées à partir d'un suivi régulier de l'hydrologique et de la communauté planctonique sur une année (Leoni et al. 2021b), ainsi que les données de la littérature, le premier objectif de ce chapitre était de représenter la dynamique de populations de *R. pulmo* au sein du réseau trophique dans l'étang de Bages Sigeon. Pour ce faire, un modèle 0D de réseau trophique planctonique initialement développé pour la scyphoméduse *Aurelia aurita* dans le fjord de Kiel (Ramirez-Romero et al. 2018) a été ajusté à *R. pulmo*. Le modèle comprend des nutriments à la dynamique des méduses dans l'écosystème. Les niveaux trophiques inférieurs ont été simulés avec un modèle NPZD classique (Fasham et al. 1990 ; Fennel 2001), couplé à un modèle de résolution du stade de développement des méduses, qui était représenté ici par les éphyrules, les méduses juvéniles et les méduses adultes de *R. pulmo*. Dans un deuxième temps, nous avons exploré la réponse de la communauté planctonique sous deux scénarios différents de réchauffement projetés pour la fin du 21<sup>ème</sup> siècle : une augmentation modérée (+0,3°C) et forte (+4,8°C) de la température prévue par le Groupe d'Experts Intergouvernemental sur l'évolution du Climat (GIEC). En raison de l'effet positif du réchauffement sur l'intensité des proliférations de *R. pulmo* (Leoni et al. 2021a), nous avons émis l'hypothèse que l'intensité des proliférations de cette méduse augmenteront et que cette dernière modifiera sa saisonnalité dans les deux scénarios futurs.

Dans l'ensemble, le modèle a capturé la dynamique de la communauté planctonique dans l'étang de Bages Sigeon pour tous les groupes de proies, à la fois en magnitude et en

nombre de pics de biomasse tout au long de l'année. Les données *in situ* pour *R. pulmo* ont montré une abondance maximale de 17,5 ind. 100m<sup>-3</sup> pour les méduses juvéniles et 1,0 ind. 100m<sup>-3</sup> pour les adultes. Dans la simulation, les abondances étaient dans le même ordre de magnitude pour les juvéniles (15,0 ind. 100m<sup>-3</sup>), et pour les adultes (3,5 ind. 100m<sup>-3</sup>), et la superposition des cohortes observées *in situ* a été simulée. Le pic de biomasse des méduses *in situ* (34,8 mgC m<sup>-3</sup>) a été observé en août, au même moment que dans les simulations, et dans le même ordre de magnitude (35,1 mgC m<sup>-3</sup>). Bien que les pics de biomasse observés tout au long de l'année n'aient pas été capturés dans la simulation, l'allure générale de la courbe des adultes a été retranscrite par la simulation, à savoir un début d'apparition des adultes, un pic de biomasse et une fin de leur présence dans la colonne d'eau. L'absence de plusieurs pics de biomasse dans le modèle était attendue en raison de la forte variabilité des estimations de la biomasse des méduses *in situ* liée à leur distribution hétérogène dans l'environnement. Dans l'ensemble, les simulations capturent la saisonnalité de *R. pulmo*, avec les abondances maximales et les biomasses maximales au cours de la même période, mais avec un schéma plus assoupli.

Dans les deux scénarios de réchauffement, les simulations ont montré une prolifération plus précoce. Le pic de biomasse se produit 10 jours avant, et environ un mois avant sous les scénarios d'augmentation modérée et forte de la température, respectivement, en comparaison avec 2019. Cependant, cette progression n'a pas été accompagnée d'abondances plus élevées. Au contraire, l'abondance maximale a diminué pour les éphyrules jusqu'à des valeurs inférieures à 10 ind. 100m<sup>-3</sup> en raison d'une augmentation de la mortalité. De plus, le pic de biomasse de méduses a diminué avec l'augmentation de la température, atteignant un minimum de 25,5 mgC m<sup>-3</sup> dans le scénario le plus chaud.

Cette étude a montré que la dynamique de la population de *R. pulmo* est principalement déterminée par la variabilité saisonnière de la température et la dynamique des proies. Cependant, notre modèle a prédit une augmentation du taux de mortalité des éphyrules et une réduction de l'abondance de *R. pulmo* dans le scénario le plus pessimiste. Alors que pour *R. pulmo* les mécanismes sous-jacents commencent à peine à être compris, notre modèle combiné aux projections climatiques, indique qu'un réchauffement des eaux méditerranéennes pourrait entraîner d'importants changements phénologiques des méduses d'ici la fin du siècle. Néanmoins, nos résultats reposent sur l'hypothèse que les conditions thermiques optimales pour l'espèce restent inchangées, ce qui sera probablement modifié en raison des capacités d'adaptation et d'acclimatation de l'espèce.

## Conclusion

Dans cette thèse, nous avons mis en évidence la diversité des réponses et des facteurs affectant l'écologie d'une espèce de méduse à différentes échelles. Dans l'ensemble, la température a été identifiée comme un facteur clé affectant la distribution, l'intensité et la fréquence des proliférations, ainsi que le moment de l'occurrence de *R. pulmo*. La disponibilité en nourriture a également été reconnue comme un facteur clé dans le développement des proliférations, et la coexistence de plusieurs cohortes au cours d'une année semble être favorisée par les changements alimentaires ontogénétiques subis par *R. pulmo*. Bien que l'espèce semble prospérer dans des conditions plus chaudes, des changements climatiques intenses et rapides peuvent être nuisibles à l'espèce. Son succès sera finalement déterminé par la capacité d'adaptation de l'espèce aux eaux plus chaudes ainsi que par sa flexibilité dans l'acquisition de nourriture dans des eaux hautement eutrophes ou stratifiées. La complexité observée pour une seule espèce souligne la nécessité de mener des recherches spécifiques à l'espèce pour identifier celles qui pourraient augmenter leurs abondances à l'avenir, et où. Ce faisant, des informations plus précises sur l'évolution des épisodes de proliférations des méduses seront obtenues, influençant le développement de mesures d'atténuation précises pour réduire leurs impacts futurs.





## TABLE OF CONTENT

<b>ABSTRACT</b> .....	<b>I</b>
<b>RÉSUMÉ</b> .....	<b>II</b>
<b>ACKNOWLEDGMENTS</b> .....	<b>III</b>
<b>RESUME EN FRANÇAIS</b> .....	<b>1</b>
<b>PUBLICATIONS</b> .....	<b>15</b>
<b>CHAPTER 1. GENERAL INTRODUCTION</b> .....	<b>17</b>
1.1   GLOBAL OCEAN UNDER ANTHROPOGENIC PRESSURES .....	19
1.1.1. <i>Biological responses to global change</i> .....	20
1.2   GELATINOUS ZOOPLANKTON .....	22
1.2.1. <i>Jellyfish populations in a changing ocean</i> .....	24
1.2.2. <i>Scyphomedusae bloom forming: current gaps</i> .....	27
1.3   JELLYFISH BLOOMS: A CHALLENGE FOR THE MEDITERRANEAN SEA.....	33
1.3.1. <i>Rhizostoma pulmo in the Mediterranean Sea</i> .....	35
1.4   OBJECTIVES.....	39
<b>CHAPTER 2. BIOGEOGRAPHY AND PHENOLOGY OF RHIZOSTOMA PULMO IN SOUTHERN EUROPEAN SEAS ..</b>	<b>41</b>
2.1   INTRODUCTION .....	45
2.2   METHODOLOGY .....	47
2.3   RESULTS .....	53
2.4   DISCUSSION.....	62
2.5   CONCLUSIONS .....	68
SUMMARY POINTS .....	69
<b>CHAPTER 3. VARIABILITY OF GROWTH RATE AND THERMOHALINE NICHES OF RHIZOSTOMA PULMO'S PELAGIC STAGES</b> .....	<b>71</b>
3.1   INTRODUCTION .....	75
3.2   METHODOLOGY .....	77
3.3   RESULTS .....	84
3.4   DISCUSSION.....	92
3.5   CONCLUSIONS .....	96
SUMMARY POINTS .....	98
<b>CHAPTER 4. ONTOGENETIC DIETARY SHIFTS OF THE MEDUSA RHIZOSTOMA PULMO</b> .....	<b>99</b>
4.1   INTRODUCTION .....	103
4.2   METHODOLOGY .....	105
4.3   RESULTS .....	109
4.4   DISCUSSION.....	117
4.5   CONCLUSIONS .....	121
SUMMARY POINTS .....	122
<b>CHAPTER 5. MODELLING A PLANKTONIC FOOD WEB INCLUDING THE POPULATION DYNAMICS OF RHIZOSTOMA PULMO UNDER A WARMING OCEAN</b> .....	<b>123</b>
5.1   INTRODUCTION .....	127
5.2   METHODOLOGY .....	129
5.3   RESULTS .....	138

5.4   DISCUSSION .....	143
5.5   CONCLUSIONS .....	147
SUMMARY POINTS .....	148
<b>CHAPTER 6. GENERAL DISCUSSION AND FUTURE DIRECTIONS.....</b>	<b>149</b>
6.1   UNDERSTANDING JELLYFISH BLOOMS REQUIRES A MULTISCALE APPROACH .....	151
6.2   MULTIPLE RESPONSES IN A CHANGING OCEAN.....	152
6.3   UNRESOLVED QUESTIONS AND WAYS FORWARD.....	156
6.4   CONCLUSION .....	158
<b>SUPPLEMENTARY INFORMATION .....</b>	<b>159</b>
<b>REFERENCES.....</b>	<b>165</b>

## PUBLICATIONS

- Article 1. LEONI V.,** Bonnet D., Ramírez-Romero E., Molinero J.C. (2021) Biogeography and phenology of the jellyfish *Rhizostoma pulmo* (Cnidaria: Scyphozoa) in southern European seas. *Global Ecology and Biogeography* 30: 622–639. <https://doi.org/10.1111/geb.13241>
- Article 2. LEONI V.,** Molinero J.C., Meffre M., Bonnet D. (2021) Variability of growth rates and thermohaline niches of *Rhizostoma pulmo*'s pelagic stages (Cnidaria: Scyphozoa). *Marine Biology* 168, 107. <https://doi.org/10.1007/s00227-021-03914-y>
- Article 3. LEONI V.,** Molinero, J.C., Crochemore S., Meffre M., Bonnet D. (2022) Ontogenetic dietary shifts of the medusa *Rhizostoma pulmo* (Cnidaria: Scyphozoa). *Hydrobiologia* 849, 2933–2948. <https://doi.org/10.1007/s10750-022-04903-y>
- Article 4. LEONI V.,** Bonnet D., Molinero J.C., Ariza A., Beltran L., Meffre, Ramírez-Romero E. (*in prep.*) Modelling a planktonic food web including the population dynamics of *Rhizostoma pulmo* (Cnidaria: Scyphozoa) under a warming ocean.

## Outreach publications

- Article 5. LEONI V.,** Cazelles N., Duron N., Juilliard F., Theys J., Molinero J.C., Simón C., Bonnet D. (*accepted - in press*) Some jellyfish like it hot! *Frontiers for Young Minds*.

## Public datasets

- LEONI V.,** Bonnet D., Ramírez-Romero E., Molinero J.C. (2021) Georeferenced semi-quantitative data of the jellyfish *Rhizostoma pulmo* (Cnidaria: Scyphozoa) from 1810 to 2019 in the Mediterranean and Black Seas, *Dryad*, Dataset, <https://doi.org/10.5061/dryad.0cfxpnw0q>



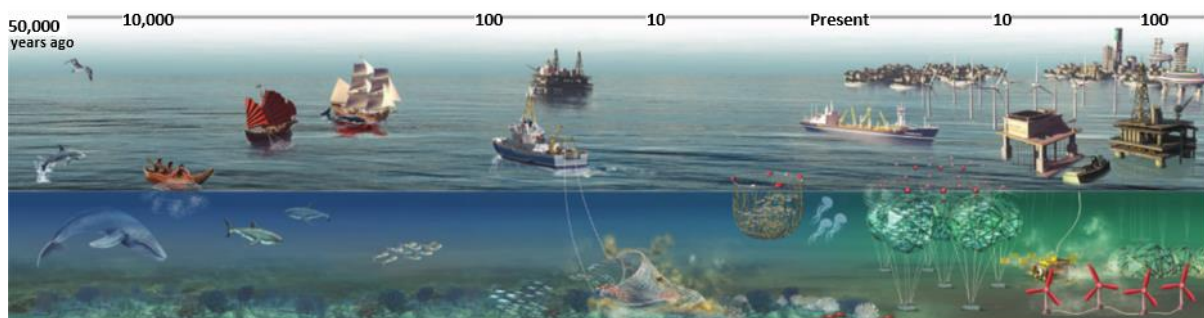
# CHAPTER 1.

## GENERAL INTRODUCTION



## 1.1 | GLOBAL OCEAN UNDER ANTHROPOGENIC PRESSURES

Today, the world human population is estimated in approximately 10 billion, the highest number in the history of humankind (Crist et al. 2017). Human activities have impacted the Earth's global environment and caused unprecedented changes in the physicochemical conditions of the atmosphere and the ocean (IPCC 2021; Fig. 1.1) Most of these anthropogenic pressures occur in coastal regions, where more than 40% of the human population lives within 100 km of the coastline (United Nations 2017).



**FIGURE 1.1.** Timeline (log scale) of changes in the ocean uses and biodiversity. The illustration represents the human-mediated temporal changes in the marine environment including overfishing, habitat destruction, eutrophication, aquaculture and ocean sprawl (Modified from McCauley et al. 2015).

Global warming is one of the most critical signals of global change that affects ocean ecosystems (Sage 2020). While climate has varied through geological time, the heating rate of the ocean is increasing at a scale of decades. Global ocean temperatures are expected to rise by 3.47°C in 2100 due to the increase of greenhouse gases in the atmosphere, fundamentally carbon dioxide (CO<sub>2</sub>) from the industrial activity (Kwiatkowski et al. 2020). Warming is not the only consequence of the industrial activity, the greenhouse gas emission will also increase the solubility of CO<sub>2</sub> in the ocean, which reduces the pH of seawater, i.e., ocean acidification, with devastating effects on shell-forming plankton and benthic species (Doney et al. 2009). Warming itself will modify major current systems and stratification processes, which will, in turn, modify oxygen availability and nutrient supply (Toggweiler and Russell 2008; Gunder and Molinero 2013).

In addition to climate forcing, other human activities are already affecting, and will continue impacting, the natural equilibrium of the ocean. Overfishing has depleted commercial species to critical levels (Link and Watson 2019, Fig. 1.1) and affected other species by trophic cascade effects (Jennings and Kaiser 1998). Together with fishing, international shipping accounts for more than 90% of the global trade (Schnurr and Walker 2019) and is one of the

main vectors to introduce exotic species (Minchin et al. 2009). Further, mounting industrial pollution in coastal areas, sewage discharge and land fertilization runoff promote coastal eutrophication (Sage 2020; Fig. 1.1). Human-made structures in the marine environment are also recognized as an important source of ecological change (Duarte et al. 2013; Bugnot et al. 2020). An expansion of artificial structures on the oceans, known as ‘ocean sprawl’, is associated with shipping, aquaculture, coastal industries, ports infrastructures, plastic waste and floating structures as buoys and pontoons (Barnes 2002; Duarte et al. 2013; Firth et al. 2016; Fig. 1.1). As artificial structures present different physical properties compared to natural substrates (Bulleri and Chapman 2010), they constitute novel habitats that are colonized by opportunistic and alien species (Glasby et al. 2007), and reduce the habitat for native ones.

The above changes have mainly affected marine ecosystems health of coastal areas and marginal seas (Bugnot et al. 2020). Further, while global projections predict productivity declines at open-ocean mid-latitudes (Bopp et al. 2013), eutrophication is reported in coastal regions and high latitudes (Kwiatkowski et al. 2020). This fosters the coastal proliferation of toxic microalgae blooms, such as cyanobacteria (Heisler et al. 2008), and the creation of anoxic zones (Diaz and Rosenberg 2008), with negative impacts on ecosystem health, food security, and economy. Semi-enclosed seas are hence particularly vulnerable to warming, which is the case of the Mediterranean Sea, where temperature is expected to rise faster than other marine systems in the world (Bopp et al. 2013), coasts are strongly affected by overbuilding (> 45% of the land cover, EEA 2006), and it is included among the most human-impacted regions worldwide (Halpern et al. 2019).

### 1.1.1. BIOLOGICAL RESPONSES TO GLOBAL CHANGE

Global change has triggered diverse biological responses in aquatic ecosystems. These responses include changes in species distribution, phenology, abundance, and demography (Poloczanska et al. 2016). A review of 1,735 biological responses of marine biota showed that approximately 82% of them were related to climate change (Poloczanska et al. 2013). Yet, species’ responses to anthropogenic impacts are heterogeneous, occurring at different rates and spatial directions (Pinsky et al. 2013).

One of the most evident consequences of warming is the shift of species distributions (Pereira et al. 2010; Lenoir and Svenning 2015). This is especially true in ectotherm organisms, which represent ~99% of the species in Earth (Atkinson and Sibly 1997) and can occupy areas within strict thermal tolerance limits. Numerous taxa have moved northward to places where



they were previously absent or uncommon (Lenoir and Svenning 2015). For example, the distribution of calanoid copepods showed a northward displacement across the North Atlantic, following the expansion of warm waters (Beaugrand et al. 2009). A study on 360 marine taxa in North America also found that shifts on species' distribution follow the speed of climate change, with the consequent reorganization of marine communities (Pinsky et al. 2013).

The timing of recurring life-cycle events influenced by seasonal and interannual variations in climate, i.e., phenology, are extremely sensitive to climate change (Asch 2015; Cohen et al. 2018). For instance, in temperate latitudes, terrestrial species are anticipating key phenological events such as migration, flowering or egg laying, at a rate of 2-5 days per decade, with 80% following the expected changes due to climate modifications (Root et al. 2003). In marine ecosystems, however, the anticipation of phenological events are occurring at faster rates, even at 50 days per decade for the case of zooplankton (Poloczanska et al. 2016). These changes are however not synchronous across trophic levels in marine communities because biological responses differ among species. Between 1958 and 2002, the variability of response across planktonic functional groups led to a mismatch between trophic levels (Edwards and Richardson 2004). This decoupling of trophic interactions can impact food web dynamics with cascading effects through trophic networks, and thus, alter ocean ecosystems as a whole. Phenology alterations have therefore broad implications in plankton communities due to the strong interdependence between trophic levels (Edwards and Richardson 2004).

Finally, human modifications of ecosystems have altered the abundances of marine populations (Poloczanska et al. 2016). Between 1970 and 2010, marine animals experienced a decline of 40% of their abundances (WWF 2014). Such reduction has been related to overfishing (Yan et al. 2021) and habitat loss (Beaumont et al. 2008), which in turn caused knock-on effects up and down in marine food webs (McCauley et al. 2015). In contrast, some marine species could increase their success in response to particular conditions caused by human activity, such as liberated niches, reduced predation, or benefiting from advantageous environmental conditions (Atkinson et al. 2004). For example, warming in northern-latitudes may restrict the success of cold adapted species, but favor suitable conditions for warm water species (Sanford 1999; Sharma et al. 2007). This exchange between winners and losers has been particularly evident in semi-enclosed seas in recent years. For instance, the impact of proliferations of harmful populations has been evidenced in the last decades. The most notorious cases are harmful algal blooms (Fu et al. 2012) and blooms of some gelatinous zooplankton species (Mills 2001), whose abundance increase in some areas has been pointed out as an indicator of deteriorated ecosystems.

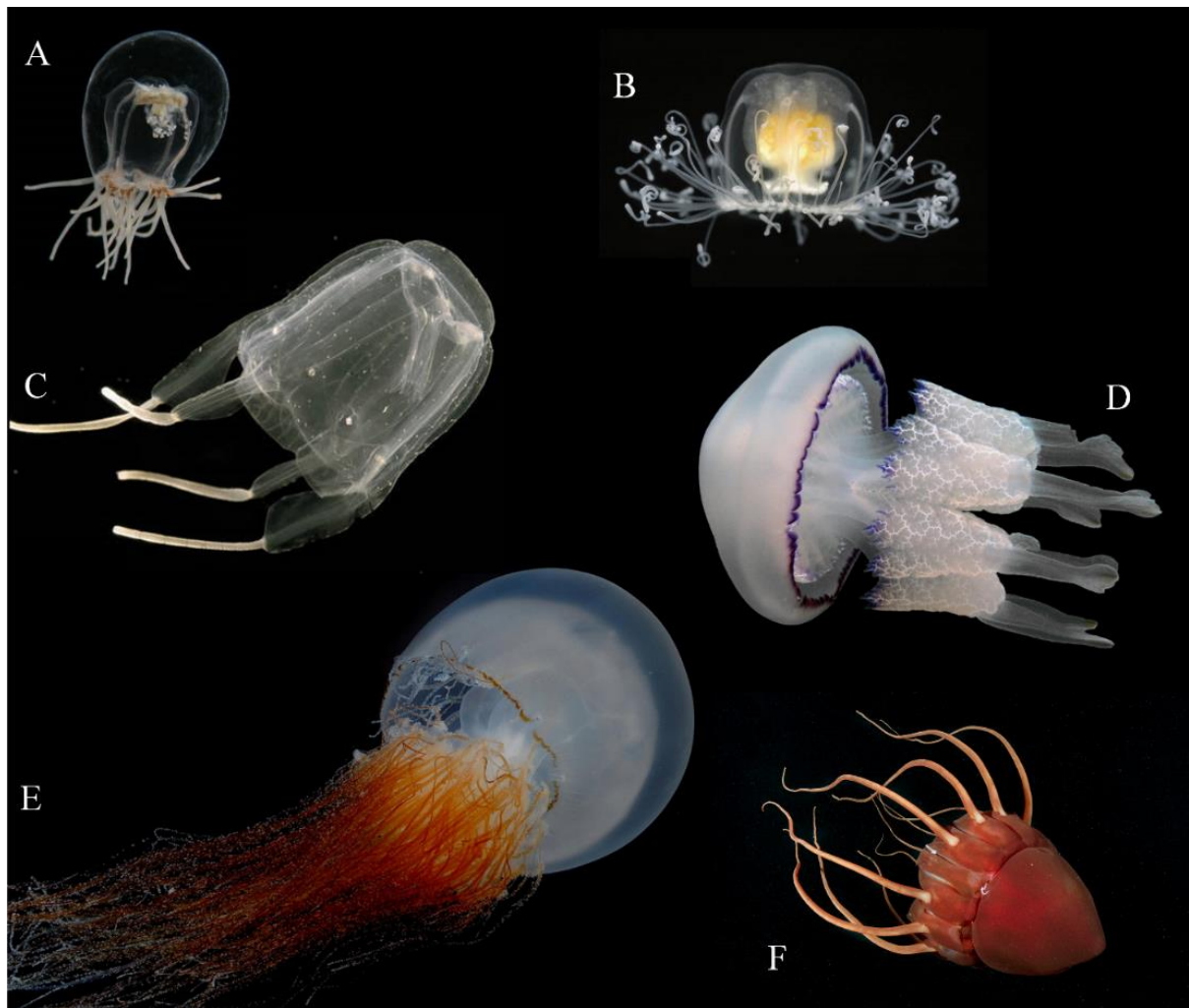
## 1.2 | GELATINOUS ZOOPLANKTON

The term ‘gelatinous zooplankton’ includes species from diverse phylums that converge on low carbon content, fast growth strategies, transparency, drifting or slow-swimming, and buoyancy (Bone 2005). Within Metazoans, this planktonic gelatinous ecotype appeared in many taxa throughout evolution (Condon et al. 2012), with some members of the phylum Ctenophora, Cnidaria and Urochordata (Kjørboe 2013) among the most important. A recent study, integrating the largest current database of gelatinous zooplankton abundance, has shown that cnidarians of the Subphylum Medusozoa represent 92% of the global gelatinous biomass (Lucas et al. 2014). This results in a total biomass around 0.04 Gt C (Bar-On et al. 2018) in the upper 200 m of the water column, excluding the deep-sea jellyfish and benthic stages. This estimation, together with the total biomass of coral reef (Subphylum Anthozoa, 0.05 Gt C) places the phylum Cnidaria as one of the Metazoans most contributing to the global biomass on Earth (~0.1 Gt C; Bar-On et al. 2018).

Cnidarians are one of the ten phylum with the greatest diversity in the marine environment (Briggs 1995). Members of the Subphylum Medusozoa, including the classes Cubozoa, Hydrozoa, Scyphozoa and Staurozoa are represented by more than 3,000 species, with varied and complex life cycles (Gibbons et al. 2010; Jarms and Morandini 2019). Among them, species of Cubozoa and Scyphozoa, but also some species of Hydrozoa, exhibit a pelagic stage during their life cycle, which are referred here as ‘jellyfish’ (Fig. 1.2). Scyphozoans, known as ‘true jellyfish’, are present on Earth since the Cambrian, and were capable of withstanding the global events that led to the extinction of arthropods, mollusks and chordates (Young and Hagadorn 2010).

Jellyfish attracted the interest of naturalists since ancient times (Haddock 2004). The current taxonomic category Scyphozoa was defined by the German scientist Ernest Haeckel, who described, between 1870 and 1890, most of the known jellyfish species. At the end of the 19<sup>th</sup> century, a period defined as the ‘golden age of gelata’ (see Haddock 2004) was coined due to a peak of taxonomic studies and life cycle descriptions of these animals. The interest in this group however decayed in subsequent decades. For instance, during research cruises, zooplankton surveys or fisheries activities, the presence of jellyfish has been overlooked or indicated as ‘a presence of gelatinous animals’ and considered as an undesirable bycatch (Haddock 2004). Practical difficulties have also contributed to this information gap. Due to their fragility, they are usually damaged when collected by nets, and are difficult to keep in good conditions with traditional fixative methods (Purcell 2009). This, along with the

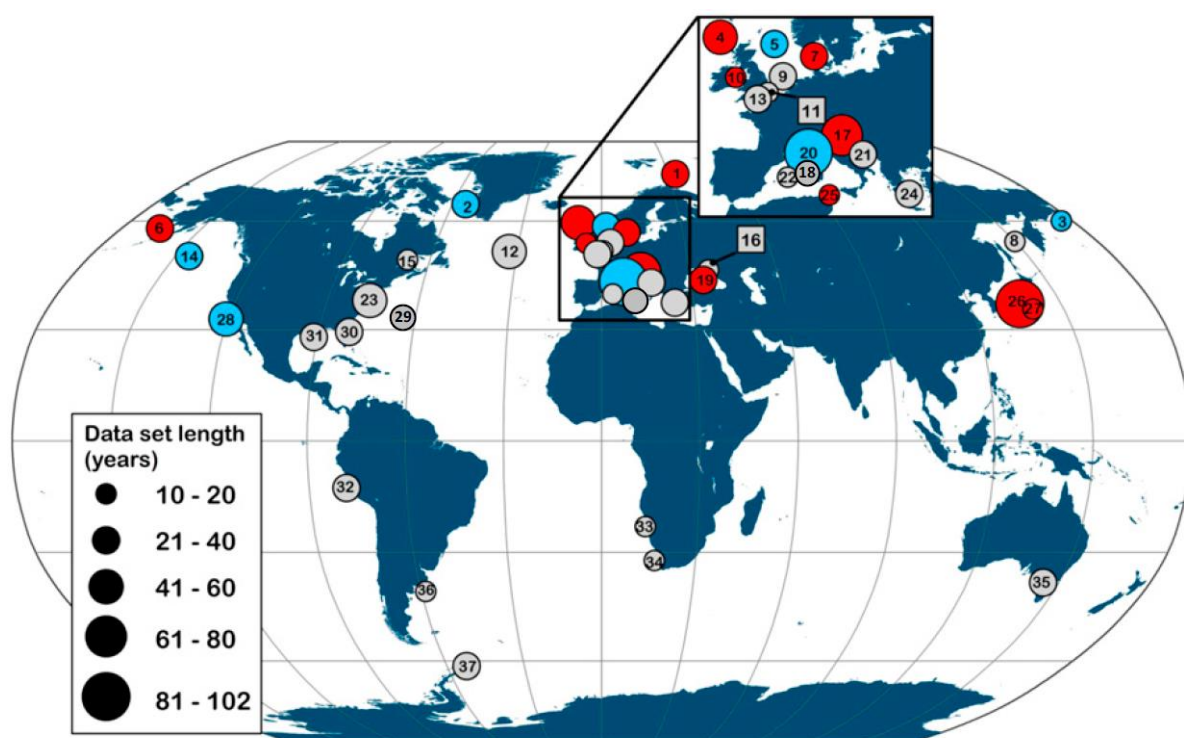
perception as unimportant components of marine ecosystems (Hays et al. 2018), contributed to the long neglect of jellyfish in ecological studies. Fortunately, the beginning of the 21<sup>st</sup> century started with a renewed interest on jellyfish ecology. The number of scientific literature has significantly increased (Sanz-Martín et al. 2016), and this present period is now regarded as the second and major golden age of gelata (Haddock 2004).



**FIGURE 1.2.** Some species of jellyfish (Cnidaria: Medusozoa) representing the diversity of the group. Hydrozoa: *Bougainvillia niobe* (A) and *Turritopsis nutricula* (B); Cubozoa: *Carybdea mora* (C); Scyphozoa: *Rhizostoma pulmo* (D), *Nemopilema nomurai* (E) and *Periphylla periphylla* (F). Source: A, B and C from <http://cifonauta.cebimar.usp.br/>; D and E from Lawley et al. (2021) and F from <https://www.bigfishexpeditions.com> (Pictures are not scaled).

### 1.2.1. JELLYFISH POPULATIONS IN A CHANGING OCEAN

The idea of a generalized global increase of jellyfish species has been present among scientists for years (see references in Sanz-Martín et al. 2016), but it was only until very recently that two global analyses have been conducted to answer this question (Brotz et al. 2012; Condon et al. 2013). Brotz et al. (2012) analyzed jellyfish data at Large Marine Ecosystem (LME) scale, identifying an increasing trend on 62% in LME coastal waters after 1950. In line with this, Condon et al. (2013) observed decadal oscillations in most areas of the world, however, large-scale increases in jellyfish populations were only identified in 27% of the analyzed coastal zones (Fig. 1.3). Interestingly, none of these studies found evidence of a global sustained increase of jellyfish, and attributed the reported increases to rising phases of decadal oscillations (Condon et al. 2013). These analyses provide the first global estimations of jellyfish populations and evince the dearth of long-term datasets in many areas to provide robust results.



**FIGURE 1.3.** Time-series of observations on jellyfish abundance (1874-2011). The diameter of the symbols is proportional to the duration of the dataset and colors indicate significant jellyfish abundance trends over time: decrease (blue), increase (red), or no trend (gray). Numbers identify the datasets described in Condon et al. (2013). Most datasets are from the northern hemisphere (87%), in particular from the Atlantic Ocean (17%) and the Mediterranean region (17%), and comprised Medusozoans (89%): JeDI project, map from Condon et al. (2013).

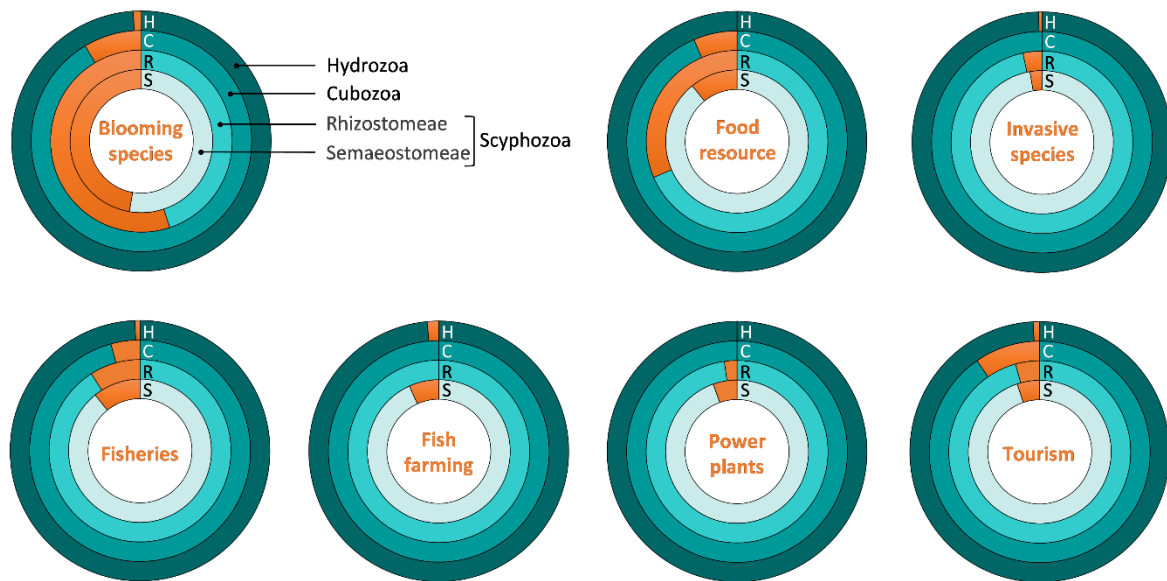
The driving forces behind this possible increase of jellyfish populations, referred sometimes as the ‘jellyfication’ of the ocean (Roux et al. 2013), are not clear yet. If such were the case, changes associated with anthropic activities seem to be the main cause of jellyfication (Purcell 2012). Among the most important: warming, which accelerates growth and reproduction (see Purcell 2005); overfishing, which operates removing jellyfish competitors and predators (Lynam et al. 2006); and eutrophication, which increases food supply and hypoxia (Purcell 2012), environmental conditions for which jellyfish are more competitive than other metazoans (Purcell et al. 2001). Other studies have pointed to ocean sprawl as beneficial for medusae, as it might increase the availability of substrates for the settlement of benthic stages (Duarte et al. 2013). However, polyps of most species are yet to be found in nature (Mills 2001; Jarms and Morandini 2019) and this supposed generalized benefit needs to be corroborated. The changing environment has also provided favourable conditions for non-indigenous jellyfish (Graham and Bayha 2007). For instance, the case of the Lessepsian jellyfish *Rhopilema nomadica* in the southeastern Mediterranean Sea (Edelist et al. 2020). Yet, the existing evidence relating jellyfish success with anthropogenic stressors is scarce, and most is limited to few species and locations (Pitt et al. 2018). The wide variability of species-specific responses to such impacts is yet to be determined, and multi-stressor analyses on broad time-space scales are inexistent.

Beyond scientific discussions on the drivers and the real extent of the so-called jellyfication, jellyfish blooms are today causing important economic losses in many coastal regions around the world (Kim et al. 2012). Over the last 50 years, the frequency and severity of negative impacts on fisheries and aquaculture have increased (Bosch-Belmar et al. 2021). The principal direct negative effects are net clogging (Graham et al. 2003), catch deterioration (Quiñones et al. 2013), longer fishing time (Palmieri et al. 2014), and the contact of artisanal fishermen during manual net collections with stinging species (Palmieri et al. 2014). Among indirect impacts on fishing, jellyfish constitute an additional hazard for fish, as they can predate on fish eggs and larvae reducing fish recruitment, or can compete for food mainly with juvenile fishes (Purcell and Arai 2001). Aquaculture activities have been also affected by jellyfish proliferation, as shown by the numerous reports of fish injuries and mortality when jellyfish — or their broken parts — enter into cages and sting fish gills or skin (Bosch-Belmar et al. 2017). Jellyfish impacts varied among economic sectors. For instance, important economic losses have been reported on desalination and nuclear power plants (Dong et al. 2010). When appearing in large quantities, jellyfish can even clog seawater intakes, producing energy shortages or the shutdown of power plants (Purcell et al. 2007). Tourism activities have also

experienced rising problems associated with jellyfish, as some species can cause medical emergencies (Kawahara et al. 2006a) or even the death (Fenner and Hadok 2002) of swimmers. This is particularly important in tropical and subtropical waters, where economic losses rise millions of dollars when jellyfish enter massively in a touristic beach (Ghermandi et al. 2015). On the other side, some countries have increased their tourism income because of jellyfish (Morandini 2022). For example, the Jellyfish Lake (Palau) and some sites in Japan receive tourists each year to dive with the scyphomedusae *Mastigias* sp. (Dawson et al. 2001) or the giant jellyfish *Nemopilema nomurai* (Graham et al. 2014). Many people are actually attracted by jellyfish. Since the staff of Monterrey Bay Aquarium managed to maintain a large collection of jellyfish in captivity in the 90s, aquariums around the world (e.g., Médusarium of Trocadero Aquarium in Paris) attract a great number of tourists each year (Purcell et al. 2007).

Despite occurring in all the oceans of the world, from coastal zones—including lakes and lagoons—to abyssal depths, jellyfish mostly interact with humans along the heavily used coastal areas. Indeed, only the ‘bloom-forming’ coastal species have been identified as a problem or an economic resource for humans (Malej et al. 2014). However, not all gelatinous zooplankton are able to form blooms (Fig. 1.4) and not all scyphozoans are responsible for these problematic proliferations (Hamner and Dawson 2009). In fact, species reported to cause economic losses are only a small portion of the total diversity, representing 10% or less of all known jellyfish (Fig. 1.4). It is remarkable that, among the total number of jellyfish species, less than 5% have been reported to interact in a positive or negative way with human activities (Fig. 1.4, Table S1.1). As a matter of fact, not even a half of scyphomedusae are blooming species, Rhizostomeae being the most important group behind these events (Fig. 1.4). Based on this, the use of the term ‘jellyfish’ in relation of bloom events is not only taxonomically simplistic but often regarded as a negative event in marine ecosystem that should be restrained. Additionally, a misconception is proliferating in scientific literature, when claiming that ‘jellyfish blooms are on the rise’ due to anthropogenic stressors, often referring to few over-studied emblematic species among hundreds. However, as highlighted by specialists in jellyfish ecology, this oversimplistic inference is not representative of the jellyfish ecological diversity (Condon et al. 2012; Pitt et al. 2018). Only 13 out of 61 genera of scyphomedusae are usually used to support these claims (Pitt et al. 2018), which are in addition dominated by the genus *Aurelia* and *Chrysaora*, the most studied gelatinous zooplankton worldwide (Mills 2001). These are, however, widespread species with a great environmental adaptability. As not all species respond equally to environmental perturbations, the approach should be reformulated. Instead of searching whether a general increase occurs, the driving questions in

jellyfish research should be species-specific, which species increase or decrease, where and why (Haddock 2004; Purcell 2005; Pitt et al. 2018).



**FIGURE 1.4.** Percentage of the total species of Medusozoa (excluding the benthic Stauromedusae and benthic Hydrozoa) capable of bloom forming and affecting human activities (indicated in orange). Of the total blooming Semaestomeae (47.3%) species, 89% belong to the genus *Aurelia* and *Chrysaora*. The number of species and references are described in detailed in Table S1.1 of the Supplementary Material.

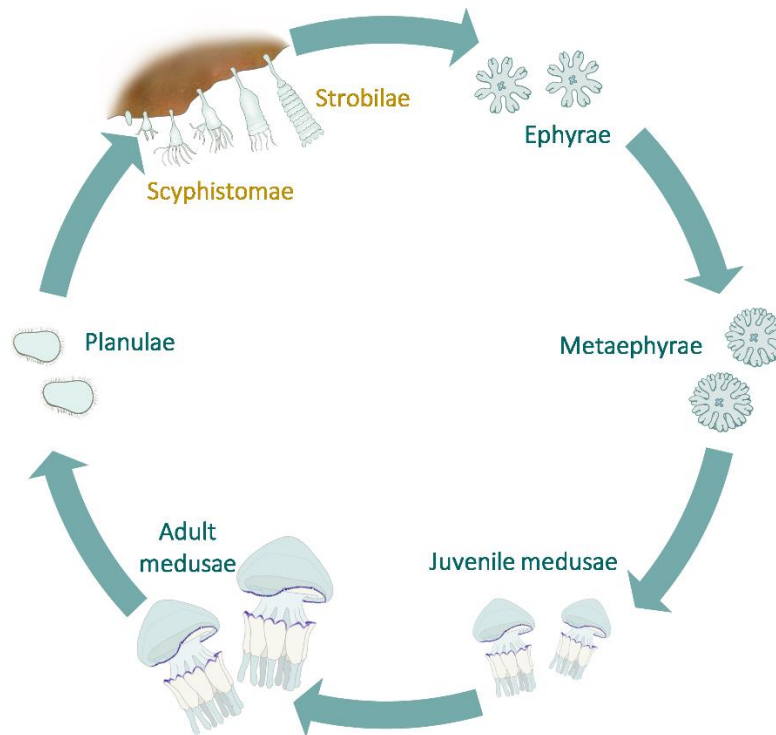
## 1.2.2. SCYPHOMEDUSAE BLOOM FORMING: CURRENT GAPS

### Life cycle

Scyphozoans species (> 200) are exclusively marine (Jarms and Morandini 2019). Most of them present a complex metagenetic life cycle, i.e., with a benthic and a pelagic phase (Arai 1997; Fig. 1.5). The benthic stage, the scyphistoma, is a polyp of a few millimeters of size which lives attached to a hard structure. Under particular environmental conditions, the scyphistoma develops into a strobila and asexual reproduction —known as strobilation— takes place. Fully developed ephyrae are released from the strobila in the water column. These ephyrae with a body diameter of a few millimeters are the initial pelagic stage. They grow rapidly and develop into metaephyrae, and later into juvenile and adult medusae. Once medusae mature (mostly dioecious), sexual reproduction takes place and small planulae are released after fertilization. These planulae swim for few days (< 4 days, Lucas et al. 2012), and once they find a suitable substrate, they fix and develop into a new generation of scyphistomae (Fig. 1.5). Some scyphozoans can spend their whole life in the pelagic domain, such as *Pelagia*



*noctiluca* (Ramondenc et al. 2019), but all species have a pelagic adult stage (medusa). During scyphozoan's life cycle, some species could extraordinarily proliferate and create 'blooms'.



**FIGURE 1.5.** Life cycle of *Rhizostoma pulmo* (described by Fuentes et al. 2011). Arrows indicate the life cycle development. Scyphistomae and strobilae (in yellow) are benthic stages of a few millimeters of size. During the process of strobilation (asexual reproduction), fully developed ephyrae are released in the water column. They grow and develop into meta-ephyrae, which later lead to juvenile and adult medusae. Planulae are the result of sexual reproduction of adult medusae stage. Note that the scheme is not size scaled. Illustrations by Justine Courboulès.

The strobilation process is a key step in the development of a bloom (Fig. 1.6). However, all we know about is restricted to laboratory studies (e.g., Holst et al. 2007; Fuentes et al. 2011; Kienberger et al. 2018; Gueroun et al. 2021). In fact, most of benthic stages of the species are yet to be found in nature (Mills 2001). Strobilation is therefore not well understood until now, and our knowledge is confined to few species. Temperature shift seems to trigger the strobilation process for some species (Han and Uye 2010; Holst 2012; Fuchs et al. 2014; Marques et al. 2019), but other environmental drivers such as a change in food supply, pH, or salinity, and internal signals have been identified (see references in Schiariti et al. 2008). The timing and amount of ephyrae liberated also differ among species, but even among individuals of the same species under equivalent environmental conditions (e.g., Kawahara et al. 2006b). While some scyphozoans are characterized by a monodisc strobilation, i.e., one strobila liberates one ephyra (see review on Schiariti et al. 2008), most of bloom forming species are



polydiscs, i.e., one strobila liberates more than one ephyra. Species from the genus *Aurelia* and *Chrysaora*, and the Family Rhizostomatidae (Order Rhizostomeae) commonly present polydisc strobilation and are the most notable blooming species (Dawson and Hamner 2009). Generally, two strategies can be observed in polydiscs species, in both cases, leading to large abundances (Lucas and Dawson 2014). Semaestomeae species commonly liberate many ephyrae during a unique strobilation event, typically one generation per year (up to 13 ephyrae released per strobila in *Aurelia* sp.; Di Camillo et al. 2010; Purcell et al. 2012), whilst Rhizostomeae can produce a few ephyrae, but can strobilate several times (*Lychnorhiza lucerna* releases three ephyrae per strobila, five times during four months; Schiariti et al. 2008). A single polyp of a bloom forming species may thereby, produce high medusae abundances. The diversity of life strategies reflects the variety of responses that each species may have in different environmental contexts and highlights the need to better understand the factors influencing each stage of development.

### **Population dynamics**

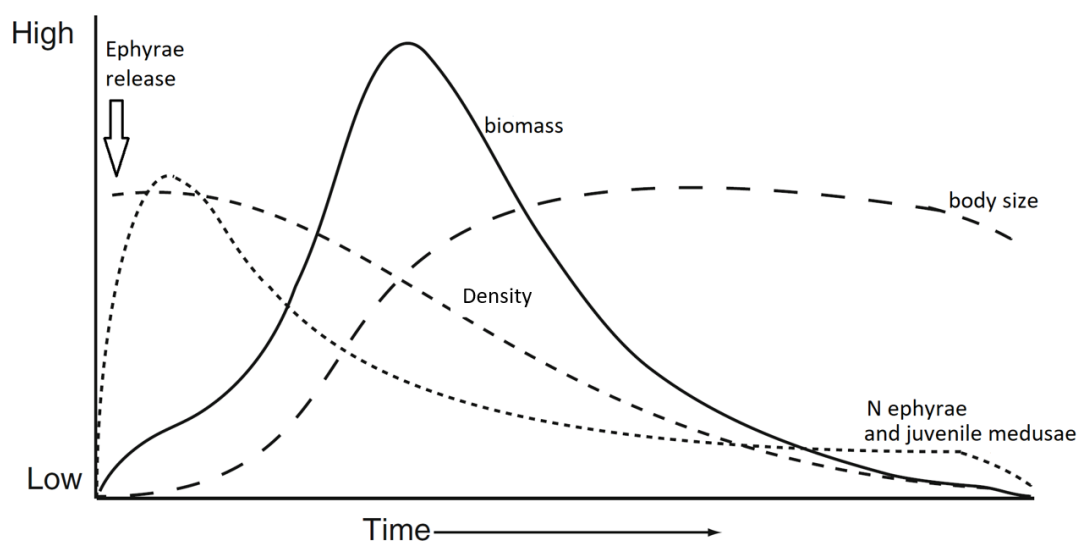
The study of the species population dynamics is fundamental to understand the processes structuring natural communities. This includes the assessment of their growth rates and interspecific interactions, as competition or predation (Hastings 2013). On one side, this basic information is necessary to design conservation plans. On the other, when it comes to commercial species, it is crucial for an adequate management of resources.

In jellyfish, once ephyrae are liberated and transformed into medusae, their growth is remarkably fast, compared to other marine species (Fig. 1.6). For example, a jellyfish bloom can reach tons of wet weight in a few weeks or months (Dawson and Hamner 2009; Lucas and Dawson 2014). Unfortunately, growth rate estimations of gelatinous animals are scarce in comparison to what we know about crustaceans or fish (Palomares and Pauly 2009). This is often due to technical limitations on their collection, manipulation and fixation (Purcell 2009). As a result, most growth estimations have been historically conducted under laboratory conditions (e.g., Astorga et al. 2012; Acevedo et al. 2013). In recent years, however, technological advances on jellyfish tagging (Fossette et al. 2016) and the analysis of statoliths on scyphomedusae (Sötje et al. 2017) have permitted to study this important physiological parameter under natural conditions.

High production of ephyrae and fast growth rate of medusae are what characterizes jellyfish population dynamics, with a typical decoupled abundance-biomass peak (Fig. 1.6). In addition, a single mature female medusa can release from ten to thousands of eggs per day,

each of them resulting in a new polyp generation. After sexual reproduction, jellyfish populations tend to collapse (Pitt et al. 2013). While this event is still not completely understood, food limitation, parasitism, cannibalism or abrupt temperature shifts have been pointed out as plausible causes (Pitt et al. 2013; Javidpour et al. 2020). Whatever the cause, what we do know is that large accumulation of dead medusae eventually reaches the bottom and becomes an important food supply for benthic species. Indeed, these massive mortality events, known as ‘jelly-falls’, are able to modify the food web and community structure of benthic ecosystems (Lebrato et al. 2012; Marques et al. 2021a).

Even if the classic description of jellyfish population dynamics can be attributed to many scyphomedusae species (Morandini et al. 2016; Fig. 1.6), a particularity of this group is the erratic and often unpredictable behavior of its populations (Ceh et al. 2015). This includes a high abundance interannual variability (e.g., Morandini et al. 2016), a non-define life span (Arai 1997; Fuentes et al. 2011), and the presence of more than one cohort in a single jellyfish season (Ceh et al. 2015; Fernández-Alías et al. 2020). Such variability underlines the relevance of population studies, to better understand their dynamics and blooms persistence. Most studies on population dynamics have focused on few widespread genera or species, but provided valuable insights on jellyfish dynamics (Lucas 1996; Buecher et al. 2001; Addad et al. 2008; Rosa et al. 2013; Marques et al. 2015b; Goldstein and Riisgård 2016). However, growth and mortality environmental drivers, as well as optimal conditions for bloom development are still not well understood for most species. In the end, this constrains the development of population dynamics models to explain the observed patterns.



**FIGURE 1.6.** Example of population dynamics of a jellyfish in a closed ecosystem, showing changes in biomass caused by life history features ( $N$  = abundance) (Modified from Lucas and Dawson 2014).

## **Trophic ecology**

Within the ecosystems, empirical evidence increased the awareness of jellyfish importance as prey. Due to novel technologies, opportunistic consumption of jellyfish has been observed in a great diversity of pelagic and benthic animals, including fishes of commercial interest, as well as many invertebrates (Hays et al. 2018). This draws attention that the role of these animals in ecosystems cannot be neglected, since it is more complex and important than what was previously thought.

Together with this growing recognition of the complexity of jellyfish as preys, bottom-up processes have been highlighted as central drivers of jellyfish populations, with food being a limiting factor for both benthic and pelagic stages (e.g., Marques et al. 2015b; Goldstein and Riisgård 2016). Under future eutrophic and warmer conditions, diverse studies hypothesized that the plankton community might shift from a diatoms-copepods-fish dominated ecosystem, to an alternative state where flagellates, microzooplankton and jellyfish will dominate (Parsons and Lalli 2002; Richardson et al. 2009; Uye 2011). However, most scyphozoan diets are still unknown, and their great morphological diversity and feeding strategies make the forecast on how species will respond even more complex (Nagata et al. 2016; Nagata and Morandini 2018). Together with this complexity, the few studies on jellyfish diet during ontogeny have identified different selectivity patterns and preferences between small and large individuals (Álvarez-Tello et al. 2016), but also among species (Purcell 2003). Understanding trophic interactions is not only crucial to define dietary niches but is also essential to incorporate this group in food web models.

## **Long-term observations of jellyfish blooms**

Long-term observations of natural populations are essential for understanding how species are adapted to the environment and to anticipate possible effects of climate change in the future. In addition to the limited information at the population level, the lack of pluriannual records on jellyfish hampers temporal studies that could otherwise identify changes in abundances and phenology (Prieto 2018).

Nowadays, taking advantage of machine learning tools and modeling, a great number of studies at a global scale on biodiversity (Benedetti et al. 2021), biogeography (Deutsch et al. 2020), phenology (Harrison et al. 2018) and predictions of marine species distribution and biomass changes (e.g., Bryndum-Buchholz et al. 2019; Lotze et al. 2019) has been performed. Nevertheless, studies of a jellyfish species along all its range of distribution are scarce (Goy et

al. 1989; Hardinge 2019). A collaborative effort has been developed to create an open-access database (JeDI) which holds *c.* 500,000 records of gelatinous zooplankton for the period 1790 to 2011 (Condon et al. 2015; Fig. 1.3). In parallel, in recent years, citizen science programs have emerged as non-traditional tools to improve spatio-temporal resolutions (Tulloch et al. 2013). They have already been widely used in terrestrial and aquatic ecosystems, including the monitoring of endangered (Schultz et al. 2017) and invasive (Zenetos et al. 2013) species, but also in marine macrofauna for cetaceans (Lodi and Tardin 2018) and sea turtles (Nordstrom et al. 2019). Recently, citizen observations on jellyfish proved to be particularly useful for large jellyfish species present on the coasts (Pikesley et al. 2014; Deidun and Sciberras 2017; Edelist et al. 2020; Marambio et al. 2021), and due to the increasing trend of jellyfish in the Mediterranean (Condon et al. 2013), scientific research, citizen science and forecasting jellyfish programs have been intensified. Among others: the CIESM JellyWatch Program (CIESM 2014), the ‘Occhio alla Medusa–Meteomeduse’ campaigns (Meteomeduse 2020, Italy), the ‘Medjelly’ project (iMedJelly 2020, Spain), the ‘Spot the Jellyfish’ campaign (Spot the Jellyfish 2020, Malta), and the ‘Découvrons Les Méduses’ citizen-science campaign (Tunisia). In particular, ‘GelAvista’ in Portugal (GelAvista 2021) and ‘La Mar de Medusas’ in Spain (CSIC 2021) are the most recent examples of jellyfish monitoring projects with the collaboration of non-specialized people. Valuable illustrations of the value of these data could be observed in Marambio et al. (2021) and Pikesley et al. (2014), where the integration of citizen science datasets and habitat modelling have allowed to forecast bloom events areas in diverse Mediterranean jellyfish species (Marambio et al. 2021). The establishment of a permanent survey of jellyfish might provide insights in the inter-annual variability of bloom episodes and their relationship to environmental conditions. Investing in collaborative strategies between scientists, administration, and citizens will minimize the cost of *in situ* data collection and maximize the scientific value of its analysis which in the end helps to design adaptative strategies.

### **Jellyfish modelling**

Understanding the population dynamics and species trophic role is a central issue for the development of reliable models (Boero et al. 2008), which can provide a mechanistic understanding of jellyfish role in the trophic food webs. However, most of the existing models for gelatinous zooplankton have been developed for the invasive ctenophore *Mnemiopsis leidyi*. They are either individual growth models (Kremer 1976; Kremer and Reeve 1989), population-based models (Oguz et al. 2008; Salihoglu et al. 2011; Shiganova et al. 2018),

biogeochemical models (Alekseenko et al. 2019) or models predicting *M. leidyi*'s occurrence (Siapatis et al. 2008; Collingridge et al. 2014) and dispersion (David et al. 2015; van der Molen et al. 2015). To a much lesser extent, models on gelatinous zooplankton have also been implemented on jellyfish. Most of these models are exclusively developed for the widespread moon jellyfish *Aurelia* spp. (Oguz et al. 2008; Melica et al. 2014; Vodopivec et al. 2017; Henschke et al. 2018; Ramirez-Romero et al. 2018), with fewer examples for other species (e.g., *Chrysaora quinquecirrha*: Brown et al. 2013; *P. noctiluca*: Malej and Malej 1992; Augustine et al. 2014; Rahi et al. 2020; *Physalia physalis*: Ferrer and Pastor 2017; Macías et al. 2021). Indeed, models are scarce for Rhizostomeae species. To our knowledge, only the population dynamics of the giant jellyfish *N. nomurai* (Xie et al. 2021) and *Cotylorhiza tuberculata* (Ruiz et al. 2012) have been simulated.

The inclusion of jellyfish in ecosystem models is actually fundamental to obtain a more realistic representation of their functional role in marine food webs. However, only 35.9% of the Ecopath-with-Ecosim projections conducted between 1984 to 2019 did actually include jellyfish (n=329; Lamb et al. 2019). It was only after 2007, that 73% of modeling approaches have taken into account these organisms as a separate group or as part of a broader plankton group (Lamb et al. 2019). Even then, none of these exercises have considered the different morphologies or changes experienced during ontogeny, omitting much of their wide trophic interactions. While this simplified representation of jellyfish in models is understandable due to the substantial lack of knowledge of these processes, it brings to surface the enormous task that we still need to accomplish in collecting fundamental ecological and physiological parameters of this key biological compartment.

### 1.3 | JELLYFISH BLOOMS: A CHALLENGE FOR THE MEDITERRANEAN SEA

The total surface of the southern European seas—including the Mediterranean and Black Seas—achieves 3 million km<sup>2</sup>. The Mediterranean Sea is regarded as one of the largest oligotrophic seas in the world (Turley et al. 2000). It is a temperate semi-enclosed ecosystem located between 30-45°N, connected to the Atlantic Ocean by the Strait of Gibraltar, to the Black Sea by the Sea of Marmara and to the Red Sea *via* the artificial Suez Canal, constructed in 1869 (Golani 1998). The Mediterranean Sea has an elongated shape of 4000 km from east to west and 800 km north to south, divided into two main basins. The western basin exchanges water with the Atlantic through the Strait of Gibraltar, with an outflow at the bottom of warm,

nutrient-rich and saline Mediterranean waters, and an inflow of colder and less saline Atlantic waters at the surface. This creates a permanent salinity gradient between the western and eastern basins. A nutrient increasing gradient from east to west, and a temperature gradient, from the temperate north to the subtropical south has been observed. The water loss through evaporation in the Mediterranean Sea exceeds the input of water through runoff and precipitation, resulting in a negative hydrological balance.

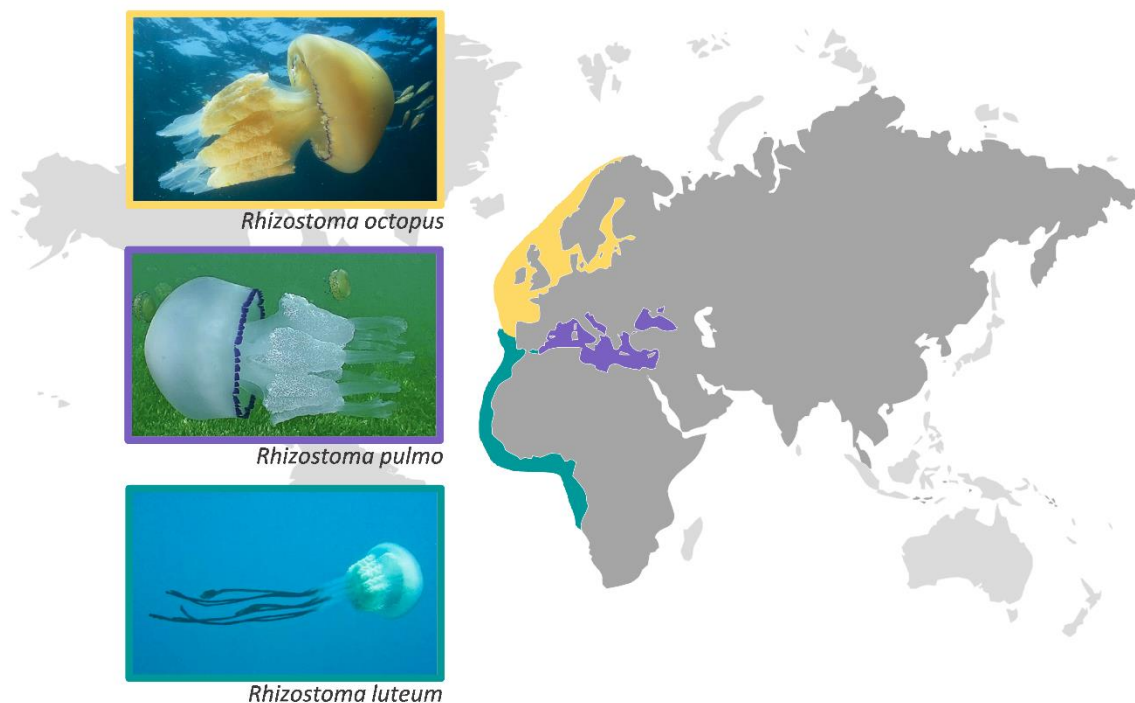
The Mediterranean Sea is considered as a biodiversity hotspot in terms of the number of species per area, where coexist a large number of endemic marine species, but also migratory ones (Coll et al. 2010, 2012). Unfortunately, due to the intense maritime traffic, numerous invasion events took place in the past, many of them with devastating effects on the ecosystem (Galil 2000). So far, nearly 1000 alien species have been introduced in the Mediterranean Sea (Katsanevakis et al. 2014), including jellyfish species. The Mediterranean and Black Seas account for a wide diversity of jellyfish species (Boero 2014). In particular, 22 species of scyphozoan have been described in the Mediterranean (Jarms and Morandini 2019). Problems associated with jellyfish therein have been related to the most common native species (Brotz and Pauly 2012; < 30% total scyphozoan diversity): the holoplanktonic *P. noctiluca*, and the meroplanktonic *Chrysaora hysoscella*, *Aurelia* spp., *C. tuberculata* and *Rhizostoma pulmo* (Palmieri et al. 2014), but also with the invasive *R. nomadica* (Ghermandi et al. 2015). As tourism and fisheries are among the most important economies for Mediterranean countries (Randone et al. 2017), these blooms have produced important economic losses in local coastal communities (Mariottini and Pane 2010; Palmieri et al. 2014).

The Mediterranean coast also presents numerous coastal lagoons. They are typically shallow, present sea connecting channels and strong environmental gradients. They are productive areas with a large variety of ecological habitats, which are important for fish, invertebrates, and provide refuges for migrating birds (Cataudella et al. 2015). However, these coastal ecosystems are highly exposed to threats related to human activities. A recent example is the massive mortality events of fishes and invertebrates observed during 2021 in Mar Menor lagoon, Spain (Sandonnini et al. 2021) due to severe eutrophication provoked by non-regulated anthropogenic activities. In particular, in the northwestern Mediterranean coastal lagoons, where many scyphomedusae coexist (*A. coerulea*, *C. tuberculata* and *R. pulmo*), numerous bloom events have been reported. Fundamentally in the Mar Menor (Spain, Pérez-Ruzafa et al. 2002; Fuentes et al. 2011; Prieto 2018), Thau (France, Bonnet et al. 2012; Marques et al. 2015) and Berre (France, Bonnet 2013) lagoons. Among these coastal Mediterranean lagoons, the Bages Sigeon lagoon (France) has been the scenario of recurrent jellyfish blooms of *R. pulmo*

since 2014, causing important societal and economic problems to the local fisheries due to net clogging, death of caught fish and stings when the nets are hauled up (S. Marin pers. comm.). Before that, only the scyphozoan species *A. coerulea* was reported in the area and blooms events were rare (Bonnet 2013). The reasons behind the outbreak of *R. pulmo* bloom events in this lagoon remains unknown.

### 1.3.1. *RHIZOSTOMA PULMO* IN THE MEDITERRANEAN SEA

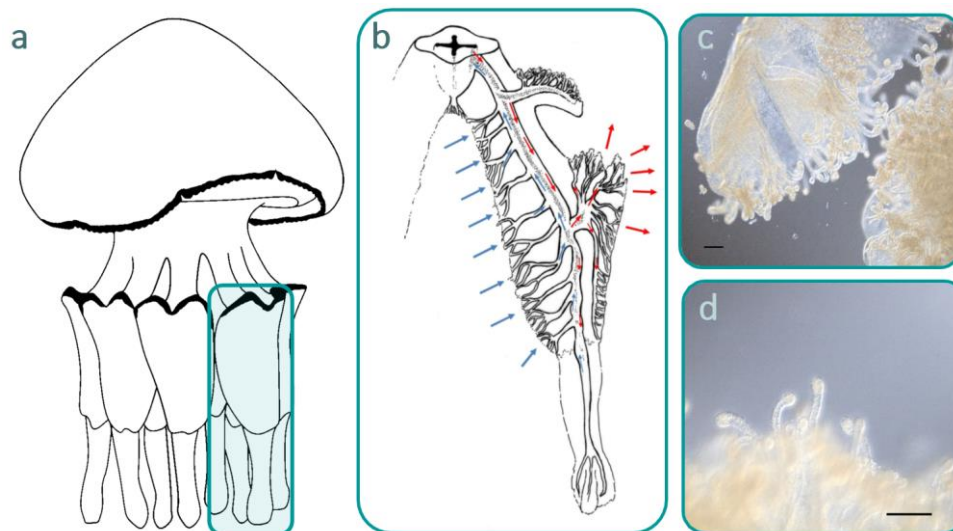
*Rhizostoma pulmo* (Macri, 1778) is one of the largest (c. 40-cm bell diameter) and most common blooming native jellyfish of the southern European seas, and one of the six species considered a nuisance (Kokelj and Plozzer 2002). This species is mainly distributed in the Western Mediterranean, Adriatic, the Ionian, the Ligurian and the Black seas, as well as in Tunisian waters (Kienberger and Prieto 2018). Despite some confusion in the literature regarding the geographic distribution of the three species of the genus *Rhizostoma* —*R. pulmo*, *R. octopus* (Gmelin, 1791) and *R. luteum* (Quoy and Gaimard, 1827)—, recent studies have shown a delimited range for each species, with only *R. pulmo* and *R. luteum* overlapping in the Strait of Gibraltar (Kienberger and Prieto 2018; Jarms and Morandini 2019; Fig. 1.7).



**FIGURE 1.7.** Distribution of the three species of the genus *Rhizostoma*: *R. octopus* (indicated in yellow), *R. pulmo* (in purple) and *R. luteum* (in green) based on Kienberger and Prieto (2018) and Jarms and Morandini (2019). Photos source: *R. octopus*: Caisey (2009), *R. pulmo* and *R. luteum*: Kienberger and Prieto (2018).

Those species belong to the Order Rhizostomeae —referred here as rhizostomids— characterized by a metagenetic life cycle (Fig. 1.5), the absence of marginal tentacles and massive bodies. Their large sizes, bell consistency and massive aggregations aroused interest in this group of jellyfish as a human food resource (Youssef et al. 2019). Since ancient times, rhizostomid jellyfish have been fished for food, and in recent years these fisheries have increased worldwide, and pharmaceutical products (e.g., antioxidants, collagen; De Domenico et al. 2019; Riccio et al. 2022) are being developed in many countries (Brotz et al. 2017). However, they are less studied than Semaestomeae and their ecology is largely unknown.

The feeding mechanism of rhizostomids, including *R. pulmo*, is peculiar. Instead of a central mouth, they use a significant portion of their large external surface, oral arms, as the primary structure to capture their prey (Fig. 1.8a, b). The ephyra central mouth develops into dactylozoid structures during the metaephyra stage, which finalized into eight oral arms in the adult medusa stage (Nagata et al. 2016). These specialized oral arms are covered with millimetric mouths from where the food is ingested (Fig. 1.8c, d). Therefore, despite the size of each mouth remain small during ontogeny, their feeding capacity increases with medusae size as the surface covered with mouths increases (Dawson and Hamner 2009).



**FIGURE 1.8.** **a.** Schematic representation of *Rhizostoma pulmo*. **b.** Incoming water flow is represented by blue arrows, outgoing flow by red arrow. **c** and **d** Detailed of the oral arms composed by millimetric mouths (scale bar = 0.2 mm). Source: *a.* Illustration modified from Justine Courboulés, *b, c* and *d* were taken and modified from Macaluso (2019).

*R. pulmo* is part of the Family Rhizostomatidae, which includes some of the largest medusae of the world, the invasive Mediterranean jellyfish *R. nomadica* and the giant Japanese jellyfish *N. nomurai*, which can also form spectacular blooms. The Rhizostomatidae have been



considered at the limit between planktonic and nektonic species, and are referred sometimes as ‘nektoplankton’ (Dawson and Hamner 2009) due to their extraordinary swimming capacities (Malul et al. 2019). These jellyfish swim by symmetrically paddling their bell and are capable of overcoming the speed of currents. This gives Rhizostomatidae advantages in terms of individual fitness, which is of vital importance to avoid stranding (Malul et al. 2019).

*R. pulmo* is a coastal species, commonly observed in lagoons (Pérez-Ruzafa et al. 2002; Fuentes et al. 2011; Gueroun 2016). Two studies on genetic variability among populations have presented contrasting results. While Ramšak et al. (2012) found no genetic structure in *R. pulmo* populations across the Mediterranean Sea, Ben Faleh et al. (2017) distinguished three phylogenetic lineages in the northern Adriatic, the western Mediterranean and the Tunisian coast. The detected genetic differentiation could be attributed to intrinsic or extrinsic barriers to genetic exchange between different populations that may have adapted to different environmental conditions. Unfortunately, differences in environmental niches have not been evaluated yet to confirm this hypothesis.

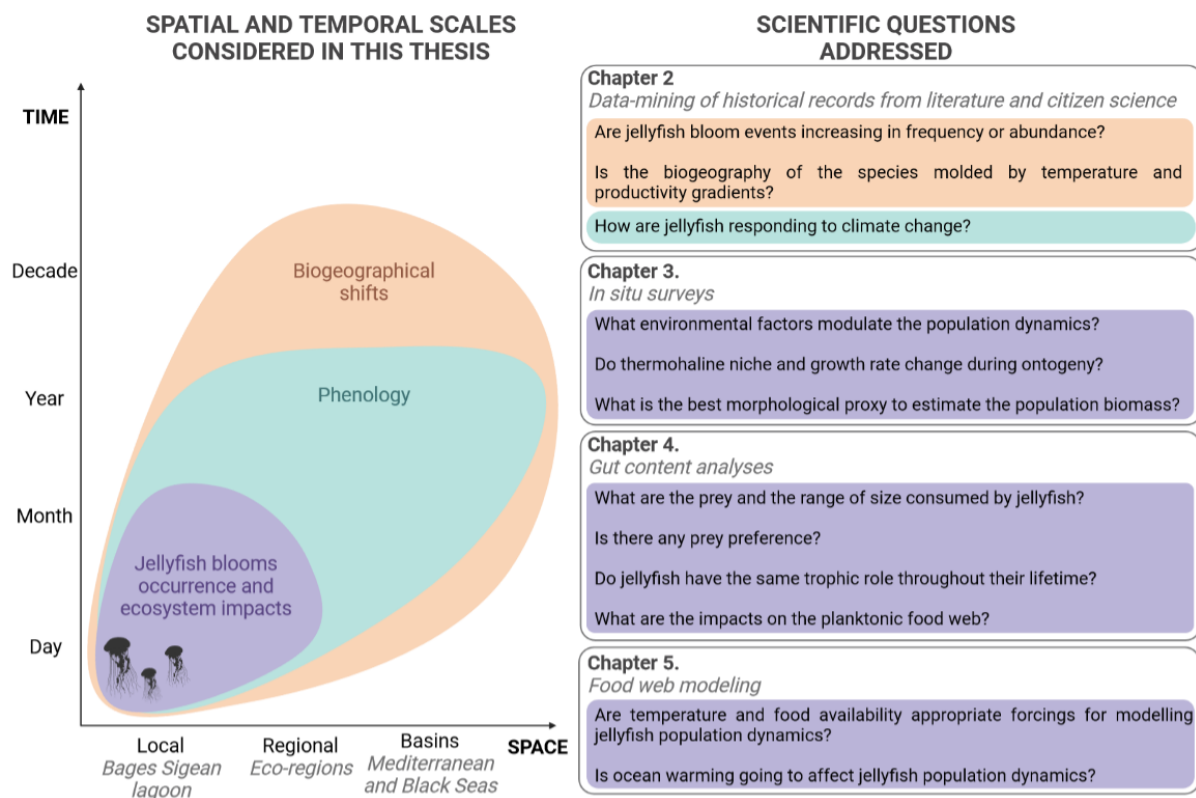
Historically, demographic (Kogovšek et al. 2010) and ecological studies (Pérez-Ruzafa et al. 2002; Lilley et al. 2009; Fuentes et al. 2011; Purcell et al. 2012b) on this species were very scarce. In recent years, the number of studies has experienced a notorious increase, related to an increasing frequency and intensity of the species blooms in many coastal areas of the Mediterranean and the Black Sea (Tinta et al. 2012; Stabili et al. 2018; Dönmez and Bat 2019; De Domenico et al. 2019; Basso et al. 2019). However, causal factors of this phenomenon, over the long term and large spatial scales, remain unknown.

The present study proposes an integrative approach to assess jellyfish ecology, looking at functional responses such as growth, thermal niches and phenology, together with trophic interactions, to quantify and evaluate the role of the species in planktonic food webs. To do so, we took advantage of a particular opportunity to follow one population of *R. pulmo* in Bages Sigean lagoon, where the species completes its life cycle. At regional scale, the study was performed gathering historical and contemporaneous data on *R. pulmo* abundance, including both published scientific literature and information obtained from citizen science records. With this multi-method design, we attempted to decipher ecological aspects of the species, working at different temporal and spatial scales. The study provides [i] novel information about the biology, trophic ecology, and biogeography of the barrel jellyfish *R. pulmo*; [ii] quantitative assessment of temporal changes on jellyfish biomass at regional and sub regional scales, and [iii] assess the role of the species in the planktonic food web by means of mechanistic modelling.



## 1.4 | OBJECTIVES

This thesis aims to provide an assessment of the biogeography, population dynamics and trophic ecology of *R. pulmo* (Fig. 1.9). This was tackled by using three main approaches. First, the biogeography and phenology of the species were assessed on the long term and at a large spatial scale. Secondly, the population dynamics and trophic ecology of a *R. pulmo* population were surveyed over one year. Thirdly, the population dynamics was modelled within a dynamic plankton food web model. To address the thesis goals, this project is structured in four interlinked chapters (Fig. 1.9). The former (Chapter 2) quantifies by means of data mining, environmental drivers shaping the species' variability in southern European seas. The second (Chapter 3) investigates, at the local scale, the effects of environmental factors on *R. pulmo* pelagic life stages dynamics and growth rates, and the third one (Chapter 4) evaluates the diet and the potential ontogenetic and seasonal dietary shifts. Finally, the results were integrated into a food web model to assess the trophic role of *R. pulmo* in the dynamics of the plankton food web (Chapter 5).



**FIGURE 1.9.** Schematic representation of the organization of this thesis, including the spatial and temporal scale considered and the scientific question addressed.



## CHAPTER 2.

# BIOGEOGRAPHY AND PHENOLOGY OF *RHIZOSTOMA PULMO* IN SOUTHERN EUROPEAN SEAS

Valentina Leoni<sup>1</sup> · Delphine Bonnet<sup>1</sup> · Eduardo Ramírez-Romero<sup>2,3</sup> · Juan Carlos Molinero<sup>4</sup>

<sup>1</sup> MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Montpellier, France

<sup>2</sup> Instituto Mediterraneo de Estudios Avanzados, IMEDEA (CSIC-UIB), Esporles, Spain

<sup>3</sup> AZTI, Marine Research, Basque Research and Technology Alliance (BRTA), Sukarrieta, Spain

<sup>4</sup> MARBEC, IRD, CNRS, Ifremer, Université de Montpellier, Sète, France

Published in **Global Ecology and Biogeography** (2021)



## Biogeography and phenology of *Rhizostoma pulmo* in southern European seas

Currently, a challenge the researchers are dealing with is to understand the extent to which jellyfish blooms frequency and intensity have increased in the last decades and to identify the causes of those changes. The bottleneck to solve this question is the lack of long-term datasets on jellyfish, mainly due to the historical neglect of gelatinous zooplankton research compared to fishes and crustaceans. As blooms are monospecific demographic events, and jellyfish species respond differently to environmental forcings and anthropogenic changes, studies at the species level might help to answer this question. Unfortunately, the vast majority of analyses at a species level is confined to a specific area and are not sustained over time, hampering the study of a species throughout its entire range of distribution.

Jellyfish have overcome historical global changes. Therefore, it would be expected that some species adapt and also take advantage of new conditions in the Anthropocene era. Numerous examples suggest this is already happening in some coastal areas, with evident impacts on human activities. In consequence, understanding the driving factors shaping large-scale patterns of jellyfish proliferations is imperative to design adaptative strategies and may provide key information on the effects of environmental changes in the marine realm. Despite the great efforts in long-term study of zooplankton, the analysis of macro medusae in the Southern European seas is very sparse. In recent years, jellyfish populations monitoring has improved with, for example, the implementation of citizen science programs.

In this context, we have gathered published data on *Rhizostoma pulmo*, the larger native jellyfish of the Mediterranean Sea, and addressed the following questions: How is the jellyfish *R. pulmo* responding to climate change? Are *R. pulmo* bloom events increasing in frequency and abundance? Is the biogeography of the species molded by temperature and productivity gradients in the Mediterranean Sea?

**Keywords:** Black Sea • Cnidarian biogeography • Gelatinous carnivore proliferations • Global anthropogenic changes • Mediterranean Sea • Warming





## 2.1 | INTRODUCTION

Compound effects of global ocean threats, such as warming, acidification, overfishing, eutrophication and habitat modifications, have triggered dramatic changes in the structure and function of marine ecosystems (Hoegh-Guldberg and Bruno 2010). Owing to their ecological and economic implications, some of the most challenging consequences for sustainability are habitat and diversity losses (Hoegh-Guldberg and Bruno 2010), the expansion of invasive species and the proliferation of harmful populations, such as toxic algae and jellyfish (Richardson et al. 2009).

The increase in massive bloom events of jellyfish (used here to refer to organisms of the phylum Cnidaria, subphylum Medusozoa; Richardson et al. 2009) is considered among the current major threats for the sustainable use of marine resources. Jellyfish temporal patterns, at species or functional group levels, have shown variations in abundance, ranging from long-term cycles (Goy et al. 1989; Kogovšek et al. 2010) to strong interannual shifts (Molinero et al. 2008). However, jellyfish biomass in temperate ecosystems appears to be increasing in recent decades (Brotz et al. 2012), expanding into new areas (Lucas et al. 2014) and experiencing phenological changes (Van Walraven et al. 2015). Underlying causes of these changes range from local to global factors. At a local scale, eutrophication modifies environmental conditions, increasing hypoxia and turbidity, and promotes enhanced small-zooplankton abundance, conditions that benefit jellyfish over fishes (Purcell et al. 2007).

Among global drivers, warming has been shown to favor some jellyfish species, increasing their reproduction rate and expanding their range of distribution to higher latitudes (Purcell 2005; Lucas et al. 2014). Warming has been also associated with changes in terrestrial and aquatic species' life history events, for example, peaks of seasonal abundance, migration, breeding, and blossoming (Edwards and Richardson 2004; Cohen et al. 2018), which may disrupt ecological interactions at the same or adjacent trophic levels (Edwards and Richardson 2004). Thereon, phenology has been proposed as the simplest process to track changes in the ecology of species in response to climate change (marine animals: Brown et al. 2016; plants: Wolkovich et al. 2014; terrestrial animals: Cohen et al. 2018). Long-term datasets are essential to uncover drivers of biomass and phenological changes (Brotz et al. 2012; Condon et al. 2013). However, the lack of historical data and sustained surveys of jellyfish populations hampers the possibility of identifying how these organisms respond to global change (Brotz et al. 2012). In recent years, citizen science has progressively gained relevance in ecology and environmental sciences as a way to increase observation and sampling efforts over wide geographical areas

otherwise difficult to cover under traditional scientific surveys (Edelist et al. 2020). Particularly, numerous citizen science projects have been launched in the Mediterranean Sea (JellyWatch program, CIESM 2014; Boero 2014), which have allowed the spatio-temporal resolution of data to be improved (Edelist et al. 2020).

The Mediterranean Sea is considered as a biodiversity hotspot (Coll et al. 2012) with coexisting temperate and subtropical biota and a large proportion of endemic species. Such biodiversity is threatened by climate change, habitat modification, resource exploitation, pollution, eutrophication, and alien species (Bianchi and Morri 2000). The Black Sea is a semi-enclosed ecosystem connected with the Mediterranean Sea by the Sea of Marmara, and about 80% of its current fauna are Mediterranean settlers (Zaitsev and Mamaev 1997). The Black Sea has experienced historical events of increasing nutrient inputs that have promoted biodiversity changes, including massive proliferations of native and invasive jellyfish species (Zaitsev and Mamaev 1997).

These southern European seas account for a wide diversity of jellyfish, both native and alien species (Boero 2014). *Rhizostoma pulmo* is one of the six species considered as a nuisance in the area (Kokelj and Plozzer 2002) and is the biggest bloom-forming jellyfish (c. 40 cm bell diameter) inhabiting this region (Jarms and Morandini 2019). Despite the potential negative impacts for tourism (e.g., because of stings) and fishing activities (e.g., by clogging nets), this species could act positively for fish populations by providing refuge to juvenile stages of commercial fishes (Mir-Arguimbau et al. 2019), and being a food resource for many marine species (Hays et al. 2018). Moreover, the carcasses of dead organisms represent an organic-rich substrate that supports rapid bacterial growth, impacting the surrounding environment (Tinta et al. 2012).

*Rhizostoma pulmo* presents a complex life cycle. The pelagic free-swimming stage (medusa) reproduces sexually and releases planulae that will settle on a hard substrate. The planulae develop into scyphistomae (polyp benthic stage), which grow and reproduce asexually by buds and podocysts. Under favorable conditions, mature scyphistomae strobilate and release ephyrae (c. eight per polyp; Fuentes et al. 2011). Each ephyra grows and develops into a new medusa. No information exists about its benthic stage in nature (Jarms and Morandini 2019). Based on genetic studies, the existence of different *R. pulmo* populations has been identified in the Mediterranean Sea (e.g., Ben Faleh et al. 2017), where regionalized hydrodynamic processes promote asynchrony of phenotypic patterns of zooplankton species (Yebra et al. 2011). In the last decade, the species has gained notoriety due to massive bloom events with negative economic impacts on tourism and fisheries, due to clogged and damaged fishing nets

and contaminated catches (Fuentes et al. 2011). However, unequivocal evidence on causal factors of this phenomenon, over the long term and coarse scales, remains elusive.

To examine biogeographical variations and temporal changes experienced by *R. pulmo* in southern European seas, we gathered a comprehensive dataset of the species' occurrence, including scientific literature and citizen reports, over the last two centuries. Here, we test hypotheses relating to global anthropogenic changes and jellyfish proliferations. We hypothesize (1) that bloom events are favored by coastal eutrophication and climate warming, due to higher food abundance and enhanced reproduction rates. Over the long-term scale, we expect (2) that the rising temperatures in the region will alter the timing of bloom events, promoting earlier and possibly massive blooms under high temperature regimes. If higher temperatures significantly affect the seasonal dynamics of the species, it is plausible (3) that temperature geographical gradients mold biogeographical patterns of *R. pulmo* blooms, although the biogeographical structure may be shaped by hydrographic dynamics that govern the Mediterranean and Black Seas' ecoregions.

## 2.2 | METHODOLOGY

### 2.2.1 | Study area

The Mediterranean Sea is the largest and deepest semi-enclosed sea in the world, with a surface area of 2.5 million km<sup>2</sup> and a water volume of 3.7 million km<sup>3</sup>. It is located in a transitional area between subtropical and temperate climates. Due to its low nutrients and chlorophyll concentrations, this basin displays a general oligotrophic character. However, some regional features, such as local winds, river discharges and municipal sewage outlets can locally enrich coastal areas. The basin is characterized by strong seasonality and marked increasing gradients from west to east and north to south of temperature. The variability of physical and chemical features affects the distribution of phytoplankton biomass, with an increasing gradient in chlorophyll concentration from east to west (Salgado-Hernanz et al. 2019). The Mediterranean Sea has been historically, and is still, exposed to intense anthropic activities, and is of particular interest due to its high biodiversity compared to its surface and volume (Bianchi and Morri 2000).

The Black Sea is a eutrophic semi-enclosed sea with a surface area of 423,500 km<sup>2</sup> and a water volume of 537,000 km<sup>3</sup>. The north-western region is the shallowest area, with a large volume of freshwater coming from rivers and this area presents the highest biological productivity (Zaitsev and Mamaev 1997).

To assess the biogeographical patterns of *R. pulmo*, we used the bioregionalization of coastal shelf areas from the Marine Ecoregions of the World (MEOW) classification. From this classification, we used the ecoregions proposed for the Mediterranean and Black Seas, defined by the dominant biogeographical forcing, such as isolation, nutrient inputs, freshwater influx, temperature regimes, currents, and coastal complexity (Spalding et al. 2007). We distinguished eight ecoregions: 1. The Alboran Sea; 2. The Western Mediterranean; 3. The Adriatic Sea; 4. The Ionian Sea; 5. The Tunisian Shelf; 6. The Aegean Sea; 7. The Levantine Sea; and 8. The Black Sea.

## **2.2.2 | Data mining**

### **2.2.2.1 | Environmental data**

We used potential environmental drivers of jellyfish bloom events based on current hypotheses linking jellyfish with temperature and productivity (primary production, Purcell et al. 2007). Temperature is probably the most important physical variable structuring marine ecosystems and is recognized to impact medusae metabolism and asexual reproduction of the scyphistomae (Lucas et al. 2012; Marques et al. 2019). We used two sources of sea surface temperature (SST) data. First, a reanalysis of monthly data was used to track the historical temperature variability in the Mediterranean and the Black Seas over the period 1870 to 2019. These data were obtained from the Met Office Hadley Centre observations datasets (Met Office 2019). Second, high spatial and daily resolution SST datasets for each ecoregion over the period 2008 to 2018 were analyzed to assess the phenology of *R. pulmo*. These data were downloaded from the Ocean Color database of the mission moderate resolution imaging spectroradiometer (NASA 2019). From these data, indices of seasonal seawater temperature were derived by calculating the mean SST for each meteorological season, winter (December, January, February), spring (March, April, May), summer (June, July, August) and autumn (September, October, November).

Eutrophication benefits jellyfish over fish through enhancing primary production and small-zooplankton abundance, hypoxia and turbidity. Here, we used chlorophyll-*a* concentration (Chl *a*) as a proxy of food abundance (Lucas et al. 2014). Chl *a* monthly data were obtained at Level 4 from the Copernicus Marine Environmental Monitoring system (CMEMS 2019) from 1998 to 2017 with a 4-km horizontal resolution.

#### 2.2.2.2 | *Rhizostoma pulmo* data

The genus *Rhizostoma* comprises three recognized species: *Rhizostoma pulmo* (Macri, 1778), *Rhizostoma octopus* (Gmelin, 1791) and *Rhizostoma luteum* (Quoy & Gaimard, 1827); however, only *R. pulmo* inhabits the Mediterranean and Black Seas (Jarms and Morandini 2019). Data on the species recorded outside these areas were not considered. An exhaustive compilation of quantitative and qualitative historical records available for *R. pulmo* medusae in the Mediterranean and Black Seas was performed.

A total of 7,359 monthly or annual records of *R. pulmo* were registered from 1810 to 2019 in the southern European seas. A list of the data sources is found in Tables S2.1, S2.2. When possible, each record was georeferenced, including the country and locality (e.g., bay, lagoon, city). Two different types of data sources were used: scientific literature from peer-review papers (Table S2.1) and citizen science data (details of available sources are provided in Table S2.2). The information from citizen science projects (e.g., CIESM JellyWatch; Occhio alla Medusa; MedusApp) has been previously screened through quality control and standardization by experts, before being available on the websites. Scientific papers were assembled through an exhaustive search on Google Scholar and Web of Knowledge. The terms used were: “*Rhizostoma*”, “*Rhizostoma pulmo*”, “Mediterranean jellyfish”, “Mediterranean medusa”, “Black Sea jellyfish”, “Black Sea medusa”, and the name of each ecoregion followed by “jellyfish”, “medusa” or “*Rhizostoma pulmo*”. Only papers where the year of recording was indicated ( $n = 39$ ) were included in this study. The compiled data were qualitative (presence/absence), quantitative (individuals per 100 m<sup>3</sup>) and semi-quantitative (categories of the number of individuals).

#### 2.2.3 | Long-term trend assessment

Historical published records and data from citizen science programs were used to build a single comprehensive database to evaluate temporal and biogeographical patterns of the species (Fig. 2.1a). As the data acquisition methods differ among research programs, we used a semi-quantitative index to assess space-time patterns of *R. pulmo* bloom events. The index ranges from 0 to 2, where 0 denotes jellyfish ‘absence’, 1 indicates the ‘presence’ of the species at low abundances, and 2 indicates the ‘bloom’. Based on personal observations on the population dynamics of *R. pulmo*, a bloom was considered here when abundance rose to more than 1 individual per m<sup>3</sup>. Details of the index construction are given in Table S2.3.

### **2.2.4 | Objective 1: Temporal bloom pattern**

Generalized linear models (GLMs) were used to test the relationship between the annual averages of the abundance index and the environmental variables. Only two records were found before 1875, therefore, the analyses were done considering data after this year. Due to the differences in the availability and length of data on environmental factors (i.e., temperature and Chl *a*), their influences were tested on different periods. The effect of temperature was tested over the period 1875-2019, while the separate and combined effects of temperature and Chl *a* were tested over the period 1998-2017. Prior to the analyses, SST and Chl *a* data were seasonally detrended by subtracting the monthly average from each value and dividing by the monthly standard deviation.

### **2.2.5 | Objective 2: Interannual phenological changes**

Jellyfish bloom phenology can be characterized by a suite of metrics: start, duration, peak and end of bloom. First, a seasonal analysis was performed for the period 1985 to 2019, which includes data of all ecoregions. The monthly mean abundance index was displayed as a traffic-light plot by each ecoregion. Only references including month and year information were included ( $n = 3,619$ ).

To evaluate phenology changes in response to changing environmental conditions, the analysis of the phenology was evaluated for the last decade (period 2008-2018), as it was the period with monthly data and more than 20 data items per year. The cumulative sums were calculated for the monthly abundance index. The annual sum was set as 100%, and the month of the 15 and 85% cumulative abundance levels for each year was determined. These levels were defined as the ‘start of season’ and ‘end of season’, respectively (Greve et al. 2005). The ‘duration of season’ was estimated as the difference between the start and end of the season. Trends in phenology dynamics (start, end or duration of the medusae season) were evaluated with a linear model (LM). GLMs were used to test the separate effects of environmental parameters (i.e., annual and seasonal SST and Chl *a* concentration) and the interactions of SST and Chl *a* with *R. pulmo* phenological descriptors.

### **2.2.6 | Objective 3: Biogeographical patterns**

The geographical information was used to map the distribution of the species ( $n = 3,448$ , from 1875 to 2019). The environmental niche of the species regarding averaged patterns of SST and Chl *a* over the last decade (2008-2018) was extracted for each *R. pulmo* observation

over the same period. To avoid bias related to the sampling effort, only one observation per satellite pixel ( $4 \times 4$  km) was considered ( $n = 915$ ).

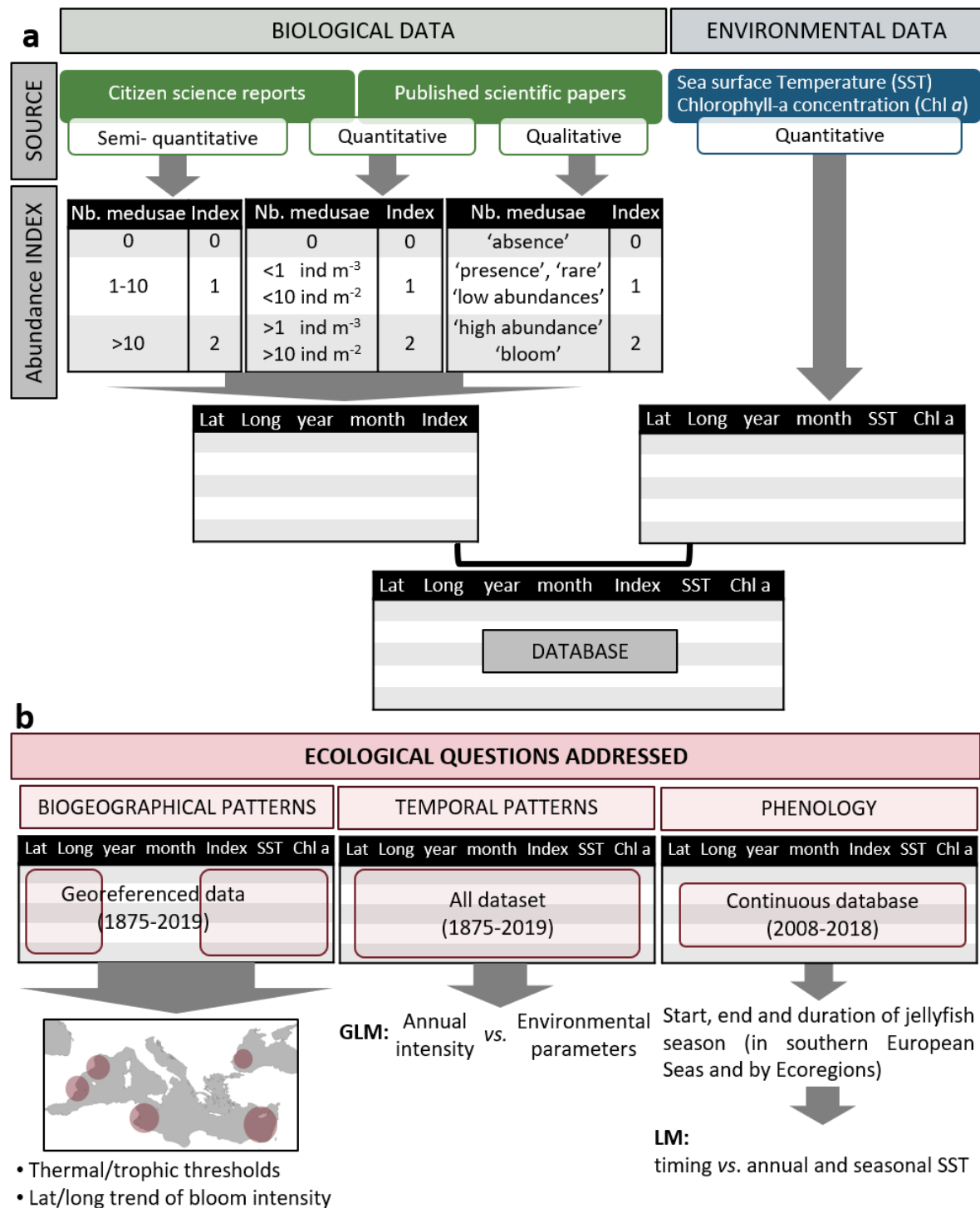
Temperature and productivity gradients governing hydrographic provinces in the Mediterranean Sea are likely to shape the biogeographical pattern of *R. pulmo* at the basin scale. This was assessed through the Mantel test, which measures the extent to which variation in dissimilarity in measured variables (e.g., bloom intensity) significantly changes over the spatial distances between sampling stations (e.g., latitudinal sites, Legendre and Legendre 1998). The Mantel test does not assume the distribution of data; instead the probabilities are computed by random permutations. Hence, the null hypothesis is tested by a randomization procedure where the value of the statistic,  $Z$ , is compared with the distribution found by randomly reallocating the order of the elements in one of the matrices. The statistical significance of Mantel correlations was assessed by Monte Carlo permutation (9,999 times). In addition, the quantile 75% of the bloom intensity was estimated by each latitudinal and longitudinal degree, and a LM was fitted between the quantiles and the latitude and longitude degrees.

#### **2.2.7 | Objective 4: Phenological differences among ecoregions**

Data were grouped in the ecoregions previously defined. Only occurrence data with month and year information were considered ( $n = 3,094$ , from 2008 to 2018). Three parameters were estimated each year in the ecoregions: (a) start of the bloom, denoted as the month of the first occurrence, that is, the month when the first record was reported in the year; (b) end of the bloom, denoted as the month of the last occurrence, that is, the last month of the year when the medusae were reported; and (c) duration of the bloom, the number of months between the months of first and last occurrences. GLMs were used to test the temporal change and the individual effects and the interactions of SST and Chl *a* with *R. pulmo* phenological descriptors. To assess the seasonality of the abundance index in the different ecoregions, the mean of the years 2008-2018 was considered in the last decade ( $n = 3,094$ ).

A step-by-step illustration of procedures for data collection and treatment, including the selection of statistical model, used in this study is provided in Figure 2.1. Data analysis was performed using the open source software R 3.6.0 (R Core Team 2020), while plots were created with the ‘ggplot2’ package (Wickham 2016) and ‘plot’. The GLMs were fitted through the function *glm*, and Mantel tests were performed with the R ‘vegan’ package (Oksanen et al. 2020) through the function *mantel*. The map illustrating the spatial distribution of records was produced using the open source software QGIS 3.4.4 (QGIS 2020). The map projection

employed was World Geodetic System 1984. The marine ecoregions layer was downloaded from the website The Nature Conservancy's maps (TNC 2019).



**FIGURE 2.1.** **a.** Schematic representation of biological (green) and environmental data (blue) collection and harmonization to build the database used in this work. **b.** Schematic representation of the procedures for the data analysis used in this study. LM = linear model; GLM = generalized linear model.



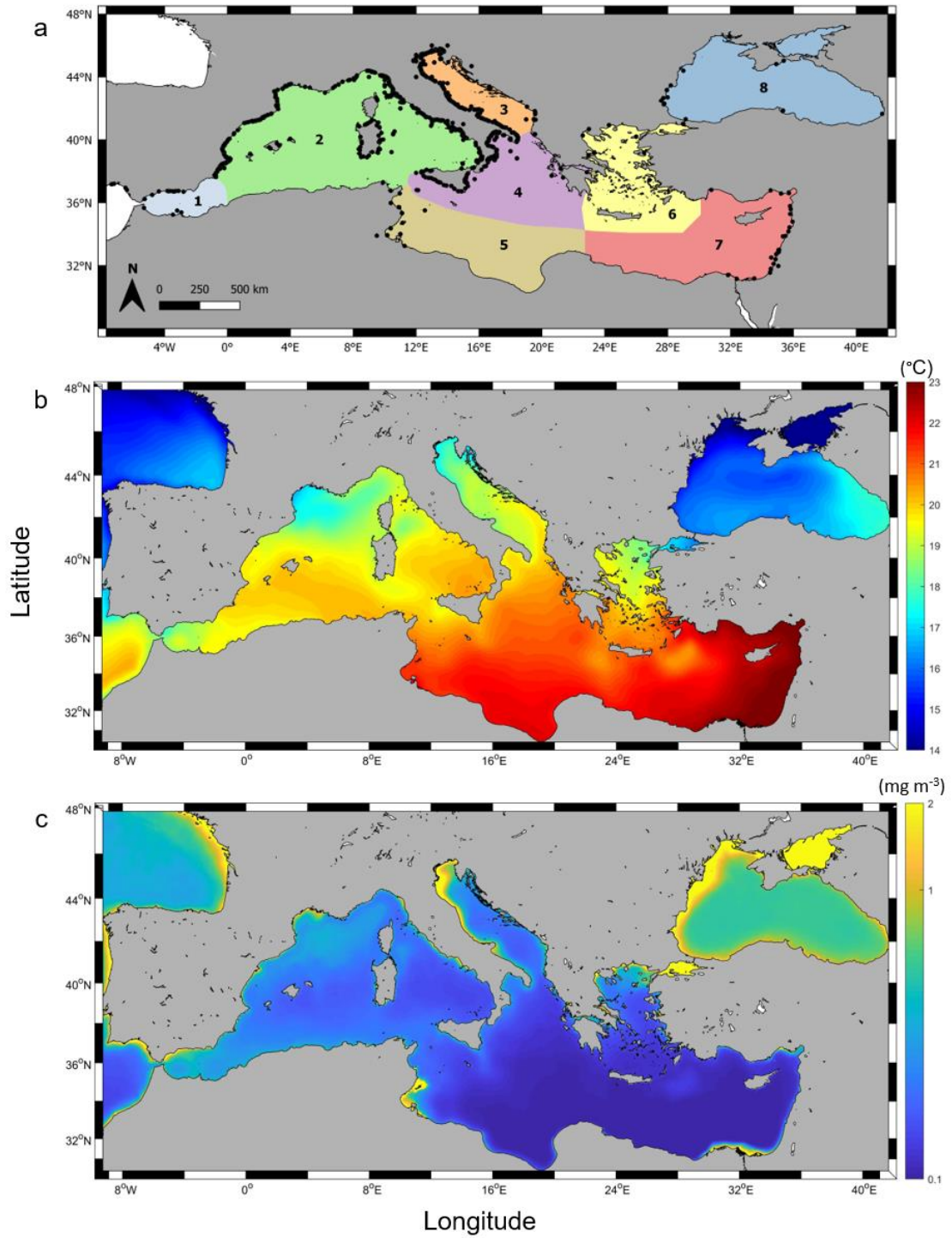
## 2.3 | RESULTS

The presence of *R. pulmo* has been recorded in all ecoregions of the Mediterranean Sea and the Black Sea (Fig. 2.2a). SST (°C) annual average during the period 2008–2018 exhibited marked increasing north to south (*c.* 17 to 22°C) and west to east (*c.* 18 to 23°C) gradients (Fig. 2.2b) in the Mediterranean Sea, where the coldest areas were the Gulf of Lion and the northern Adriatic Sea. The Black Sea was the region with the lowest SST values (14–18°C). Outflowing surface Black Sea waters partially explain the lower SST values in the Aegean Sea compared with the Ionian Sea at the same latitude. Chl *a* (mg m<sup>-3</sup>) showed an overall eastward decreasing pattern over the Mediterranean Sea (*c.* 0.5 to 0.1 mg m<sup>-3</sup>). However, productive areas in the northern Adriatic Sea and along the Tunisian coast with high Chl *a* concentrations (*c.* 2 mg m<sup>-3</sup>) were detected. Likewise, the Black Sea displayed the highest values of Chl *a* (*c.* 0.7 to 2 mg m<sup>-3</sup>; Fig. 2.2c).

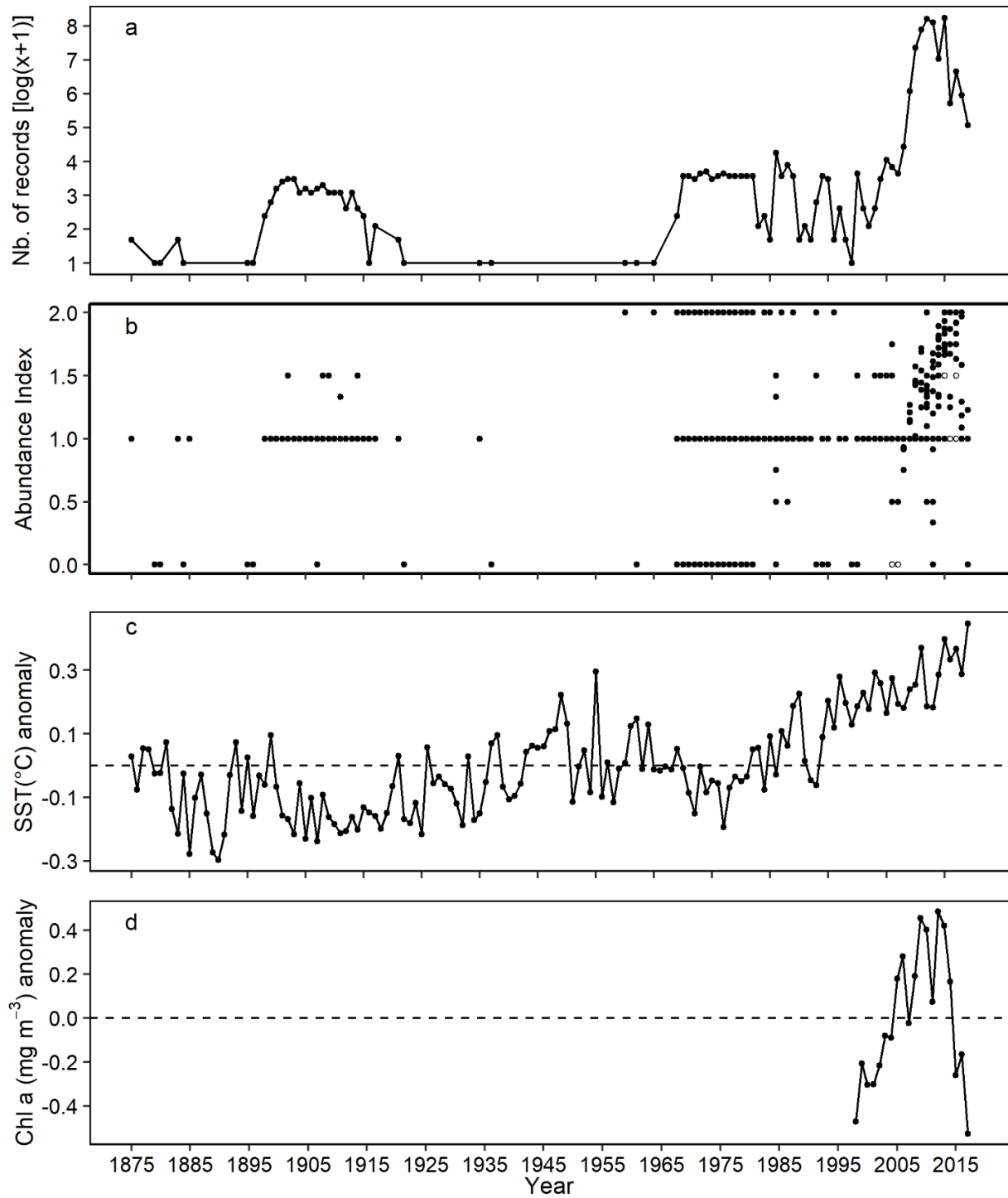
### 2.3.1 | Objective 1: Temporal bloom pattern

The long-term records of *R. pulmo* over the period 1875 to 2019 mainly covered the periods 1895 to 1925 and 1965 to 2019, while scattered data were collected before 1895 and between 1925–1965. The pattern of variability of *R. pulmo* bloom events showed sustained high numbers between 1875 and 1920 with a decline afterward. Similarly, high values were observed from the late 1960s to the early 1980s, followed by a marked variability until the early 2000s and a conspicuous increase in the last decade (Fig. 2.3a).

An overall substantial increase in frequency and intensity of the abundance index was observed in recent decades (Fig. 2.3b). From 1965, the observation effort has been sustained and a progressive abundance index increment was observed. The intensity of events was partially explained by the increasing trend in temperature anomalies (Fig. 2.3c) during the period 1875–2019 in the Mediterranean Sea (GLM,  $p < 0.05$ , % deviance explained = 23%). However, the interaction SST\*Chl *a* and the individual effect of Chl *a* (Fig. 2.3d) did not show a significant effect on the bloom intensity (GLM,  $p > 0.05$ ).



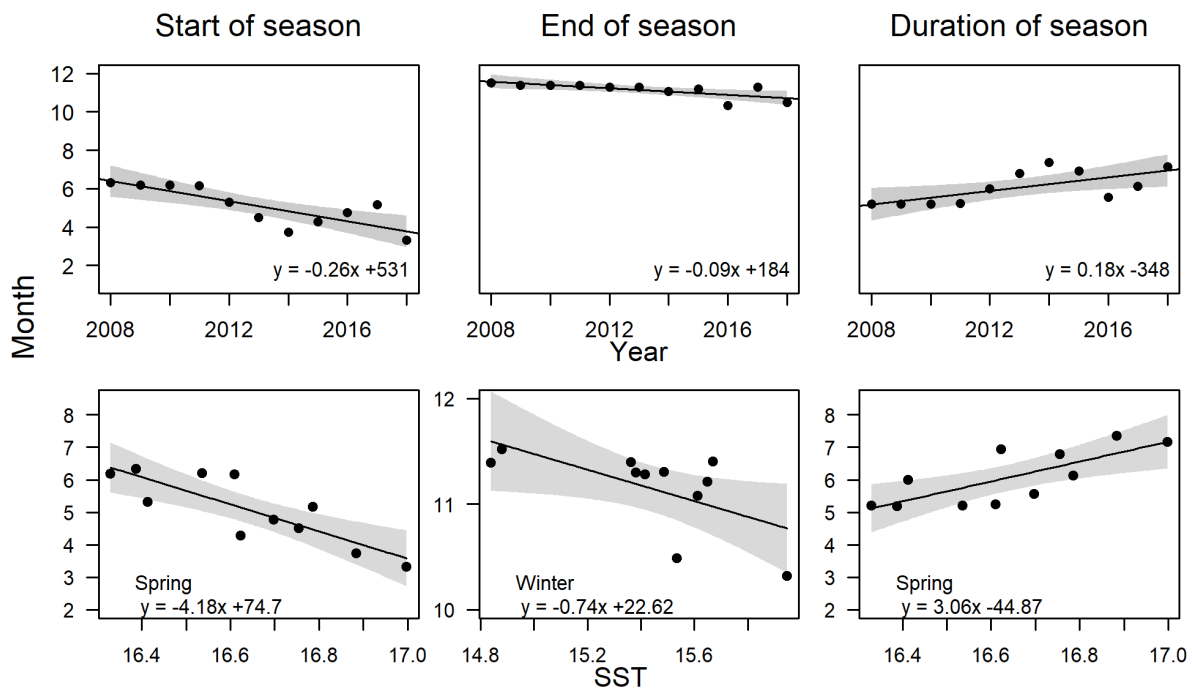
**FIGURE 2.2.** **a.** Georeferenced records of *Rhizostoma pulmo* (black dots) in the ecoregions of the southern European seas and the Atlantic Ocean from 1875 to 2019. Ecoregions: Alboran Sea (1), Western Mediterranean (2), Adriatic Sea (3), Ionian Sea (4), Tunisian Shelf (5), Aegean Sea (6), Levantine Sea (7) and Black Sea (8). **b.** Sea surface temperature (°C) for the period 2008-2018 and **c.** chlorophyll-a mean concentration (mg m<sup>-3</sup>) for the period 2008–2018 in the Mediterranean and Black Seas.



**FIGURE 2.3.** **a.** Number of annual bloom events of *Rhizostoma pulmo* in southern European seas from 1875 to 2018. **b.** Monthly mean by year from 1875 to 2019 of the abundance index (0: jellyfish absence, 1: low abundances, 2: bloom). Full dots = Mediterranean Sea, empty dots = Black Sea. **c.** Annual standardized anomalies of sea surface temperature (SST) from 1870 to 2019. The dashed line indicates the overall average value for the entire period. **d.** Chlorophyll *a* (Chl *a*) annual standardized anomalies from 1998 to 2017. The dashed line indicates the average value for the period 1998–2017.

### 2.3.2 | Objective 2. Phenological changes

At the Mediterranean scale, the start and end of the season of *R. pulmo* have moved forward in the last 10 years (Fig. 2.4; LM start of season:  $p < 0.01$ ,  $r^2 = 0.61$ , slope =  $-0.27$ , end of season:  $p < 0.01$ ,  $r^2 = 0.49$ , slope =  $-0.09$ ) and were negatively correlated with an increasing annual SST (LM, start of season:  $r^2 = 0.66$ ,  $p < 0.01$ , slope =  $-4.1$ , end of season:  $r^2 = 0.45$ ,  $p < 0.05$ , slope =  $-1.3$ ). From 2009 to 2011, the medusae season started in June, while in 2018, jellyfish occurred 2 months before, in April. The end of the season arrived earlier in the year, changing from December in 2008 to October in 2018. However, the duration of the medusae season has increased significantly in the last 10 years (Fig. 2.4; LM,  $p < 0.01$ ,  $r^2 = 0.39$ , slope =  $0.18$ ) from 5 to 7 months. These changes were significantly correlated with annual SST (LM,  $r^2 = 0.45$ ,  $p < 0.05$ , slope =  $2.8$ ), which showed a significant increase (LM,  $p < 0.01$ ,  $r^2 = 0.55$ , slope =  $0.05$ ) from  $19$  to  $19.7^\circ\text{C}$  in 10 years.



**FIGURE 2.4. Top panel:** Advancing start of season of *Rhizostoma pulmo* [linear model (LM),  $p < 0.01$ ,  $r^2 = 0.61$ ], end (LM,  $p < 0.05$ ,  $r^2 = 0.48$ ) and increasing duration of season (LM,  $p < 0.01$ ,  $r^2 = 0.39$ ). Grey areas indicate 95% confidence limits. For each year from 2008 to 2018, the number of records is as follows: 2008:  $n = 21$ ; 2009:  $n = 148$ ; 2010:  $n = 572$ ; 2011:  $n = 977$ ; 2012:  $n = 1,342$ ; 2013:  $n = 1,198$ ; 2014:  $n = 402$ ; 2015:  $n = 1,393$ ; 2016:  $n = 112$ ; 2017:  $n = 284$ ; 2018:  $n = 141$ . **Bottom panel:** Linear relationship between spring sea surface temperature (SST) and the start (LM,  $p < 0.01$ ,  $r^2 = 0.66$ ) of the seasonal cycle for *R. pulmo*, winter SST and the end of the season (LM,  $p < 0.05$ ,  $r^2 = 0.32$ ), and spring SST and the duration of the season (LM,  $p > 0.01$ ,  $r^2 = 0.52$ ). Grey areas indicate 95% confidence limits.

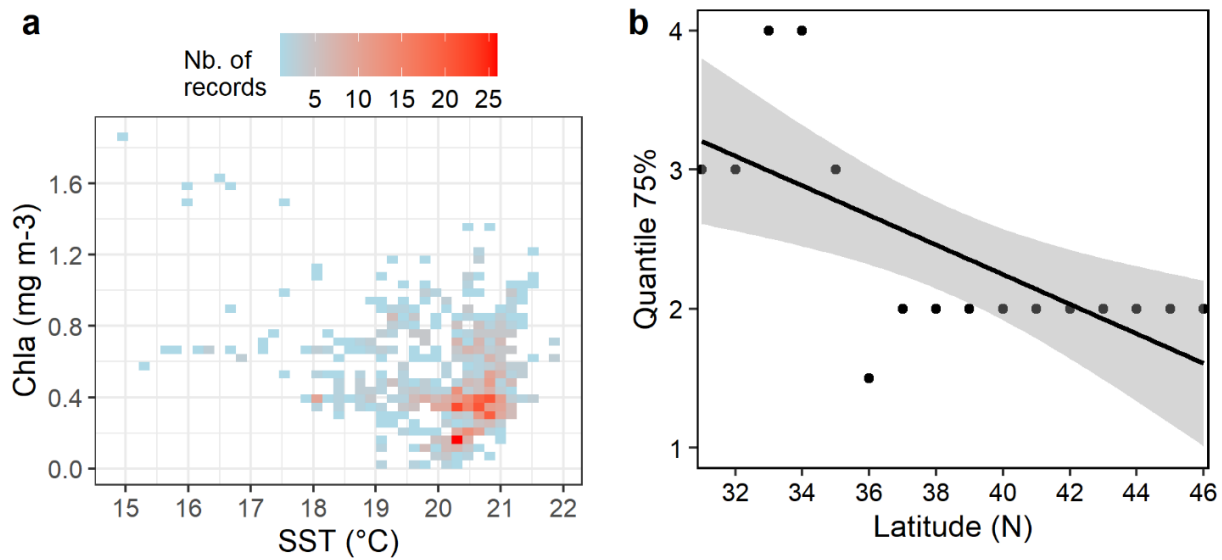
Spring temperature was significantly correlated with the start of the season (LM,  $r^2 = 0.66$ ,  $p < 0.01$ ) and duration of the season (LM,  $r^2 = 0.52$ ,  $p < 0.01$ ) (Fig. 2.4), meaning that during warm springs the species appeared earlier, and the duration of the season was prolonged. Winter temperature was significantly correlated with the end of the season (LM,  $r^2 = 0.32$ ,  $p < 0.05$ ; Fig. 2.4). No correlation was detected for summer or autumn temperatures against the estimated phenology metrics or with seasonal Chl *a* concentration.

### 2.3.3 | Objective 3: Biogeographical pattern

The presence of *R. pulmo* has been recorded in all ecoregions of the Mediterranean Sea and the Black Sea (Fig. 2.2a). A higher number of records was observed in the northern Mediterranean Sea (the Adriatic Sea and the north-western Mediterranean Sea) in comparison with the southern coast or the Black Sea. The few records in the Gulf of Cadiz (Atlantic Ocean) were of stranded individuals.

In the last decade, records of the species were observed between 15 and 22°C (Fig. 2.5a). However, most of the records were reported for temperatures between 20 and 21°C. They were associated with a wide spectrum of Chl *a* values (from 0.1 to 2 mg m<sup>-3</sup>), without a clear effect of chlorophyll concentration.

A positive and significant correlation was observed between the bloom intensity and the latitudinal and longitudinal gradients (Mantel test, 9,999 permutations,  $p = 0.001$ , observed correlation  $r = 0.31$ ). Furthermore, the species displayed a latitudinal trend in the quantile 75% of the bloom intensity (Fig. 2.5b). Northern locations (low temperature) showed less intense bloom events, while southern locations (high temperature) exhibit the most intense blooms events (LM,  $p < 0.05$ ,  $r^2 = 0.41$ , slope = -4.21). No significant longitudinal gradient was detected (LM,  $p > 0.05$ ).

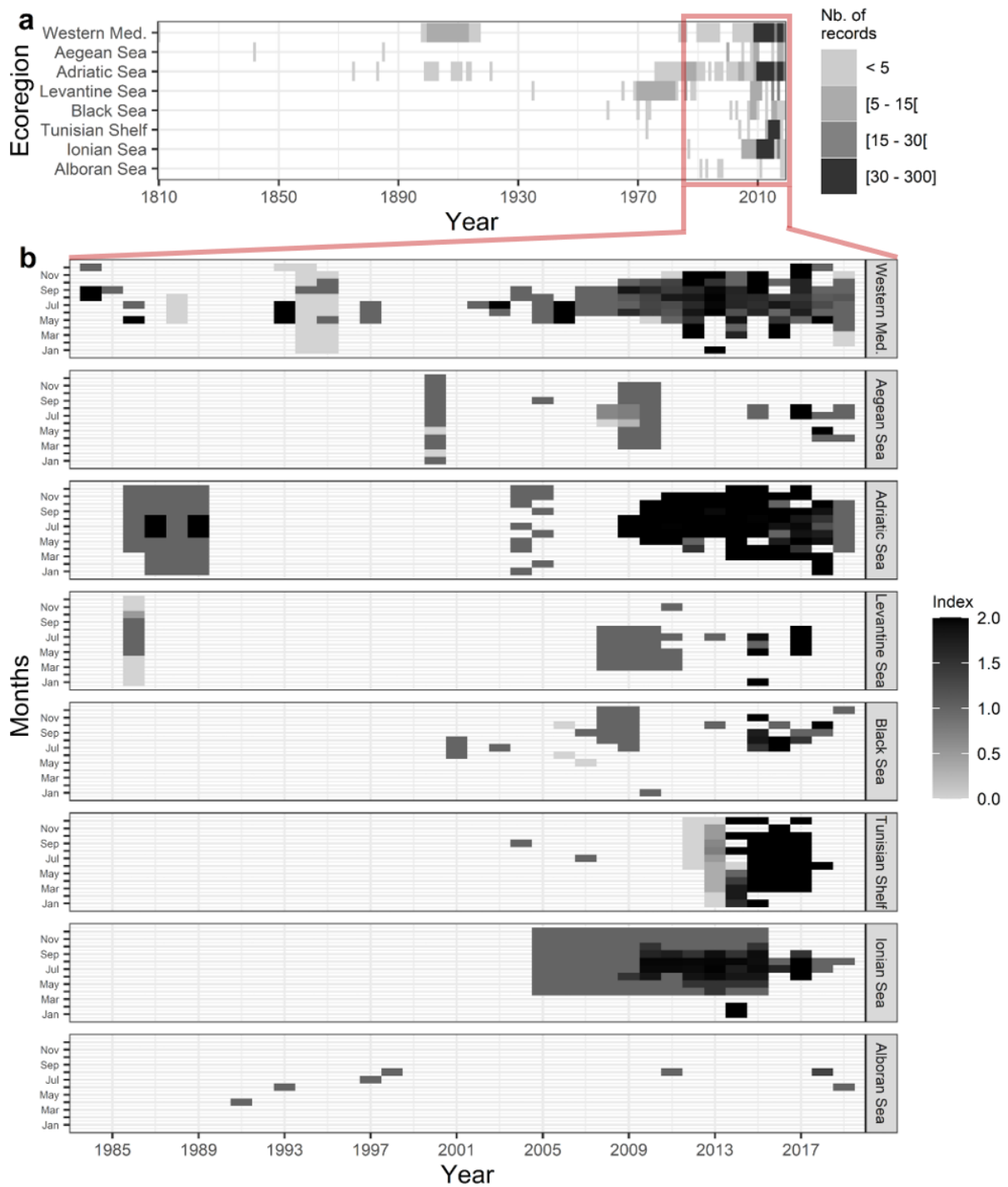


**FIGURE 2.5.** **a.** Thermal (°C) and trophic (Chl *a*) thresholds of *Rhizostoma pulmo* in the last decade (2008–2018). The colour scale, from lightblue to red, denotes the increase in the number of records. SST = sea surface temperature. **b.** Latitudinal trends of the 75% quantile of *R. pulmo*'s bloom intensity (Linear Model,  $p < 0.05$ ,  $r^2 = .41$ , slope =  $-4.21$ ). Grey areas indicate 95% confidence limits.

### 2.3.4 | Objective 4: Phenological differences among ecoregions

The number of presences recorded was heterogeneous both in time (1810–2019) and among ecoregions (Fig. 2.6a). The ecoregions with the greatest spatial coverage (i.e., with the oldest records) were the Western Mediterranean and Adriatic Seas. The third oldest record was observed in the Aegean Sea, followed by an extended period without records until 2000. Two periods of records, the first one between 1960 and 1980, and the second after 2000, are observed in the Black Sea. In all ecoregions, the number of records was fewer than 15 per year before 2005, followed by an increased number of records, with more than 200 records per year particularly in the Western Mediterranean, the Adriatic and the Ionian Seas, and the Tunisian Shelf. The records in the Ionian and the Alboran Seas appeared in both cases after 1975. Records in the Alboran Sea were of stranded specimens and started after 1990 until 2019.

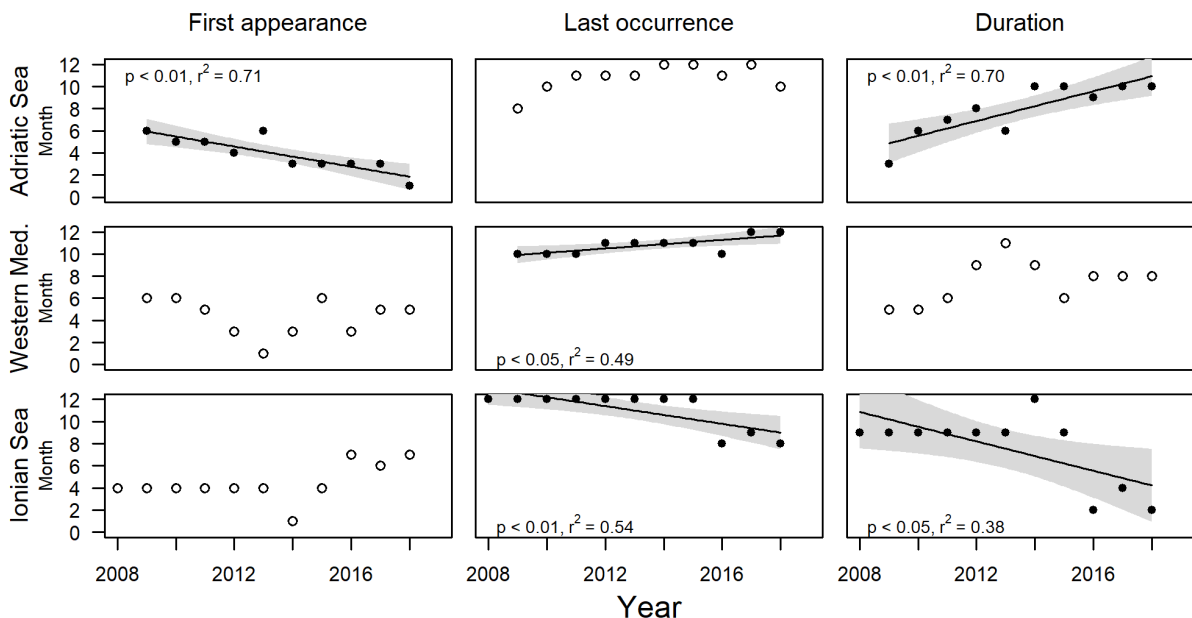
The monthly abundance index in the southern European seas' ecoregions during the period 1985–2019 (Fig. 2.6b) showed high variability at both seasonal and interannual scales. The abundance index experienced an increase after 2009 in most of the regions without a clear seasonality. The areas with the highest observations were the Western Mediterranean, the Adriatic and the Ionian Seas. We, therefore, used only data of the Adriatic Sea, the Western Mediterranean and the Ionian Sea, which had continuous records to evaluate the patterns of phenological parameters over 2008–2018. The month of first and last appearance and the duration of the bloom showed varied patterns among ecoregions (Fig. 2.7).



**FIGURE 2.6. a.** Interannual variability of the number of records (presence only) of *Rhizostoma pulmo* from 1810 to 2019, in the southern European seas ( $n = 7,128$ ). The color scale, from light grey to black, denotes the increase of the number of records (by intervals). White areas represent the absence of data. **b.** Seasonal and interannual variability of the average intensity of *R. pulmo* abundance, from 1985 to 2019, in the southern European seas ( $n = 3,619$ ). The color scale, from light grey to black, denotes the magnitude of jellyfish abundance (0: jellyfish absence, 1: low abundance, 2: bloom). White areas represent the absence of data.



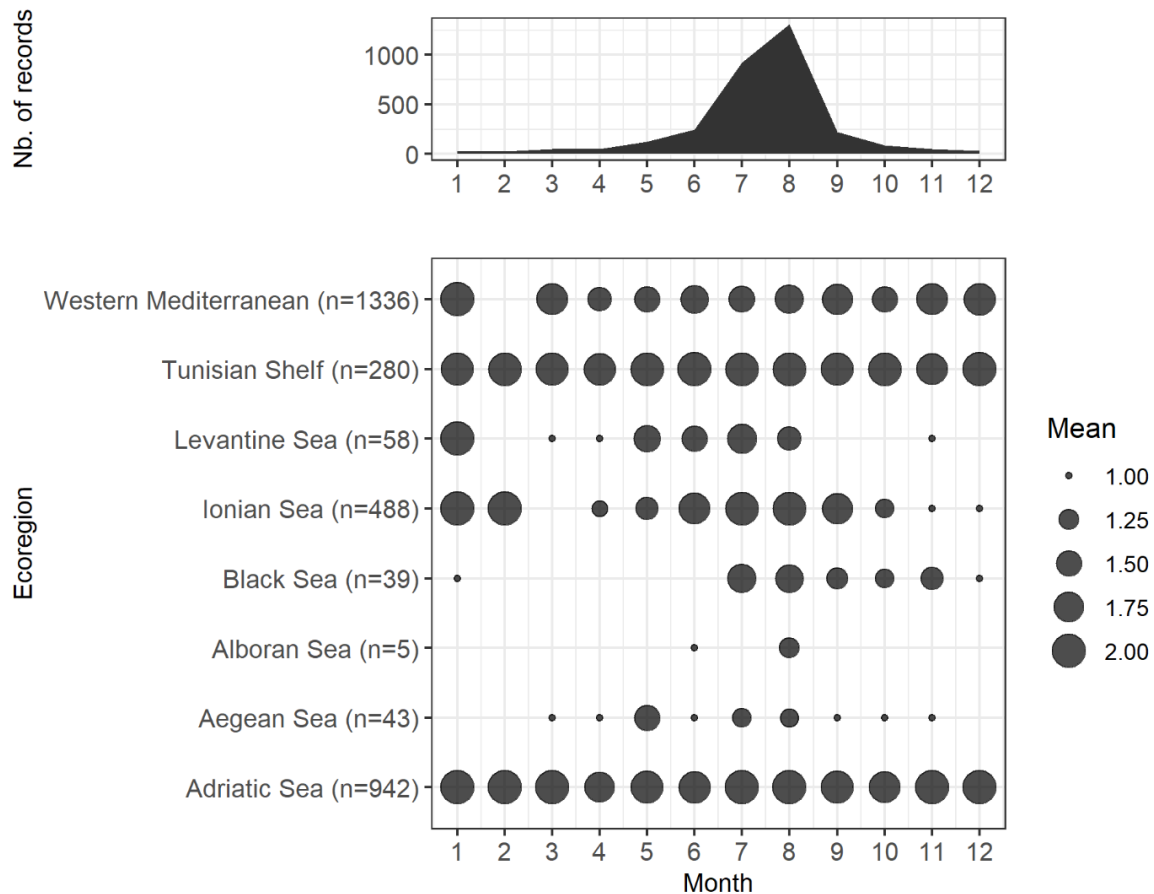
In the Adriatic Sea, a significant trend towards earlier appearances was noticed (LM,  $p < 0.01$ ,  $r^2 = 0.71$ , slope =  $-0.45$ ), resulting in a linear increase in duration (LM,  $p < 0.01$ ,  $r^2 = 0.70$ , slope =  $0.67$ ). These changes were, at least partly, shaped by temperature variability, as shown by a positive correlation between the duration of the bloom and winter SST (LM,  $p < 0.05$ ,  $r^2 = 0.41$ , slope =  $2.18$ ). None of the phenological parameters estimated for the Adriatic Sea showed a significant relationship with Chl  $a$ . In the Western Mediterranean, the first occurrence of the species was mostly between January and June during the studied period. However, the month of the last occurrence moved from October in 2008 to December after 2017 (LM,  $p < 0.05$ ,  $r^2 = 0.49$ , slope =  $0.19$ ), and was significantly correlated with annual SST (LM,  $p < 0.05$ ,  $r^2 = 0.45$ , slope =  $1.83$ ). None of the phenological parameters estimated for the Western Mediterranean showed a significant relationship with seasonal SST or Chl  $a$ . In turn, in the Ionian Sea the month of the last occurrence shifted from December during 2008 to 2015, to September–October during 2016–2018 (LM,  $p < 0.01$ ,  $r^2 = 0.54$ , slope =  $-0.40$ ), resulting in a linear decrease in duration (LM, 2008–2018:  $p < 0.05$ ,  $r^2 = 0.38$ , slope =  $-0.66$ ) from more than eight months to less than five. The month of last occurrence was correlated with spring temperature (LM,  $p < 0.05$ ,  $r^2 = 0.31$ , slope =  $-3.88$ ). We did not find any statistical support for the potential relationship between productivity, as indexed by Chl  $a$ , and jellyfish phenology.



**FIGURE 2.7.** Phenological interannual changes of *Rhizostoma pulmo* at ecoregion scale from 2008 to 2018. Linear models identified significant patterns in the month of first appearance (Adriatic Sea), the month of last occurrence (Western Mediterranean and the Ionian Sea) and the duration of the medusae presence (Adriatic and Ionian Seas). Grey areas indicate 95% confidence limits.



Overall, the observed number of events recorded displayed a great number of records from June to September (Fig. 2.8). The average annual cycle, as well as the monthly mean of the abundance index, markedly varied among ecoregions (Fig. 2.8).



**FIGURE 2.8. Top:** Number of monthly records of *Rhizostoma pulmo* in southern European seas (2008–2018). **Bottom:** Average seasonality of the abundance intensity of *R. pulmo* by ecoregion over the period 2008–2018. The absence of a circle indicates the absence of data. Symbol size and scale number denote the magnitude from 1 (low abundance) to 2 (blooms) ( $n$  = number of records).

*R. pulmo* was present all year round on the Tunisian Shelf and in the Adriatic Sea, with constant high abundance all year round. These areas coincide with the most productive coasts in the Mediterranean Sea (Fig 2.2c). In the Western Mediterranean the species was present all year round except in February. The westernmost records reported in the Alboran Sea were scarce ( $n = 5$ ), with low bloom intensity values concentrated in the summer months. The eastern basin of the Mediterranean Sea, including the Aegean, Ionian and Levantine Seas, showed remarkable variability. The Aegean Sea was the ecoregion where the species was restricted to summer, spring and autumn months, and showed variable monthly abundances. In the Ionian Sea, the species appeared all year round except in March, with variable intensities. In the

Levantine Sea, the species was present in high abundances during the summer months, although it has been reported as well in January and sporadically in November. Finally, in the Black Sea, *R. pulmo* appeared in summer and disappeared at the beginning of winter, with high variability in its abundance during the year. Despite all these differences, the species was present in almost all ecoregions during the summer months, and in all ecoregions in August. It is important to highlight that a great heterogeneity of data exists among ecoregions; the Western Mediterranean, the Tunisian Shelf, and the Adriatic and Ionian Seas being the ecoregions containing the majority of the data (more than 200 records in the last decade by ecoregion).

## 2.4 | DISCUSSION

This study provides a synoptic picture of the biogeographical and phenological patterns of the largest, and one of the most common, jellyfish in the southern European seas.

### 2.4.1 | Environmental drivers of demographic changes

The observed increase of the intensity and frequency of *R. pulmo* blooms events over the last decade, concurrently with positive temperature anomalies, suggests that this species benefits from warm temperatures. In particular, bloom events are observed when the temperature is between 20 and 21°C (Fig. 2.5a). Experimental evidence has shown that *R. pulmo* produces more buds and ephyrae per scyphistomae at high temperatures, that is, between 21 and 28°C, compared to the production at lower temperatures, that is, 14°C (Purcell et al. 2012b). Similar effects have been reported in other species, with enhanced growth rates and sexual reproduction in the medusae stage under warm temperatures (Purcell 2005; Lucas et al. 2012), while scyphistomae can increase their asexual reproduction and the rate of ephyrae release (Holst 2012; Marques et al. 2019). However, as *R. pulmo* scyphistomae have never been found in nature yet, it is not possible to predict if temperature rises could favour *R. pulmo* benthic populations in nature.

A recent up-phase of an oscillation pattern of jellyfish populations has been hypothesized to explain the current perception of a global increase in jellyfish over the past decade (Condon et al. 2013). We do not discard this hypothesis. Nevertheless, due to the rise we observed, aligned with an accelerating rate of change in environmental conditions in the southern European seas (i.e., temperature, extreme climatic events, pollution, substrate availability; Lejeusne et al. 2010), an increase greater than expected by that oscillation could

be taking place for *R. pulmo*. Furthermore, similar results were observed for scyphomedusae and cubomedusae species in the Mediterranean (*Cotylorhiza tuberculata*, Prieto et al. 2010; *Phyllorhiza punctata*, Durgham 2011; *Carybdea marsupialis*, Canepa et al. 2017; *Rhopilema nomadica*, Edelist et al. 2020) and Black Seas (*Aurelia aurita*, Mutlu 2009). The 12-year periodicity of blooms found for *P. noctiluca* in the 1870s and 1980s (Goy et al. 1989) shifted to a quasi-annually periodicity in the XXI century (Daly Yahia et al. 2010). *R. pulmo* occurrence showed a periodicity of 4 and 6–8 years from 1875 to 1922 in the Adriatic Sea. From 2003 to 2006 its abundance increased, but then dwindled after 2006 (Kogovšek et al. 2010). The increase we have detected may represent the rising phase of this periodicity.

Together with the abundance increase, the enhanced duration of the *R. pulmo* medusae season (an increase from 5 to 7 months for the period 2008–2018) could have resulted from several processes acting on the early life stages of the scyphomedusae, but also from a longer survival of adult stages (Boero et al. 2016). This greater duration may be favoured by the earlier bloom events (advancing 5.9 days year<sup>-1</sup>) during warmer spring years and also to an extended period of strobilation (Purcell et al. 2012b). One plausible explanation for the former is an earlier strobilation with high temperature conditions, as observed for *Aurelia* spp. (Purcell et al. 2007) and for *R. pulmo* under experimental conditions (days until first ephyrae shift from 85.5 at 14°C to 9.5 at 28°C, Purcell et al. 2012b). The ephyrae of *R. pulmo* in the Western Mediterranean Sea have been observed in the field during spring and early summer (from April to May along the Catalan coast and Mar Menor Lagoon, Spain; Fuentes et al. 2011), and from April to June in Bages-Sigean Lagoon, France; D. Bonnet and V. Leoni, 2019, personal observations). It is known that the ontogenetic rate of development of *R. pulmo* ephyrae depends on temperature and feeding conditions (Fuentes et al. 2011). A negative relationship of spring SST with the start of the jellyfish season suggests a higher growth rate under warm springs, thus adult specimens are observed earlier in the year. A bottom-up process due to an effect of spring temperatures on lower trophic levels can also be hypothesized, as it could increase the abundance of prey or change its taxonomic composition (Molinero et al. 2008; Mozetič et al. 2010).

On the contrary, warmer winters lead to an earlier jellyfish season end, particularly in the Eastern basin, for example, the Ionian Sea (Fig. 2.4 and 2.6). Warmer waters promote prolonged stratification, as recorded during late summer and autumn in recent decades in the Mediterranean Sea (Macias et al. 2013). Under the lengthening of summer conditions, exhaustion of dissolved surface nutrients concurrently with warm temperatures could hamper

primary production, as recorded in the Eastern Mediterranean (Salgado-Hernanz et al. 2019), and even trigger mass mortality events in marine communities (Coma et al. 2009).

Phenology studies on jellyfish are rare and restricted to a few species. The main phenological changes that have been observed are an early start or an early peak of the jellyfish blooms, most of them partially explained by an increase in winter or spring SST (Table 2.1). However, these studies are not included yet in global analyses on marine animals (e.g., Poloczanska et al. 2016). In addition to the variability in the phenological response of each species (Table 2.1), the areas where these studies have been conducted may add more variability, as observed among ecoregions for *R. pulmo*. The coldest areas in the Mediterranean Sea are experiencing a fast warming, and many thermophilic species have shown an early occurrence or a late disappearance (Lejeusne et al. 2010), as observed in the Western Mediterranean and Adriatic Seas for *R. pulmo* (Fig. 2.6).

#### **2.4.2 | Metapopulation of *R. pulmo* in southern European seas**

Phenology trends observed for *R. pulmo* differ among the three ecoregions analyzed (Western Mediterranean, Adriatic and Ionian Seas; Fig. 2.6). In the last decade, warming may have caused *R. pulmo* to persist longer during the year in the Western Mediterranean Sea. The temperature and the duration of the phytoplankton bloom have increased in this area since 1998 (see Lejeusne et al. 2010; Salgado-Hernanz et al. 2019), and the abundance of small-sized phytoplankton therein has increased in response to the expansion of summer stratification (e.g., Bay of Calvi, Goffart et al. 2002). The phytoplankton community shift in the Adriatic Sea, from early spring diatom blooms to nanoflagellate dominance (Mozetič et al. 2010), could affect the timing of the first appearance of *R. pulmo*, due to its capacity to predate microzooplankton (Dönmez and Bat 2019), which in turn graze preferentially on small phytoplankton (Kamburska and Fonda-Umani 2006).

In addition, the different seasonal patterns detected in the Mediterranean and Black Sea ecoregions (Fig. 2.8) can be interpreted as spatially isolated *R. pulmo* populations adapted to diverse environmental conditions. In the Adriatic Sea and Tunisian Shelf, the medusae are present throughout the year with high bloom intensities, coinciding with the most productive zones (highest Chl *a* values). In the Black Sea, although highly productive, *R. pulmo* was only present during the summer and autumn months. Therein, the high seasonal temperature variability compared with any other Mediterranean ecoregion (Shaltout and Omstedt 2014) may explain the absence of medusae during the coldest months (January to April). The Black Sea is the only ecoregion where winter and spring temperatures drop under 10 and 12°C,

respectively. On the eastern coast of the Mediterranean (Aegean and Levantine Seas), the highest abundances were mainly recorded in the warmest months ( $> 18^{\circ}\text{C}$ ). These differences suggest that the life cycle is temperature-dependent, but also that a seasonal bottom-up process is acting at local scales (Hoover et al. 2006), where different nutrient input dynamics can partially shape this seasonality.

Geographical differences in the species' seasonality could contribute to the genetic structure observed in *R. pulmo* (Ben Faleh et al. 2017), which is also determined by small-scale hydrodynamic and oceanographic patterns that constrain population connectivity (such as temperature and salinity fronts, gyres; Berline et al. 2014) despite high dispersive potential. Similar geographical differentiation in the Mediterranean and Black Seas has been observed in other jellyfish (Ramšak et al. 2012), copepods (Yebra et al. 2011), chaetognaths (Peijnenburg et al. 2006), shrimps (Luttikhuisen et al. 2008), fish (Borsa et al. 1997) and bivalve species with a planktonic larva stage (Mariani et al. 2002). This evidence suggests that contemporary hydrographic barriers, together with the impacts of Pleistocene climate shifts, modulate the limited gene flow among populations and mold the distribution of marine organisms (Deli et al. 2018). The most remarkable of these physical barriers is the restricted water exchange between the Black Sea and the Mediterranean. Likewise, the narrow Strait of Messina could limit the gene flow between populations of the Western Mediterranean and populations of the Adriatic Sea, as the unidirectional water flow at the Siculo-Tunisian strait influences the West–East Mediterranean connectivity (Pérez-Losada et al. 2007). In addition, it has been suggested that the Aegean-Ionian isolation is due to a quasi-circular circulation (Pérez-Losada et al. 2007).

For big jellyfish, swimming capacities allow them, to some extent, to avoid current advection to open waters and to maintain the population core together to facilitate reproduction events (Lee et al. 2013). This ability also favours the planulae settlement in shallow-water benthic habitats. Indeed, interannual scyphistomae survival has been suggested to be critical for the re-occurrence of medusae patchy bloom events in the same area (Lee et al. 2013). The extent to which marine taxa are widely dispersed or not in the marine realm requires thorough biogeographical assessments based on recent technological advances, including individual-based dispersal models (Lee et al. 2013), genetic tools and electronically geo-localized sensors. In the case of jellyfish, this will shed light not only on understanding how animals interact with their environment, patterns of dispersion and connectivity, but also on the degree of geographical restrictions jellyfish may have, as benthic-pelagic species are closely dependent on the coast.

**TABLE 2.1.** Phenological changes in jellyfish species (medusae stage). Geographical area and time of period studied are indicated. Nature of change is indicated: When linear correlation was observed, the rate of change of day per year is indicated. When sea surface temperature (SST) had a significant effect, the rate of change of days per degree is indicated. Advance = the species appeared earlier; Later = the species appeared later; - = non-significant change.

Species	Geographical area	Period of time studied	Phenology change						References
			First occurrence		Peak of bloom		Last occurrence		
			Nature of change	Driver of change	Nature of change	Driver of change	Nature of change	Driver of change	
<i>Aurelia aurita</i>	Wadden Sea, Netherlands	1960-2010	Advance 6 to 8 days	Winter SST	Advance 4 to 7 days	Winter SST	-		Van Walraven et al. (2015)
	Flødevigen Bay, Norway	1992-2011	-		Shift unimodal (1993-2005) to bimodal (2006-2011)		-		Hosia et al. (2014)
<i>Chironex fleckeri</i>	Darwin harbor, Australia	1991-2004	Advance	Annual SST					Jacups (2010)
<i>Chrysaora hysoscella</i>	Wadden Sea, Netherlands	1960-2010	Advance		-		29 days later	Summer SST	Van Walraven et al. (2015)
<i>Cyanea</i> spp.	Wadden Sea	1960-2010	Advance		-		-		Van Walraven et al. (2015)
	Flødevigen Bay, Norway	1992-2011	-		1.86 days later		-		Hosia et al. (2014)
<i>Rhizostoma octopus</i>	Wadden Sea, Netherlands	1960-2010					-		Van Walraven et al. (2015)
<i>Rhizostoma pulmo</i>	Mediterranean Sea	2008-2018	Advance	Spring SST			Advance	Winter SST	This study
	Western Mediterranean	2008-2018	-				Later	Annual SST	This study
	Adriatic Sea	2008-2018	Advance	Winter SST			-		This study
	Ionian Sea	2008-2018	-				Advance	Spring SST	This study
Trophic groups									
Gelatinous carnivores*	Mondego Estuary, Portugal	2003-2013			Advance 48.8 days	Spring SST			D'Ambrosio et al. (2016)

\* Includes hydromedusae and siphonophores species.

Despite the probable existence of metapopulations, the species seems to respond to cues at larger scales. The significant latitudinal pattern of bloom intensity (Fig. 2.8b) observed for *R. pulmo* following temperature gradients warns of a potential increase in bloom events and a geographical expansion if the phenomenon of tropicalization experienced in the Mediterranean is enhanced. In other jellyfish species, such as the invasive *Rhopilema nomadica*, a geographical expansion to new areas has been associated with temperature shifts in the Mediterranean Sea (Edelist et al. 2020). In the case of *R. pulmo*, the increasing number of records in the Black Sea was aligned with an increase in the abundance of the species in the late 1990s (Mutlu 2001).

### 2.4.3 | Scope and caveats of our study

Few long-term scientific surveys exist to assess historical and current trends in jellyfish populations. Nevertheless, new technologies allow communication of sighting information to diverse initiatives (e.g., GBif, JellyWatch), increasing citizen participation in the study of gelatinous zooplankton (e.g., Nordstrom et al. 2019; Edelist et al. 2020), invasive species (Zenetos et al. 2013) or conservation of marine (Nordstrom et al. 2019) and terrestrial ecosystems (Schultz et al. 2017). Here, we have used both quantitative and qualitative data produced by scientific surveys and citizen science, which have proved useful to depict regional temporal patterns of the species and their relationships with environmental changes.

Citizen science is on the rise, and is suggested as a powerful strategy to increase the acquisition of biological data for large-scale ecological studies that are difficult to obtain through conventional scientific methods. Edelist et al. (2020) have shown its advantages by mapping the entire spatial distribution of the invasive jellyfish species *R. nomadica* in the Mediterranean Sea, which would otherwise be difficult through standard protocols of cruise-based sampling.

We acknowledge that our database has limitations regarding the heterogeneous spatial and temporal distributions of the records; however, it currently is the most comprehensive dataset to evaluate biogeographical and phenological patterns of the largest jellyfish species in the Mediterranean Sea. Indeed, the spatial heterogeneity does not alter our results, as the areas used in the analysis of latitudinal trends offer a valuable geographical gradient to test whether the magnitude of blooms covaries along with the latitudinal gradients of temperature. Time-wise, periods with no records are observed in the entire study period, whilst annually, the typical concentration of records during some seasons (e.g., summer months) has been detected. Nevertheless, this temporal variability did not affect our results as only the period with the

highest effort and a large temporal coverage during one year were considered in phenological analyses.

It must also be noted that, in some records, there could be confusion between *R. pulmo* and *R. luteum*, especially in the Alboran Sea, since the distributional ranges of the species overlap there (Kienberger and Prieto 2018). Another caveat is the limited number of environmental descriptors to depict regional scale patterns. However, these descriptors are among the most important molding the biogeography of plankton. Moreover, our results align with the current hypotheses linking jellyfish dynamics with anthropogenic changes. Future studies should include more variables, such as overfishing, oxygen concentration, zooplankton and phytoplankton composition, considering as well the potential interactions among environmental variables at local scales (for example, freshwater nutrient inputs).

## 2.5 | CONCLUSIONS

Few studies have been performed on jellyfish phenological changes and biogeography compared with other marine species, including other zooplankton groups. Here, despite data restrictions, a broadscale general pattern has been elucidated for *R. pulmo*. The species displayed marked accelerated changes in the last decade, both in phenology and in population size, which were linked to increasing temperatures. Our results provide support to the hypothesis that global warming benefits temperate-subtropical metagenetic jellyfish, and that enhanced temperatures promote earlier bloom events, which can have wide implications for food web trophodynamics. Furthermore, the latitudinal temperature gradient shapes the biogeographical patterns of the species, supporting our original hypotheses. However, we reject the hypothesis linking the rise of jellyfish bloom events with an increase in eutrophication. Our results point out a predominant role of temperature not only in influencing biogeographical patterns but also in affecting the timing of seasonal dynamics. Hence, enhanced warming may therefore boost phenological responses, unbalancing established patterns in trophic interactions with wide consequences for the recruitment of higher trophic levels.



## SUMMARY POINTS

- *R. pulmo* is present in all ecoregions of the Mediterranean Sea and the Black Sea, between 15 and 22°C, but most of the records were reported between 20 and 21°C.
- Overall, a substantial increase in the magnitude and frequency of *R. pulmo* blooms was observed in recent decades, concurrently with positive sea surface temperature anomalies. This suggests that the species benefits from warm temperatures.
- Bloom intensity was not correlated with the interannual variability of primary production (chlorophyll *a*).
- *R. pulmo* has experienced phenological changes in the last 10 years in the Mediterranean Sea: warmer springs favored an earlier start (advance of 5.9 days year<sup>-1</sup>) and a longer duration (from 5 to 7 months) of the jellyfish season. Warmer waters could promote an earlier strobilation, but also enhance medusae survival.
- The most intense blooms were detected at low latitudes, suggesting that the latitudinal temperature gradient shapes the biogeographical patterns of the species.
- Spatial isolated *R. pulmo* populations, adapted to diverse environmental conditions, could explain the great variability observed at both interannual and seasonal scales among ecoregions.



## CHAPTER 3.

# VARIABILITY OF GROWTH RATE AND THERMOHALINE NICHES OF *RHIZOSTOMA* *PULMO*'S PELAGIC STAGES

Valentina Leoni<sup>1</sup> • Juan Carlos Molinero<sup>2</sup> • Marie Meffre<sup>1</sup> • Delphine Bonnet<sup>1</sup>

<sup>1</sup> MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Montpellier, France

<sup>2</sup> MARBEC, IRD, CNRS, Ifremer, Université de Montpellier, Sète, France

Published in **Marine Biology** (2021)



## **Variability of growth rates and thermohaline niches of *Rhizostoma pulmo*'s pelagic stages**

Analyzing monospecific data at multiple locations has allowed us to capture basin-scale drivers of *R. pulmo* biogeographic patterns (Chapter 2). Yet, those analyses across locations hide variations at population level. Indeed, besides the influence of climate patterns, population dynamics is closely linked to the variability of local processes.

Unlike in the open ocean, species living in coastal and shallow-water habitats often experience strong intra- and interannual fluctuations of biotic (e.g., food availability) and abiotic (e.g., temperature, salinity) factors, which is shaped by climate change. To predict how these changes affect ecological processes, and finally jellyfish blooms, it is essential to identify, quantify and contextualize the current dynamics of jellyfish abundances, as well as their life-history traits. In this line, a population perspective, on how the environment molds the species, complements the previous analyses and may help to better understand the observed intra-specific variability. In particular, growth is an ideal proxy of environmental variability. Historically, an emphasis has been put on the growth of copepods, although invertebrates other than crustaceans can dominate the total abundance and biomass of meso- and macrozooplankton. Rhizostomeae jellyfish are among the most important blooming species, but our knowledge of their life-history traits is scarce. In addition, fisheries focusing on this group are growing in popularity, which further emphasizes, the need for monitoring and quantifying basic population parameters, and for identifying reliable biomass proxies.

In this chapter, we moved from a basin scale to a local scale, to focus on one population of *R. pulmo* and investigated its seasonal demographic variability under natural environmental conditions. Here we addressed the following questions: What environmental factors modulate the population dynamics? What is the best morphological proxy to estimate *R. pulmo* population biomass? Do thermohaline niche and growth rate vary during ontogeny and between Mediterranean populations?

**Keywords:** Barrel jellyfish • Population dynamics • Mediterranean Sea • Morphological traits • Biomass estimations



### 3.1 | INTRODUCTION

Jellyfish blooms are conspicuous natural events in coastal marine ecosystems, but over the last decades, their frequency and intensity have increased in middle latitudes (Graham et al. 2014). Identifying drivers of jellyfish population dynamics and quantifying favourable environmental windows throughout their life cycle is necessary to understand the variability of these bloom events. They are also required parameters to model population dynamics and to improve ecosystem models, which have long oversimplified the role of jellyfish. In particular, for jellyfish with metagenetic life cycles, semi-enclosed ecosystems provide substrates for benthic stages and refuges for pelagic stages from the advection by currents (Marques et al. 2015a), which favour the populations' development. Coastal lagoons may be considered as large mesocosms to survey ecological processes that are difficult to assess in open sea conditions, i.e., population growth, and to identify the environmental conditions these organisms face during the ontogeny (Bonnet et al. 2012; Marques et al. 2015b; Fernández-Alías et al. 2020).

*Rhizostoma pulmo* (Macri, 1778) is one of the most abundant and biggest jellyfish inhabiting coastal areas and semi-closed lagoons in the Mediterranean and Black Seas (Fuentes et al. 2011; Leoni et al. 2021a). Research on *R. pulmo* ecology has been scarce (Pérez-Ruzafa et al. 2002; Daly Yahia et al. 2003; Lilley et al. 2009), although in recent years, the population dynamics, ecological role and biogeography of the species have gained interest (e.g., Fuentes et al. 2011; Ben Faleh et al. 2017; Dönmez and Bat 2019; Basso et al. 2019; Fernández-Alías et al. 2020). At the basin scale, the species has shown an increase in abundance and frequency of blooms in the last decades (Leoni et al. 2021a). These massive blooms constitute a potential food resource and open the possibility for developing a Mediterranean jellyfish fishery (Leone et al. 2019).

The current knowledge on the wide distribution of the species in the Southern Mediterranean seas points towards a metapopulation composed of at least three genetically distinct populations (Ben Faleh et al. 2017), probably linked with the Mediterranean hydrographic provinces. Restricted ecological niches may explain those geographically distinct populations (Kingsford et al. 2000; Ramšak et al. 2012; Dawson et al. 2015; Ben Faleh et al. 2017). Hutchinson (1957) defined the ecological niche as the range of tolerance of a species when all environmental factors are considered, including interspecific competition and dispersal. In particular, the realized niche represents the fundamental niche modified by external factors such as competition that can narrow the breadth or dispersion, that can expand

it (Helaouët et al. 2011). Temperature (Lucas et al. 2014) and salinity (Zhang et al. 2012) are well-known key factors shaping jellyfish species' geographic distribution. As observed for other ectotherm animals (Gilbert and Lattanzio 2016), these environmental niches may vary during jellyfish ontogeny (ephyrae and medusae, Bonnet et al. 2012; Marques et al. 2015b), suggesting that they may be more size-dependent than species-specific. In this context, characterization of environmental niches sheds light on the ecological partitioning of the species and metapopulation dynamics and can help to understand the ecological role of each stage of development of the species.

Environmental conditions additionally shape growth patterns in marine populations (Bhaud et al. 1995). Determining the population growth rate and its interaction with the environment is critical for stock assessment in harvested populations (Sparre and Venema 1998), including bloom-forming jellyfish (López-Martínez et al. 2020). Nevertheless, these data are still scarce in jellyfish fisheries (Omori and Nakano 2001). Scyphozoa growth estimation is challenging due to technical limitations on their collection, manipulation or fixation (Purcell 2009). Growth estimations have been realized rearing individuals under laboratory conditions (e.g., Astorga et al. 2012; Acevedo et al. 2013), though they are restricted to small size species or early medusae stages. In the field, however, studies are far less numerous (López-Martínez et al. 2020).

Bell diameter frequency distribution is usually the most used proxy to estimate the population growth (Houghton et al. 2006; Palomares and Pauly 2009) and indirectly the population biomass (Nogueira and Haddad 2006). Recently, a new approach based on statoliths size and number (Sötje et al. 2017) has emerged to assess the growth of scyphomedusae in the field. Lately, jellyfish cohorts monitoring together with multi-model inference approaches have proven valuable to estimate population dynamics and growth of the harvest medusae *Stomolophus meleagris* (López-Martínez et al. 2020). These authors showed that the von Bertalanffy model provides the best growth estimation of multicohort jellyfish species, supporting the use of this model to assess jellyfish growth (Palomares and Pauly 2009). Some efforts have been made to synthesize growth rates estimations of scyphozoan species (Palomares and Pauly 2009; Uye and Brodeur 2017), although all together the species of the Subphylum Medusozoa have not been considered.

In a global change scenario, determining environmental niches and growth rates is critical to understand jellyfish species' plasticity under changing marine ecosystems. Here, we assess a field survey of *R. pulmo* in Bages Sigean lagoon (France), a small semi-enclosed lagoon connected to the Mediterranean Sea, that is inhabited perennially (1) to evaluate



underlying factors shaping the species' population dynamics and (2) to determine thermohaline niches of the species' pelagic life-stages (ephyrae, juveniles and adults) in Bages Sigeon, and for ephyrae and medusae from Mar Menor (Spain) and Bizerte (Tunisia) lagoons. Using multimodal analysis and the von Bertalanffy model, we assessed (3) the species' population growth and mortality rates. Additionally, (4) we addressed our results in a broader context to identify growth patterns in the Medusozoa and (5) we performed a comparative multi-trait assessment to determine the best morphological proxy to estimate *R. pulmo* biomass.

## 3.2 | METHODOLOGY

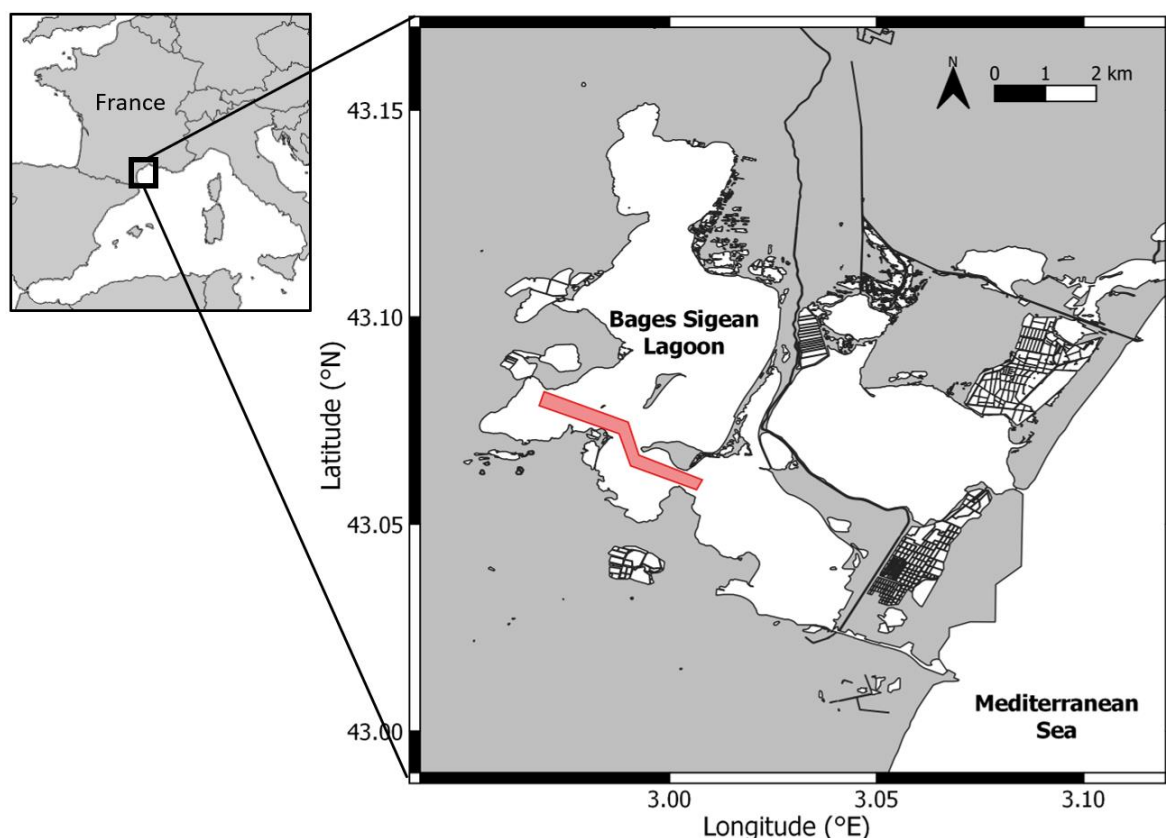
### 3.2.1 | Study area

The study was performed in the Bages Sigeon lagoon (Fig. 3.1), on the French Mediterranean coast (43°05'12.72"N; 3°00'35.3"E). It is a small (38 km<sup>2</sup>) and shallow lagoon (mean depth 2 m, maximum 4 m) connected to the Mediterranean Sea by a unique and narrow channel (Port La Nouvelle, 60 m width). The main freshwater and nutrients inputs come from the northern coast of the basin. Two main areas can be distinguished: the northern area, characterized by low salinity values (from 15 to 29) and the southern area with higher salinity values (from 20 to 35; Fiandrino et al. 2017). Therein, many economic activities coexist, including artisanal fisheries (e.g., eels and sea bass), sport (kitesurf, sailing) and tourism. The lagoon is included in a protected area (Parc Naturel Regional de la Narbonnaise en Mediterranee).

The single previous study on gelatinous zooplankton in the lagoon during 2010–2011 (Bonnet 2013) did not report the presence of *R. pulmo*, which inhabits Bages Sigeon lagoon since 2014 only (Stephane Marin, pers. comm).

### 3.2.2 | *In situ* monitoring

A bimonthly sampling was performed from February to November 2019 ( $n = 16$ ) during the daytime (between 09:00 and 12:00 AM). Due to weather conditions, only one sampling was carried out in some months (February, March, September, October and November). The sampling area (Fig. 3.1, red polygon) was chosen based on previous exchanges with fishermen, who indicated the presence of the species every year in this zone since 2014.



**FIGURE 3.1.** Map of Bages Sigean lagoon (Aude, France). The sampling area is indicated as a red polygon.

### 3.2.2.1 | Environmental parameters

Environmental parameters were measured twice at each sampling date to characterize the physical environment. Salinity and temperature data were recorded in sub-surface ( $< 0.5$  m) with a multiparameter probe (Hanna HI 9829) and visibility with a Secchi disk. Water samples (150 mL) were collected in triplicate and stored in darkness and fresh conditions to estimate chlorophyll *a* concentration afterward. Back to the laboratory, water triplicates were filtered on Whatman GF/F filters and stored at  $-30^{\circ}\text{C}$  until extraction and measurement by spectrofluorimetry (LS 50B Perkin Elmer).

### 3.2.2.2 | Zooplankton composition analysis

Zooplankton was collected with plankton nets towed horizontally under the sub-surface due to the shallow depth in the area. Meso zooplankton and macrozooplankton samples were performed with 200- $\mu\text{m}$  (0.54 m diameter  $\times$  2.5 m length) and 700- $\mu\text{m}$  (0.78 m diameter  $\times$  2 m length) mesh nets, respectively, and were fixed in formalin 4%. The volumes filtered by the nets were determined using flowmeters. Zooplankton organisms were identified and counted in a Bogorov chamber under a stereomicroscope Leica using taxonomic guides (Trégoubouff

and Rose 1978; Hecq et al. 2014) and their abundances were estimated from subsamples and expressed as the number of individuals per cubic meter.

### 3.2.2.3 | Medusae stage of development

Based on Fuentes et al. 's (2011) criteria of development, ephyrae of stages 2, 4, 6 and 7 were identified in the lagoon. Regarding medusae stages, size classes were determined and juveniles were defined as individuals without gonads and adults as individuals with gonads. Although gonads started to appear on some individuals of 12 cm of bell diameter (BD), they were present in all individuals > 15 cm. We therefore used 15 cm as the size threshold to distinguish juveniles from adults' specimens. Photos of each stage are shown in Figure S3.1.

### 3.2.2.3 | Medusae abundance estimations

*R. pulmo* undergo a wide range of size, from ephyrae (from 1 mm) to adults with *c.* 40 cm of BD, weighting up to 2 kg. Two sampling methods were combined to better estimate the abundance of *R. pulmo* pelagic stages and to capture this heterogeneity of size. Ephyrae and juvenile medusae were collected by a 700-µm zooplankton net with a flowmeter and abundances were estimated and expressed as the number of individuals per cubic meter. In the sampling area (Fig. 3.1), two stations within a distance of 3 km were sampled at each date to have a better representation of the abundances. An average of both values was then calculated. For adults, this monitoring was coupled with a non-intrusive count from the boat in the same area (Fig. 3.1). Medusae were identified and counted simultaneously by two observers on each side of the boat, along 1 km transects twice. The exact length of each transect (*L*) was defined by GPS coordinates of departure and arrival points. On each side of the boat, a 3 m wide band (*w*) was considered as the maximum visibility distance, and depth visibility (*d*) was based on Secchi disk measurements. All samplings were performed under calm weather conditions, and detectability at Secchi depth was assumed to be 100%. Individuals counted (*n*) were attributed to three size categories: < 15 cm, 15–30 cm and > 30 cm BD. Counts for adults (BD > 15 cm) were then converted in terms of individuals per cubic meter (*X*) based on the formula:

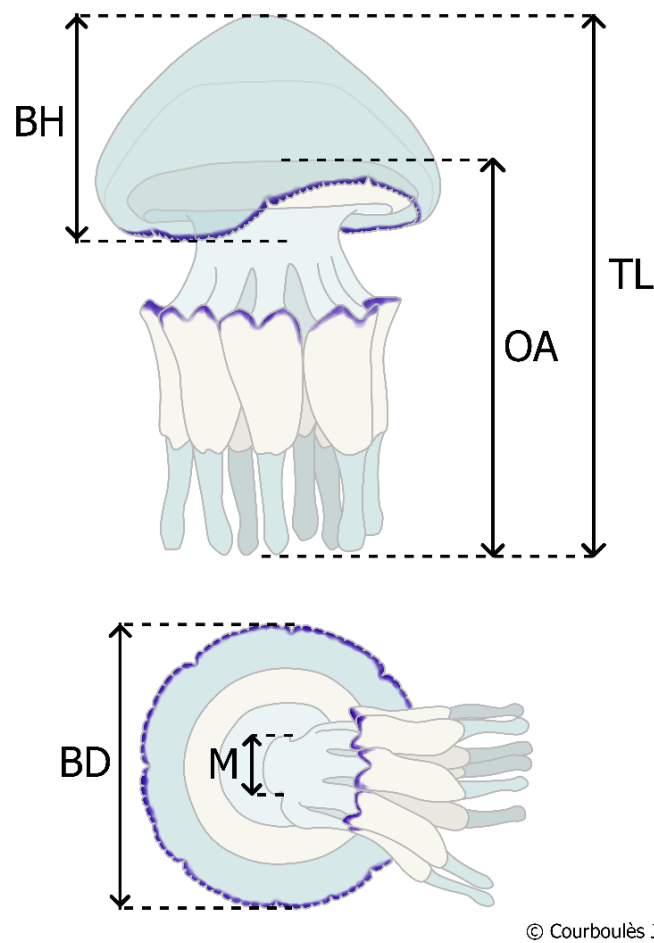
$$X = n / (w \times L \times d)$$

### 3.2.2.4 | Biometrical measurements and biomass estimations

In parallel to net collections, more than 400 specimens were randomly collected by dip nets and conserved in big containers on board with seawater to be measured on land. Each

specimen was gently dried with paper and weighted with a balance (precision  $\pm 0.1$  g). We further performed a multi-traits assessment to determine the best allometric estimation for the wet weight (WW). Morphological measurements: bell diameter (BD), total length (TL), bell height (BH), manubrium diameter (M) and oral arms' length (OA) were recorded on each medusa collected (Fig. 3.2 and S3.2). Those measurements were taken with an ichthyometer (precision  $\pm 0.1$  cm) and a digital caliber (precision  $\pm 0.01$  cm). To estimate the growth rates of the species, calculations were based on BD measurement.

Biomass estimation ( $\text{g m}^{-3}$ ) of juveniles ( $\text{BD} < 15$  cm) was obtained from specimens caught with the 700- $\mu\text{m}$  net and weighted. For adults ( $\text{BD} > 15$  cm), biomass estimation was performed using the individual data from dip nets. Once the number of specimens by category (15–30 cm and  $> 30$  cm) was obtained from visual counts, the same number of organisms from dip nets for each size category was aleatory chosen and its individual weight (g) was considered to estimate the biomass per cubic meter ( $\text{g m}^{-3}$ ).



© Courboulès J.

**FIGURE 3.2.** Morphological measurements recorded on each *Rhizostoma pulmo* medusa collected: bell height (BH), total length (TL), oral arms' length (OA), bell diameter (BD) and manubrium diameter (M).

### 3.2.3 | Statistical analysis

#### 3.2.3.1 | Objective 1: drivers of *R. pulmo* population dynamics

Generalized Linear Models (GLM) were run to assess the relevance of potential environmental drivers (temperature, salinity, chlorophyll *a* concentration and mesozooplankton and macrozooplankton abundances) on *R. pulmo*'s abundances seasonal changes. Explanatory variables were selected with a limit of  $p = 0.05$  and models with and without interactions were selected based on the Akaike's Information Criteria (AIC). Models were fitted in R `stats` through the function *glm*.

#### 3.2.3.2 | Objective 2: Thermohaline niches of each stage of development

We used a nonparametric test of association between environmental factors (temperature, salinity) and the abundance of each pelagic developmental stage of *R. pulmo* (ephyrae, juveniles and adults). The approach encompasses a cumulative frequency method and a Monte Carlo randomization (Paramo et al. 2003). It is based on the maximum absolute difference between the cumulative frequency distribution (CFD) of an environmental factor and the abundance weighted CFD of that environmental factor. First, the relative CFD was calculated for temperature and salinity. Then, the CFD for each environmental variable was weighted by the abundance of each *R. pulmo* pelagic stage. The comparison of unweighted and weighted CFD indicates the association of the population with the environmental variable. If the density of the population is randomly distributed in relation to the environmental variable, the cumulative pattern will increase similarly in the two curves and they will not be significantly different. In turn, if the population is related with a specific range of the environmental variable, the slope of the weighted CFD should be steeper than the unweighted environmental variable (Molinero et al. 2009). This allows testing, by a randomization procedure, the degree of association between the species abundance and environmental factors. The same analysis was performed to estimate the thermohaline niche of the medusae stage pooling together juveniles and adults' abundances.

To have a broader picture of *R. pulmo* niche, we compiled data from previously reported locations, Mar Menor lagoon, Spain (Fernández-Alías et al. 2020) and Bizerte lagoon, Tunisia (Gueroun 2016) to compute the thermohaline niche of ephyrae and medusae stages. The estimations of abundances of *R. pulmo*'s ephyrae and medusae in both lagoons were performed following the methodology used in the present study (Gueroun 2016; Fernández-Alías et al. 2020).

### 3.2.3.3 | Objective 3: Growth and mortality rates

*Identifications of cohorts:* Size frequency histograms of BD size classes of 0.5 cm were created for each month from specimens caught by dip nets and counted by the visual method. To avoid bias in the frequency distribution of jellyfish caught by dip nets and the *in situ* distribution observed visually from boat, the size classes of jellyfish were compared by a nonparametric Wilcoxon test.

Cohorts were determined by multimodal analyses by matching monthly frequency distribution of 0.5 cm BD class to log-normal distributions according to the presumed number of cohorts (López-Martínez et al. 2020) based on maximum-likelihood estimation for grouped data. If the distributions significantly represented the data ( $p < 0.05$ ), then the number of estimated cohorts was retained. This technique is classically recommended to analyze the size frequency distribution of a population with overlapping age groups, to identify the distributions that best fit to the size frequency histograms. This was performed using the *mix* function of the ‘mixdist’ package (Macdonald and Du 2018). Once the cohorts were identified, the specimens were grouped by cohort and treated independently for subsequent analyses.

*Growth rate estimations:* The von Bertalanffy growth model (VBGM) has been used in numerous studies to quantify the growth of fish (Ogle and Isermann 2017), crustaceans (Indarjo et al. 2020) and mollusks (Ford et al. 2020). It has been also demonstrated to be an appropriated way to estimate jellyfish growth (Palomares and Pauly 2009; Fernández-Alías et al. 2020). For *R. pulmo*, once the number of cohorts was defined, a von Bertalanffy function (Beverton and Holt 1957; Ogle 2013) was estimated for each cohort as:

$$L_{(t)} = L_{\infty}(1 - (e^{-k(t-t_0)}))$$

where  $L_{(t)}$  is the length at age  $t$ ,  $L_{\infty}$  is the asymptotic length at which growth is zero,  $k$  is the growth coefficient (in month or year),  $t$  is the age at size  $L_{(t)}$  and  $t_0$  is the age at which the organisms would have had zero size (initial condition parameter).

Starting parameters values for the model ( $k$  and  $L_{\infty}$ ) were estimated individually for each cohort following the methodology in Ogle (2013). Typically, this equation is utilized when both age and body size are known. Here, the age of the jellyfish was considered by month during one year. Once the cohorts were defined, specimens were monthly grouped and the initial values estimated using the BD as size, with the function *vbStarts* of the ‘FSA’ package. Then, these values were used to fit the model. This was performed with the ‘FSA’ and ‘nlstools’ packages (Baty et al. 2015; Ogle et al. 2021). Once the VBGM was obtained for each cohort,

growth curves were fitted between the age (in months) and the BD. Somatic growth rates (mm of BD per day) were determined from the average of the slopes obtained for each month. In addition, the same method was used to estimate the growth rate for juveniles and adults of each cohort independently.

*Literature review:* To gain further perspective on jellyfish growth, a literature review of growth rate estimations (mm of BD per day) of Medusozoa species was made through a search on Google Scholar. The terms used were: ‘Jellyfish growth rate’, ‘Medusae growth rate’ or the name of each Class/Order followed by ‘growth rate’. Available data of BD were assembled from different studies and growth rates were uniformly re-calculated as a linear regression fitted to BD data from all individuals collected. Both medusae and ephyrae were considered—as different groups when possible—when a continuous period was available. *Aurelia* spp.’s growth rates reviewed by Marques et al. (2015b) were included in the analysis, but not showed in details in the synthesis.

Growth rates were compared among taxonomic Orders by an ANOVA test. The effect of individual mean size on the growth rate values was evaluated with a Linear Model (LM) fitted between the mean BD and the estimated growth rate.

*Mortality rates estimations:* Mortality is a key component to understand the jellyfish population dynamics. Mortality rates were estimated using the Chapman–Robson method (Chapman and Robson 1960). This method assumes that the catches at each age on the descending limb of the catch curve follow a geometric probability distribution. The catch of jellyfish at each age is proportional to the number of jellyfish observed by age, considering the age as months. This distribution was used to derive a maximum-likelihood estimator for the survival parameter of the distribution, used later to estimate mortality. This analysis was carried out with the function *chapmanRobson* of the ‘FSA’ package (Ogle et al. 2021).

#### 3.2.3.4 | Objective 4: Biomass assessment

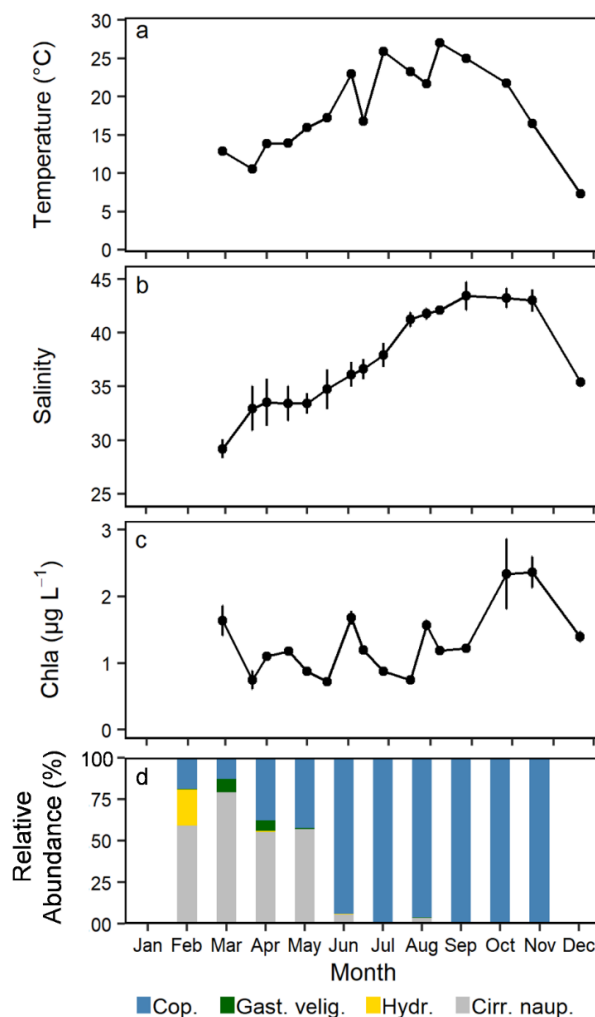
To determine the reliability of allometric relationships to estimate the WW, nonlinear regressions were fitted between individual WW and morphological measurements. The selection of the best trait was based on the best fitted curve ( $r^2$ ), but also considering the easiest measurement to acquire in the field.

All the analyses were performed using the open source software R 3.6.0 (R Core Team 2020) and plots were created with the ‘ggplot2’ package (Wickham 2016). The map was performed using the open source software QGIS 3.4.4 (QGIS 2020).

### 3.3 | RESULTS

#### 3.3.1 | Environmental conditions

Mean depth of the sampling area was  $1.8 \pm 0.1$  m. Temperature showed a typical seasonal cycle in the lagoon, with highest values recorded in August ( $27.2^{\circ}\text{C}$ ) and lowest in November ( $7.2^{\circ}\text{C}$ ; Fig. 3.3a). Salinity displayed an increasing trend during the year, reaching values higher than previously reported (Fiandrino et al. 2017) in the lagoon during summer (44.7 in August) and minimum values in winter (28.3 in February; Fig. 3.3b). Chlorophyll *a* showed a main seasonal peak in autumn ( $2.4 \mu\text{g L}^{-1}$  in October) and a noticeable monthly variability. Three smaller peaks were also observed in February, June and July and the minimum value was measured in March ( $0.7 \mu\text{g L}^{-1}$ ; Fig. 3.3c).



**FIGURE 3.3.** **a.** Average seasonal cycles of temperature ( $^{\circ}\text{C}$ ), **b.** salinity and **c.** chlorophyll *a* ( $\mu\text{g L}^{-1}$ ) during 2019 in Bages Sigeon lagoon (France). Curves represent the mean and error bars the standard error by sampling date. **d.** Monthly relative abundance (%) of the main mesozooplankton groups (Cop. = Copepoda, blue; Gast. velig. = Gastropoda veliger larvae, green; Hydr. = hydromedusae, yellow; Cirr. naup. = Cirripedia nauplii, grey).



### 3.3.2 | Zooplankton composition

Zooplankton abundance displayed a marked seasonal variability (data not shown). The copepods *Acartia clausi*, *Paracalanus parvus* and *Pseudocalanus elongatus* and the cirripeds nauplii contributed at least to 80% of the total mesozooplankton abundance (Fig. 3.3d). We therefore used these taxa for posterior statistical analysis as representative of the mesozooplankton community.

A temporal succession in the gelatinous zooplankton community was observed. This community showed a dominance of the small (less than 1 cm of BD) hydromedusae *Rathkea octopunctata*, *Odessia maeotica*, *Ptychogena crocea* and *Podocoryne minima* during Spring. They all disappeared in May when the scyphomedusae *R. pulmo* and *Aurelia coerulea* abundances increased (data not shown).

### 3.3.3 | Objective 1. *R. pulmo* population dynamics and its environmental drivers

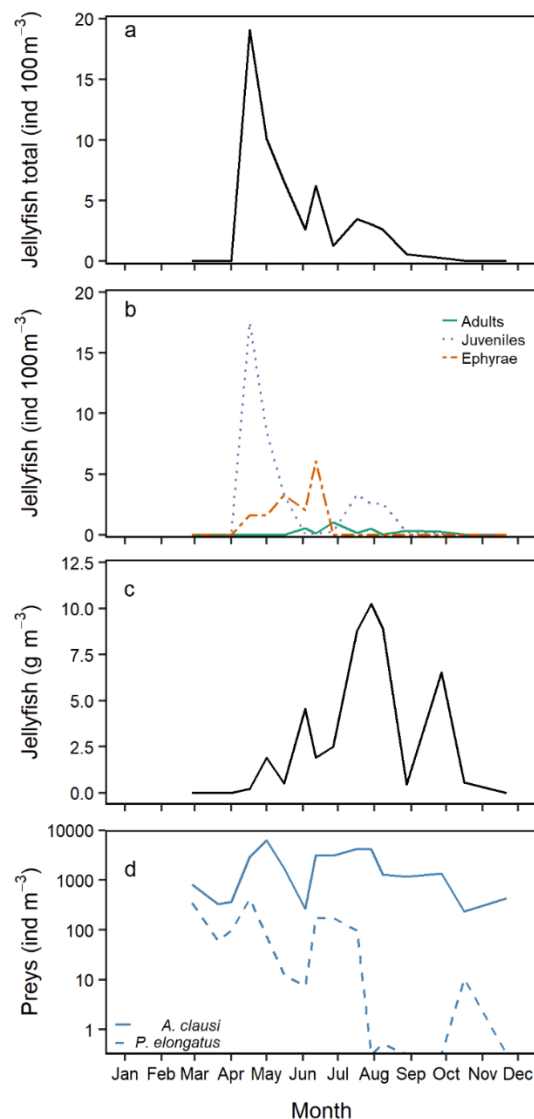
The visual counting was performed for 2 km ( $L$ ) with a 1.2 m visibility depth ( $d$ ). Total abundance of *R. pulmo* pelagic stages presented three peaks: a maximum in April and two smaller in June and July (Fig. 3.4a). Ephyrae occurred from April to June, with a maximum abundance in June ( $6.1 \text{ ind } 100 \text{ m}^{-3}$ ). Juveniles appeared from April to September, with a peak in April ( $17.5 \text{ ind } 100 \text{ m}^{-3}$ ), and adults from May to October, rising a peak at the end of June ( $1.0 \text{ ind } 100 \text{ m}^{-3}$ ; Fig. 3.4b). *R. pulmo* total biomass ( $\text{g m}^{-3}$ ) was estimated for the medusae stages (juveniles and adults) and presented three peaks (June, July and September), with a maximum in July ( $10.2 \text{ g m}^{-3}$ ; Fig. 3.4c). When the last adults were observed, the bottom of the lagoon was full of dead medusae (V. Leoni personal observation). In November, no individual occurred.

The temporal variability of *R. pulmo* abundance was positively correlated to the abundance of the copepods *A. clausi* and *P. elongatus*, with an explained variance of 51% (GLM,  $p < 0.05$ ; Fig. 3.4d). Environmental parameters —temperature, salinity or chlorophyll  $a$ — did not show any significant correlations with *R. pulmo* abundance.

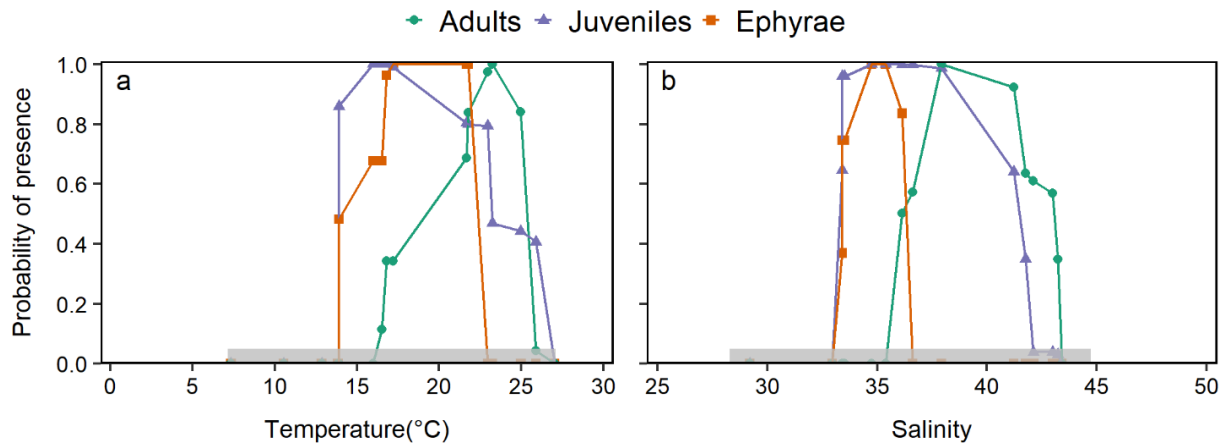
### 3.3.4 | Objective 2. Thermohaline niches of each stage of development

Niches of salinity and temperature in Bages Sigean differed among the three pelagic stages of development of *R. pulmo* (Fig. 3.5). Ephyrae showed the narrowest thermal window ( $13.9\text{--}21.8^\circ\text{C}$ ), with the highest probability of occurrence at  $20.2^\circ\text{C}$ . In contrast, juveniles occurred in a largest range of temperature (from  $13.9$  to  $25.9^\circ\text{C}$ ) and their maximum probability of presence was at a lower temperature ( $16.8^\circ\text{C}$ ) than ephyrae. The maximum probability of

adults' occurrence was at 23.2°C, a warmer temperature than for juveniles or ephyrae. Adults were present between 16.5 and 25.9°C. Regarding salinity, ephyrae occurrence was associated to a narrow range (33.4–36.1) and juveniles showed a noticeable wider range (33.4–41.8). However, both ephyrae and juveniles displayed a maximum of probability of occurrence at a salinity of 35.1. Similarly, as for temperature, adults were found at higher salinities (36.1–43.2), with a maximum at 37.9.



**FIGURE 3.4.** **a.** Temporal variability of the total abundance (ind 100 m<sup>-3</sup>) of the three pelagic stages of *Rhizostoma pulmo*. **b.** Abundance for each developmental stage (ephyrae in dashed orange line; juveniles < 15 cm in dotted purple line; adults > 15 cm in continuous green line). **c.** Temporal variability of the medusae total biomass (g m<sup>-3</sup>, juvenile and adults together). **d.** Abundance of the two copepods species (*Acartia clausi*: continuous blue line and *Pseudocalanus elongatus*: dashed blue line) showing a significant correlation with *R. pulmo* total abundance (Note that Y axis is represented in logarithmic scale). Data were collected in Bages Sigean lagoon (France) during 2019.



**FIGURE 3.5.** **a.** Environmental niche of temperature and **b.** salinity of ephyrae in orange, juveniles in purple and adults medusae of *Rhizostoma pulmo* in green in Bages Sigean lagoon (France) during 2019. Grey bars represent the range of the environmental variable during the study period.

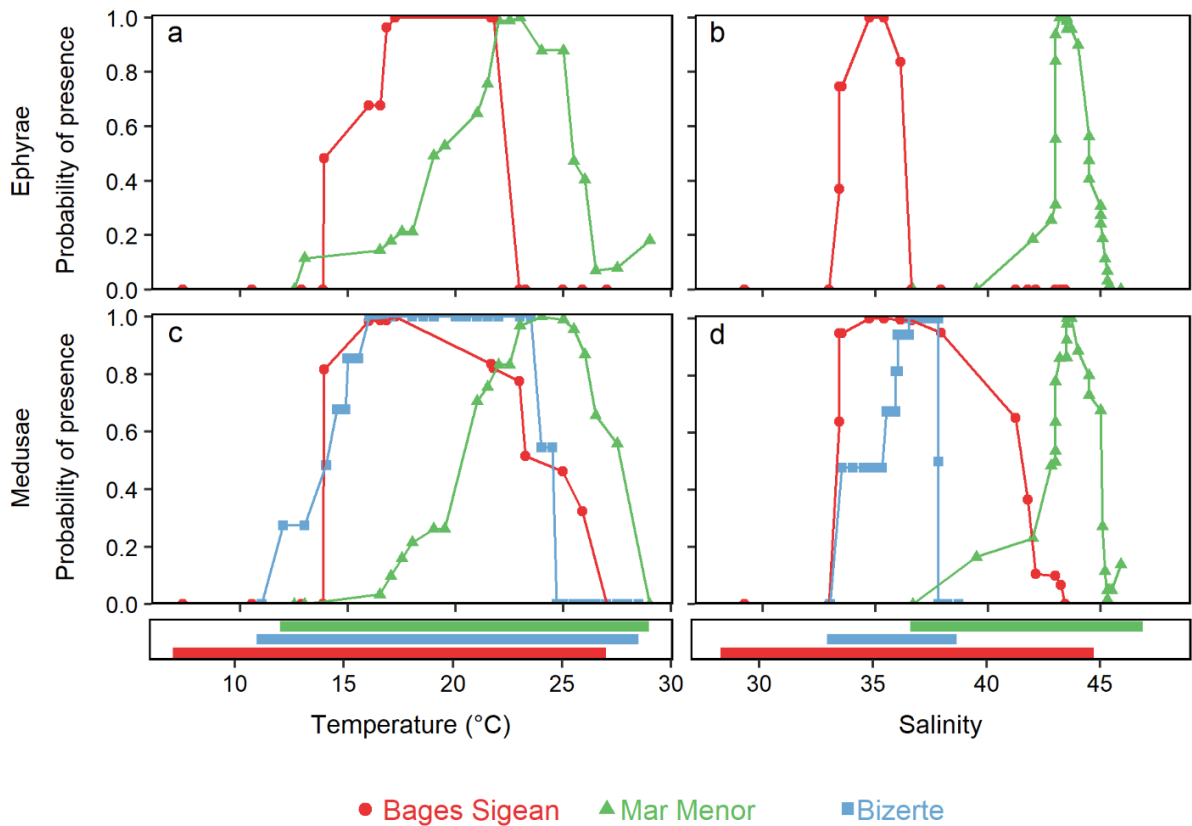
When comparing ontogenetic niche partitioning among areas, we found that *R. pulmo* occurs at higher temperature (13.0–29.0°C) and salinity (39.5–45.9) ranges in Mar Menor, compared with Bages Sigean and Bizerte lagoons (Fig. 3.6). Medusae from Bages Sigean and Bizerte showed similar thermal windows and a maximum probability of presence at close temperatures (mean around 19.8°C in Bizerte and at 17.2°C in Bages Sigean, Fig. 3.6c). Although the salinity range of medusae occurrence in Bages Sigean was the widest, the maximum probability of occurrence was at lower salinity (35) than in Bizerte (37.2, Fig. 3.6d).

### 3.3.5 | Objective 3. *R. pulmo* growth and mortality rates

For most sampling dates, a wide range of medusae size was observed in the lagoon (Fig. 3.7a), indicating the probable existence of more than one cohort during the year. Multinomial analysis showed the presence of three cohorts of *R. pulmo* overlapping during 2019. The first cohort occurred from April to September, the second from May to October, and the third from June to October. Graphically, the multinomial analysis showed modal progressions through time from April to September 2019 (Fig. 3.7b).

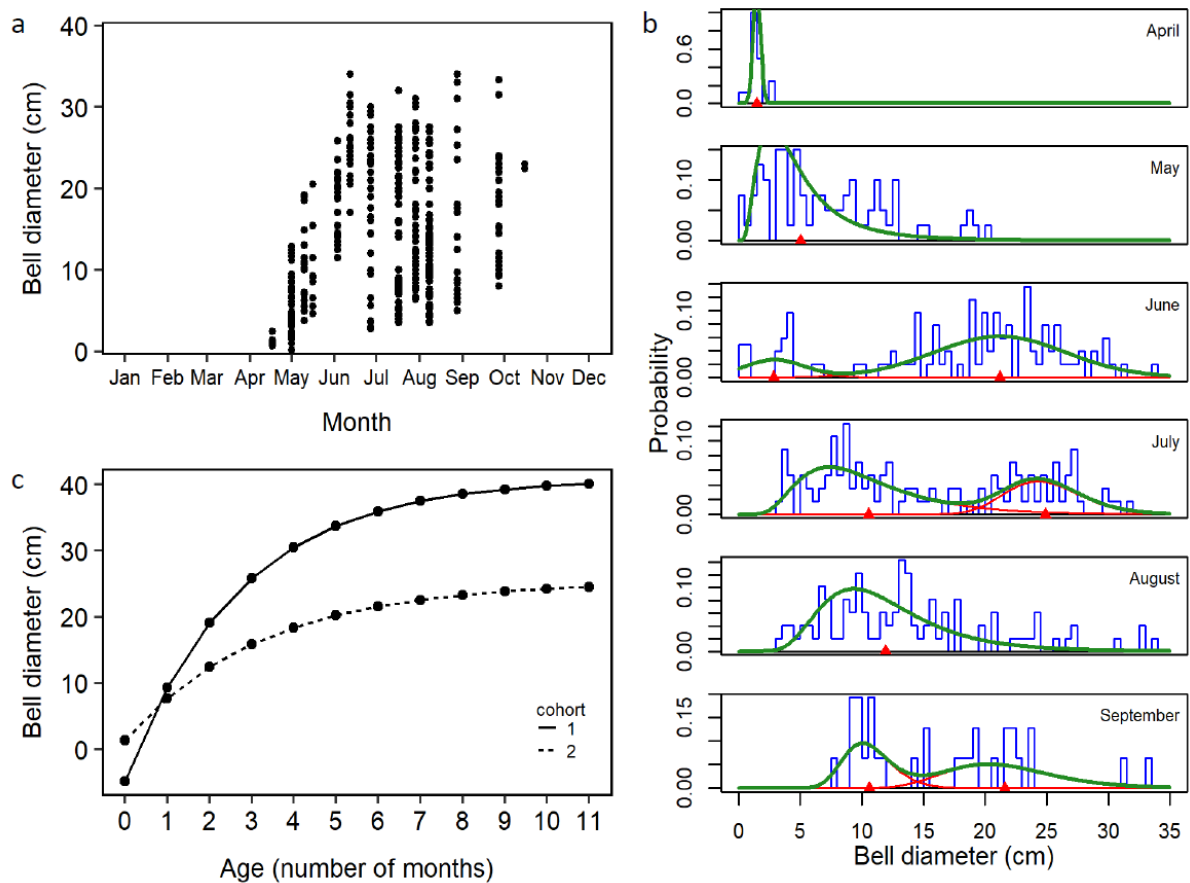
The growth parameters estimated with VBGM are presented in Table 3.1. Figure 3.7c depicts the fitted growth curves of VBGM for the two first cohorts, as there were not enough individuals collected to parameterize the third cohort. The projected growth curve on the age-length data showed a pronounced curvature in the youngest medusae. Even so, the growth curve for the second cohort showed a lower asymptotic value compared to the first one. On average, medusae grow 2.3 mm day<sup>-1</sup> for the first cohort, and 1.5 mm day<sup>-1</sup> for the second cohort. Regarding each developmental stage separately, juvenile growth rates were much

higher than those determined for adults, with 4.7 and 2.4 mm day<sup>-1</sup>, for the first and second cohorts, respectively. Adults' growth rates were 1.8 and 0.9 mm day<sup>-1</sup>, for the first and second cohorts, respectively. Moreover, the  $L_{\infty}$  was higher for the first cohort than the second cohort (Table 3.1). The monthly mortality rates were 52.6% and 61.3% for the first and second cohorts, respectively.



**FIGURE 3.6.** **a-b.** Thermohaline niche for ephyrae and **c-d.** medusae of *Rhizostoma pulmo* in three coastal Mediterranean lagoons: Bages Sigeon lagoon in red (France, 2019), Mar Menor lagoon in green (Spain, 1997) and Bizerte lagoon in blue (Tunisia, 2012–2014). Horizontal lines represent the range of the environmental variable (temperature or salinity) during the study period for each region.

A literature review on the growth rate of jellyfish species (Table 3.2) revealed a heterogeneity between taxonomic groups, the Scyphozoa being the most studied species. Differences among Classes, but also among Orders of each Class have been identified (Fig. 3.8a), with Rhizostomeae species presenting the highest growth rates. If the mean BD is considered to explain this variability (Fig. 3.8b), an increase of the growth rate is revealed with an increase of the size of the jellyfish. We observed also that Rhizostomeae species are the largest jellyfish for which growth has been studied.



**FIGURE 3.7.** **a.** Individual bell diameter (cm) of *Rhizostoma pulmo*. **b.** *R. pulmo* size class distribution multinomial analysis in Bages Sigean lagoon (France) from April to September 2019. Blue lines show the observed bell diameter frequencies and green lines show theoretical modal groups of the species. Red symbols indicate a significant mode identified. **c.** Growth curves described by the von Bertalanffy growth model for two of the three cohorts identified for *R. pulmo* in Bages Sigean lagoon.

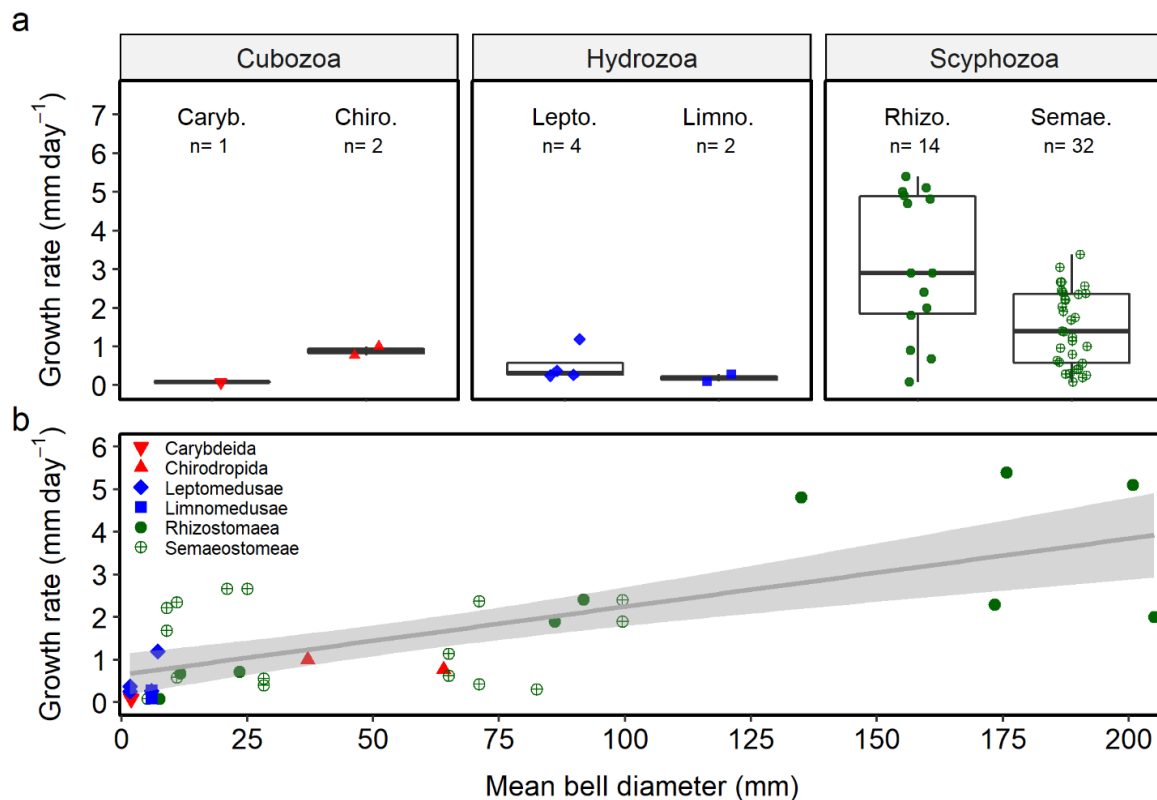
**TABLE 3.1.** Growth parameters estimated by von Bertalanffy growth model for the different cohorts of *Rhizostoma pulmo* in Bages Sigean and Mar Menor lagoons.  $L_{\infty}$  is the asymptotic size at which growth is zero.  $k$  is the growth coefficient ( $\text{year}^{-1}$ ). The parameter  $t_0$  is included to adjust the equation for the initial size of the organism and is the time at which the organism would have had zero size (initial condition parameter)

Study area	Cohort	$k$ ( $\text{year}^{-1}$ )	$L_{\infty}$ (cm)	$t_0$	Reference
Bages Sigean lagoon (France, 2019)	1	4.47	40.95	0.02	Present study
	2	3.76	25.31	-0.01	
	3	NA	NA	NA	
Mar Menor lagoon (Spain, 1997)	1	3.19	46.36	-0.04	Fernández-Alías et al. (2020)
	2	3.44	46.36	-0.08	
	3	3.10	46.36	-0.07	
	4	3.00	46.36	-0.13	

**TABLE 3.2.** Literature review of growth rates (mm per day) of jellyfish species.

Class	Order	Species	Growth rate range (mm day <sup>-1</sup> )	Nb. of cohorts per year	Strobilation type (nb. ephyrae release)	Medusae size (min-max) in mm	Stage	Study area	Reference
Scyphozoa	Rhizostomeae	<i>Catostylus mosaicus</i>	4.81 (max)	1 to 3	Mono/polydisc	20.0 - 250.0	Young medusae	Botany Bay and Lake Illawarra, New South Wales (Australia)	Pitt and Kingsford (2003)
		<i>Cephea cephea</i>	0.71	-	Monodisc	2.0 - 45.0	Young medusae	Laboratory conditions (28°C) (Japan)	Sugiura (1966)
		<i>Cotylorhiza tuberculata</i>	5.40	1		1.5 - 350.0	Ephyrae	+ Bay of Vlyho (Greece)	Kikinger (1992)
			5.00 - 5.10	2		1.5 - 400.0	Medusae	+ Bay of Vlyho (Greece)	Kikinger (1992)
			0.08	-	Monodisc	2.1 - 13.0	Ephyrae	+ Laboratory conditions	Astorga et al. (2012)
		<i>Mastigias papua</i>	2.90	-		2.2 - 18.0	Medusae	Laboratory conditions (20°C) (Spain)	Sugiura (1964)
		<i>Nemopilema nomurai</i>	0.92	1		18.0 - 110.0	Metaephyrae	+ Laboratory conditions	Kawahara et al. (2006)
			3.77	-	Polydisc (3-7)	18.0 - 110.0	Young medusae	Laboratory conditions (22-28) (East Asia)	
		<i>Phyllorhiza punctata</i>	2.00	1 or 2		10.0 - 400.0	Medusae	Laguna Joyuda (Puerto Rico)	Garcia (1990)
			0.74	-		46.0	Ephyrae	+ Vlyho Bay (Lefkada, Greece)	Abed-Navandi and Kikinger (2007)
	Semaestomeae	<i>Rhizostoma pulmo</i>	1.50 - 2.30	3	Polydisc (8 -18)	6.7 - 340.0	Medusae	Bages Sigeon lagoon (France)	Present study; Paspalef (1938)
		<i>Rhizostoma octopus</i>	2.90	-	Polydisc (1-12)		Medusae		Thiel (1966); Krüger (1968)
		<i>Rhizostoma luteum</i>	0.68	-	Monodisc	4.0 - 19.4	Ephyrae	Laboratory conditions (17°C)	Kienberger et al. (2018)
			2.41	-		19.4 - 164.0	Medusae	Laboratory conditions (17°C)	
			-	1 (potentially 3)		-	Medusae	La Herradura (Spain)	
		<i>Rhopilema nomadica</i>	1.89	-	Polydisc (5-6)	2.0 - 170.0	Ephyrae	+ Laboratory conditions (NA)	Lotan et al. (1994)
							Medusae		
		<i>Stomolophus meleagris</i>	3.10	3	Polydisc (1-3)		Ephyrae	+ Gulf of California (Mexico)	López-Martínez et al. (2020)
	Semaestomeae	<i>Aurelia</i> sp. (a)	0.19 - 3.38	-	Polydisc		Medusae	Synthesis multisite report	Marques et al. (2015b)
			0.59 - 2.67	1		10.0 - 31.9	Medusae	Thau lagoon (France)	Marques et al. (2015b)
		<i>Cyanea</i>	0.40 - 0.80	1		20.0 - 70.0	Medusae	Niantic River, Waterford	Brewer (1989)
		<i>Pelagia noctiluca</i>	0.09	2	Holoplanktonic	0.5 - 10.0	Ephyrae	Gulf of Trieste (Adriatic Sea)	Malej and Malej (1992)
			0.25	-			Ephyrae	Laboratory conditions (19°C)	Avian (1986)
			0.28 - 0.30	1		20.0 - 145.0	Medusae	Straits of Messina (Central Mediterranean Sea)	Rosa et al. (2013)
Cubozoa	Chirodropida	<i>Chiropsalmus</i> sp.	1.00	3 to 4	Monodisc	3.0 - 71.0	Medusae	Port Douglas, North Queensland (Australia)	Gordon et al. (2004)
		<i>Chiropsalmus quadrigatus</i>	0.77	-	Monodisc	18.0 - 110.0	Medusae	Matagorda Bay, Texas (USA)	Guest (1959)
		<i>Chironex flackeri</i>	3.20	-		0.6 - 190.0	Medusae	Cape York (Australia)	Gordon and Seymour (2012)
	Carybdeidae	<i>Carybdea marsupialis</i>	0.08	-			Medusae	Laboratory conditions (NA)	Acevedo et al. (2013)
Hydrozoa	Limnomedusae	<i>Craspedacusta sowerbii</i>	0.28	-		1.0 - 11.1	Medusae	Laboratory conditions (29°C)	Marchessaux and Bejean (2020)
			0.12	-			Medusae	Laboratory conditions (21-30°C)	Folino-Rorem et al. (2016)
	Leptomedusae	<i>Clytia</i> spp.	0.27	-	Colony	2.0 - 10.0	Medusae		Matsakis (1993)
		<i>Clytia hemisphaerica</i>	0.25 - 0.37	-	Colony	1.0 - 2.5	Medusae	Laboratory conditions (18-20°C)	Lechable et al. (2020)
			1.19	-	Colony	2.5 - 12.0	Medusae	Laboratory conditions (18-20°C)	

(a) Data from *Aurelia* spp. previous review by Marques et al. (2015b) are not included in details in this table



**FIGURE 3.8.** **a.** Growth rate (mm day<sup>-1</sup>) for each Medusozoa Order (Caryb. = Carybidae, Chiro. = Chirodropida, Lepto. = Leptomedusae, Limno. = Limnomedusae, Rhizo. = Rhizostomeae, Sema. = Semaestomeae) by Class (Cubozoa, Hydrozoa and Scyphozoa). Dots represent each data (n). **b.** Linear significant relationship between mean bell diameter (BD) and growth rate (GR) ( $GR = 0.02 \times BD + 0.64$ ,  $p < 0.01$ ,  $r^2 = 0.44$ ). Grey area indicates the 95% confidence limits. Both analyses were performed with published data of jellyfish growth rates (literature review in Table 3.2).

### 3.3.6 | Objective 4. Biomass assessment

Significant relationships were obtained between WW and all morphological parameters measured (Table 3.3). In fact, all the morphological traits considered in the present study are good indicators to estimate the biomass of *R. pulmo*. In particular, the BD and the TL of the individuals presented both the best fit ( $r^2$ ).

**TABLE 3.3.** Relationships between wet weight (WW, in g) and morphological traits (in cm) measured in *Rhizostoma pulmo*. n: number of specimens.

Morphological trait (cm)	n	Function	$r^2$
Bell diameter (BD)	485	$WW = 0.09 * BD^{2.91}$	0.98
Total length (TL)	455	$WW = 0.19 * TL^{2.63}$	0.97
Oral arm's length (OA)	258	$WW = 1.15 * OA^{2.52}$	0.96
Bell height (BH)	384	$WW = 0.95 * BH^{2.82}$	0.95
Manubrium diameter (M)	353	$WW = 47.81 * M^{2.68}$	0.92

### 3.4 | DISCUSSION

Semi-enclosed coastal lagoons can be considered as large mesocosms, offering unique opportunities to study jellyfish dynamics. Here, we provide evidence of a bottom-up control on the population dynamics of *R. pulmo* in Bages Sigeon lagoon, which is further shaped by multiple recruitment pulses on a yearly basis. In addition, we also show different thermohaline niches for western Mediterranean populations of *R. pulmo*.

#### 3.4.1 | Population dynamics of *Rhizostoma pulmo* in coastal Mediterranean lagoons

Multiple recruitment pulses have been described in many scyphozoan (Calder 1982) and cubozoan species (Table 3.2). However, the underlying causes of such patterns are still far from understood (Houghton et al. 2007). In the present study, we identified three abundance peaks of *R. pulmo* ephyrae during one year. This multi-cohort pattern agrees with previous observations in Mar Menor, where four ephyrae abundance peaks were detected (Fernández-Alías et al. 2020). Under laboratory conditions, thermal shocks stimulate scyphistomae strobilation in some species (Holst 2012; Marques et al. 2019). For *R. pulmo*, empirical observations have shown that only one thermal shock may induce more than one strobilation event (Anais Courtet, Paris Aquarium, pers. comm.), with the possibility that the same scyphistomae strobilates twice (Purcell et al. 2012b). We suggest that multi-strobilation may be a common feature for some species (Calder 1982; Houghton et al. 2007) including *R. pulmo*, whilst interannual variability in the number of cohorts (Kikinger 1992) has been associated to the delta of temperature prior strobilation.

The seasonal dynamics of *R. pulmo* in Bages Sigeon during 2019 was characterized by a peak of medusae abundance during spring (April) and a disappearance during winter (November). This trend supports previous observations in Mar Menor during 1997 (Fernández-Alías et al. 2020). In both lagoons, first ephyrae appeared at the beginning of spring (April) and medusae seemed to grow inside the lagoons throughout the year, as all pelagic stages were observed. Fuentes et al. (2011) recorded a quite similar seasonal distribution during three consecutive years (2007, 2008, 2009) on the Catalan coast (Spain). On both French and Spanish Mediterranean coasts, seasonal patterns of temperature, salinity and chlorophyll *a* concentration are similar, which may explain the quasi-synchronous annual pattern of *R. pulmo* in the lagoons. Despite a similar seasonality, *R. pulmo* abundances seem to exhibit marked variability. Maximum abundance detected in Bages Sigeon during 2019 was 19.1 ind 100m<sup>-3</sup>, while in 1997 in Mar Menor it was 2.6 ind 100m<sup>-3</sup> (Fernández-Alías et al. 2020), but interannual



abundance variability are also to be considered (D'Ambrosio et al. 2016). In the Southern Mediterranean coast, *R. pulmo* was observed in the bay of Bizerte (Tunisia) mainly during summer–autumn months: in September 1994, May, September and October 1995 (Daly Yahia et al. 2003) and from September to November 2013 (Gueroun 2016). In 2014, the species appeared in Bizerte lagoon during winter–spring months (January to April), which probably corresponds to some individuals capable of entering in the lagoon to withstand the winter. In all cases, *R. pulmo* was observed at low abundances ( $< 1 \text{ ind } 100\text{m}^{-3}$ ) therein and in specific months, which suggests that the species is transported from adjacent areas.

The thermal window of *R. pulmo* medusae in the Mediterranean Sea in the last decade, based on medusae semi-quantitative data and satellite temperature data, was identified between 15 and 22°C (Leoni et al. 2021a). Our results support the reported range, but also showed that at local scales, the width of the thermal niche is larger, with a potential thermal niche from 13 to 29°C, although major abundances were found at temperatures  $> 15^\circ\text{C}$ . The ability of *R. pulmo* to dwell a wide range of temperatures is probably due to the capacity of temperate ectothermic species to tolerate changing temperatures as observed for marine copepods (Molinero et al. 2009).

Except for the low winter temperature measured in the shallow Bages Sigean lagoon, temperature values were comparable in the three lagoons. However, we have shown that the species presents different realized niches in the three evaluated geographic regions: Tunisia, Spain and France (Fig. 3.6). For *R. pulmo*, at least three genetically distinct populations have been identified in Tunisia, North Adriatic and Western Mediterranean (coast of Spain and Italy) Sea (Ben Faleh et al. 2017). Population genetic differentiation among distant areas has been also observed for others scyphozoan species (Kingsford et al. 2000; Ramšak et al. 2012; Dawson et al. 2015; Glynn et al. 2015). In those distinct jellyfish populations, physiological adaptation to temperature variability has been observed (Dawson et al. 2015; Gotoh et al. 2017). Here, the niche variation we observed on *R. pulmo* is likely indicative of local adaptation and phenotypic plasticity of *R. pulmo* populations from the Western Mediterranean. Future biogeography studies of this species should include not only the French population, but also those from other ecoregions of the Mediterranean to identify its potential divergence.

Ontogenetic variations in the thermohaline niche were also revealed, as observed in *A. coerulea* in Thau lagoon (Bonnet et al. 2012; Marques et al. 2015b). The maximum ephyrae abundance was reached in June, in concurrence with a peak of temperature. This agrees with laboratory observations, where *R. pulmo* scyphistomae produced more buds and ephyrae under warm (21 to 28°C) than cold conditions (14°C; Purcell et al. 2012b). The widest range of

temperature observed for young medusae in Bages Sigean is probably due to the continuous ephyrae production under different environmental conditions. This underlines that plasticity in juvenile stages is probably higher than in mature sexual medusae. The detection of juveniles' abundance peak (April 17) before ephyrae abundance peak (June 12; Fig. 3.4b) was probably due to a combination of a fast growth rate (4.7 mm day<sup>-1</sup>) of early pelagic stages, and a low-frequency sampling (April sampling occurred in April 1 and 17), which did not allow to capture the ephyrae short term dynamics. Moreover, the use of fixed sampling stations for monitoring free-living species, transported with current generated by the winds in the area, may explain the lack of ephyrae detection prior to the peak of juveniles. Overall, adults in Bages Sigean were observed under warmer waters conditions than younger stages, which agrees with summer blooms reported for many Mediterranean jellyfish species (Boero 2014). Salinity ranges differ between lagoons, but the optimal salinity values for ephyrae in Bages Sigean and medusae from Bages Sigean and Bizerte were similar. In Bages Sigean and Mar Menor, ephyrae presented a different but restricted range of salinity, probably because of their short period of development, as new released ephyrae of approximately 1 mm should grow only 9 mm before developing into a small medusae.

Despite that drivers of jellyfish population dynamics are still not well understood, increasing evidences on the role of food availability have been provided by in situ monitoring (Lucas 1996; Buecher et al. 2001; Rosa et al. 2013; Marques et al. 2015b; Goldstein and Riisgård 2016). For *R. pulmo*, bottom-up processes appeared to be main drivers of the pelagic population dynamics in Bages Sigean, in agreement with previous research in Mar Menor (Fernández-Alías et al. 2020) and Bizerte (Addad et al. 2008) lagoons, or for the Rhizostomeae *N. nomurai* in Dalian Sea, China (Xie et al. 2021). In Bages Sigean, copepods play a key role in shaping *R. pulmo* abundances. In this regard, increasing knowledge on the diet of the species (Pérez-Ruzafa et al. 2002; Dönmez and Bat 2019) is required to evaluate not only the role of plankton community in the dynamics of the species, but also the feeding pressure of *R. pulmo* on the ecosystem.

The voracious food-consumption of scyphomedusae (Acuña et al. 2011), together with the fast growth rates (several mm per day, Table 3.2), induces rapid development of large individuals in short periods of time. The growth coefficients ( $k$  in years<sup>-1</sup>) of *R. pulmo* varied from 3.76 to 4.47, but are consistent with those reported for other scyphozoans: *S. meleagris* (3.97 to 5.79), *Phyllorhiza punctata* (4.69), *C. hysoscella* (4.30) and *A. aurita* (3.83) (Palomares and Pauly 2009; López-Martínez et al. 2020). However, Fernández-Alías et al. (2020) reported lower values (3.00 to 3.44) for *R. pulmo* in Mar Menor, probably due to the

fact that they used a different method for cohort identification and defined a unique  $L_{\infty}$ , whilst we defined a specific value for each cohort. In Bages Sigean, *R. pulmo* growth varied between cohorts and during ontogeny. We suggest that this difference may be partly due to the overlapping between adults from the first cohort with juveniles of the second cohort, which could induce competition for food. This, together with the natural seasonality of the zooplankton community in the lagoon, might limit their growth rate but also the maximum size raised by adults from the second cohort. In addition, growth can be reduced in adult stages (> 15 cm) when resources are reallocated to reproduction (Lucas and Lawes 1998). *R. pulmo* start to present gonads when their BD is larger than 15 cm. Based on age estimations derived from our study, medusae could reach sexual maturity within 1 to 2 months, as estimated for *Catostylus mosaicus* (Pitt and Kingsford 2003b).

In comparison with other Class of Medusozoa (Table 3.2), scyphozoan species show the fastest growth and the biggest BD. A great proportion of the variability of Medusozoa's growth rate was explained by the medusae size ( $r^2 = 0.44$ , Fig. 3.8b). Despite most of the studies have been realized on *Aurelia* spp., a greater diversification is observed in the studies on Suborder Rhizostomeae, with 11 species analyzed compared to 3 species of Semaestomeae. In contrary, Hydromedusae and Cubomedusae showed similar rates, but less than 10% of these species have their growth rates estimated. The fast growth rates of scyphomedusae could explain their relatively short longevity (< 1 year; Arai 1997). A maximum longevity of 7 months was identified for *R. pulmo* in Bages Sigean, as previously reported in the Mediterranean Sea (Leoni et al. 2021a). Similar estimations have been made for Rhizostomeae species as *S. meleagris* (8 months; López-Martínez et al. 2020) and *N. nomurai* (7 months; Sun et al. 2015) and for the Semaestomeae *A. coerulea* (7–8 months; Bonnet et al. 2012; Marques et al. 2015b) and *A. solida* (6–7 months ; Gueroun et al. 2020). However, some species could live longer than one year in nature, like *C. mosaicus* (13 months; Pitt and Kingsford 2003b). Few individuals of *R. pulmo* were observed to survive winter conditions in Mar Menor where temperature did not drop under 10°C (Fuentes et al. 2011), suggesting that its lifespan can be sometimes longer. In addition, some jellyfish species kept in captivity under optimal conditions may live for multiple years (e.g., *Cassiopeia* sp., 4 years; *A. aurita*, 2 years; Zahn 1981). In this regard, *in situ* mortality of medusae seems to be age-independent.

Seasonal declines in jellyfish abundance are typically observed in temperate regions (e.g., Lucas 1996). Therein, many factors could explain these massive mortality events, including the release of gametes (Omori et al. 1995), low temperatures and food availability. The sharp abundance decreases with massive stranded individuals observed in winter months

could be triggered by the decrease of temperature. It is possible that medusae do not survive winter conditions in Bages Sigean where temperature typically decreases under 7°C (PNRNM 2021), as the adults' thermal niche is the warmest among all life stages. If temperature minimum is the cause behind this mortality event, warming trend in the NW Mediterranean Sea (0.04°C year<sup>-1</sup>; Salat and Pascual 2002) could induce a temporal expansion of these events if food availability is not limited for the population.

### 3.4.2 | Jellyfish population biomass estimations

Jellyfish demographic features, such as BD frequency distribution, size at sexual maturity, growth rates, diameter–weight relationships, abundance and biomass, are crucial for resources management. Nevertheless, population biomass estimations are still missing for many jellyfish species (Lucas et al. 2014). Non-invasive technologies based on images (Cimino et al. 2018; Schaub et al. 2018; Raoult and Gaston 2018) provide new opportunities to monitor these populations covering large study areas. However, those methods require determining allometric relationships to estimate medusae biomass. Although BD is the most used morphological trait for biomass or growth rate estimations on Scyphomedusae (Nogueira and Haddad 2006), for some Rhizostomeae species, TL has proven to be more appropriate (López-Martínez et al. 2020). In these organisms, OA are an important fraction of the biomass of the medusae compared with the other groups. Here, we observed a tight correlation between all morphological traits considered and the WW (Table 3.3). Due to the swimming behavior of these medusae in parallel to the water surface (Raoult and Gaston 2018), and because measuring the BD can be a difficult task due to the bell consistency on the biggest specimens (i.e., hard collagen umbrella difficult to flatten), TL should be preferred on *R. pulmo* to obtain an accurate estimation of WW, and subsequently, of biomass (g m<sup>-3</sup>).

## 3.5 | CONCLUSIONS

We have shown that a bottom–up control shaped *R. pulmo*'s population dynamics in the Bages Sigean lagoon during 2019 and that the growth rate and environmental windows of the species presented ontogenetic variability. Experimental studies may provide complementary information (see Purcell et al. 2012) to understand the physiological responses of each stage of development under future scenarios of significant water temperature changes. These results stress the need to consider jellyfish ontogeny and differences among Medusozoans into food web models. At the Mediterranean basin scale, the variability of the

realized thermohaline niche of *R. pulmo* among geographic regions sheds light on the plasticity of the species. These results may reflect genetic divergences of the studied populations, so future investigations should include genetic identification of these Mediterranean populations. As *R. pulmo* is currently in the spotlight as a potential fishery resource, the identification of distinct populations is crucial for its sustainable exploitation (González et al. 2020) to avoid overfishing on jellyfish stocks (Getino Mamet et al. 2019). In addition, the methodology we used to estimate growth rate for a multicohort species is recommended in jellyfish stocks assessment. We expect that the ecological information provided in the present study help to elucidate the biogeography and ecology of one of the most common species in the Mediterranean Sea.

## SUMMARY POINTS

- During one year, we found a succession of cohorts that showed some degree of overlapping, from April to September, May to October and June to October. This multicohort pattern has previously been observed in Mar Menor lagoon and is probably a common feature of this species.
- *R. pulmo* occurs between a temperature range of 13 to 29°C, with major abundances at temperatures higher than 15°C.
- Overall, the population presents three abundance peaks: The highest in April, and two smaller in June and July, while the maximum biomass was reached in July. All jellyfish disappeared in November, probably not surviving under winter conditions (< 7°C).
- Jellyfish seasonality seems to be driven by the abundance of copepods, suggesting a bottom-up control of *R. pulmo* in Bages Sigean lagoon.
- An ontogenetical shift in the favored environmental windows was detected for *R. pulmo*, as previously observed in other jellyfish species. Adults' maximum probability of occurrence was at warm waters, in agreement with summer blooms reported for many Mediterranean jellyfish species.
- *R. pulmo*'s growth rates differ between cohorts and developmental stages: Juveniles grow faster than adults, and individuals from the first cohort grow faster than the second one. These differences could be driven by the natural seasonality of food resources in the lagoon.
- Bell diameter and total length were identified as the best morphological descriptors of growth and are the recommended proxies of biomass estimation in jellyfish stocks assessment.
- The species presents different realized niches in the three evaluated geographic regions: Tunisia, Spain and France. This result suggests the existence of a metapopulation in the Mediterranean Sea.

## CHAPTER 4.

# ONTOGENETIC DIETARY SHIFTS OF THE MEDUSA *RHIZOSTOMA PULMO*

Valentina Leoni<sup>1</sup> • Juan Carlos Molinero<sup>2</sup> • Sandrine Crochemore<sup>1</sup> • Marie Meffre<sup>1</sup> • Delphine Bonnet<sup>1</sup>

<sup>1</sup> MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Montpellier, France

<sup>2</sup> MARBEC, IRD, CNRS, Ifremer, Université de Montpellier, Sète, France

Published in **Hydrobiologia** (2022)





## **Ontogenetic dietary shifts of the medusa *Rhizostoma pulmo***

Recent studies have challenged the notion that gelatinous animals are trophic dead ends and have demonstrated that they play a critical role in marine food webs as predators and prey. This group feeds on a wide variety of prey and uses diverse feeding strategies, including active hunting, passive trapping, or filter feeding. The trophic links that both preys and predators have with gelatinous zooplankton animals, known as the ‘jelly-web’, are complex. Characterizing these links is challenging due to the difficulties associated with their collection, which becomes even harder when studying large organisms. Scyphomedusae are a common component of the coastal food webs that reach large sizes, in some cases reaching more than 1 meter. The voracious consumption of these organisms during bloom events may alter the structure of the food web, but the timing of the species life cycle will determine their impact in the food web. However, few studies have evaluated the trophic role of one species during its entire life cycle.

In the previous chapter, seasonal variations in food availability were identified as a critical factor in *R. pulmo* population dynamics, as already observed for several gelatinous zooplankton species. Nevertheless, a gap of information exists on the trophic ecology of these species, and the predatory impact on the plankton community is still incipient.

This chapter aims to describe the intra-annual trophic ecology of *R. pulmo* pelagic stages in Bages Sigeon lagoon and to assess its potential variability during ontogeny. In this context, the purpose of this chapter was to answer these questions: What is the taxonomic identity of prey and the range of size consumed by this jellyfish? Do *R. pulmo* have the same trophic role throughout its lifetime? Is there any prey preference? What is the impact of the species in the planktonic food web?

**Keywords:** Gut content • Barrell jellyfish • Mediterranean Sea • Developmental stages



## 4.1 | INTRODUCTION

Assessing the trophic role of species, i.e., what they eat and in what proportions, is fundamental to understand energy fluxes and ecosystem functioning (Cury et al. 2008). In marine ecosystems, gelatinous zooplankton are increasingly recognized as conspicuous prey (Hays et al. 2018), consumers (Robinson and Graham 2014), and prominent players in biogeochemical cycles (Lebrato et al. 2019). Cnidarians represent approximately 92% of the total global biomass of gelatinous zooplankton (Lucas et al. 2014), with scyphomedusae species developing the largest individual body weight and forming spectacular blooms (Dawson and Hamner 2009). Due to their voracity on lower trophic levels (Purcell 1992), scyphomedusae blooms impact the whole food web structure in coastal marine ecosystems, thereby shaping the ecosystem functioning and services (West et al. 2009).

Despite the central role of scyphomedusae and their impact on local economies (Bosch-Belmar et al., 2021), the trophic ecology of this taxon is often misrepresented, as the large majority of studies have focused on two genera, *Aurelia* and *Chrysaora*. The remaining 85% of scyphomedusae species are overlooked. Consequently, ecosystem models have historically oversimplified their role as predators (Pauly et al. 2009), although recent evidence has shown a wide variation in their trophic role which changes not only across species, but also throughout their ontogeny (Fleming et al. 2015).

During their life cycle, scyphozoans display a wide range of sizes, from few millimeters up to 1 meter. The few studies that have addressed their ontogenetic dietary shifts have identified diverse responses. For instance, benthic and pelagic stages trophic niches of some species widely overlap (*Aurelia coerulea*; Marques et al., 2021), others shift their trophic level with size (*Lychnorhiza lucerna*; Nagata et al., 2015 and *Cyanea nozakii*; Wang et al., 2020), or modify prey preferences and diversity (*Stomolophus meleagris* and *Aurelia aurita*; Larson, 1991; Graham & Kroutil, 2001; Álvarez-Tello et al., 2016). Such diet changes have been associated with shifts in mouth size, prey encounter probability, or small-scale currents generated by bell pulsations (Costello and Colin 1995; Nagata et al. 2016).

Among the methods used to determine the trophic role, four have been implemented on scyphozoans' diet analyses (Pitt et al. 2009): gut content, grazing experiments, stable isotope (SI) and fatty acid (FA) analyses. SI and FA analyses provide the signal of the assimilated food, but require a previous knowledge of the prey's signal in the environment (Pitt et al. 2009). In turn, gut content analysis provides information on recently ingested food, although it does not allow detecting the assimilated one, and therefore underestimate preys that are digested rapidly

(Purcell, 1997; Båmstedt & Martinussen, 2000). Notwithstanding this limitation, it remains the most direct method for prey identification (Purcell 2018). A protocol to standardize the assessment of scyphomedusae gut content has been only recently provided (Nagata and Morandini 2018). To date, however, gut content analyses on jellyfish have generally based their conclusions on a small sample size, and overlooked the predators and prey seasonality, which are not only crucial to define dietary niches but are also essential to incorporate this group in food web models.

By virtue of their relative shallowness and protection from the open sea, semi-enclosed ecosystems, such as coastal lagoons, are exceptional places to study jellyfish trophic interactions in natural environments (Marques et al. 2021b). Bages Sigean (France) (43°05'12.72" N; 3°00'35.3" E) is a small Mediterranean coastal lagoon (38 km<sup>2</sup>, mean depth of 2 m) located in a protected area (Cesmat et al. 2012). The lagoon is a shelter for migrant birds and fishes, and an important biodiversity reservoir (PNRNM 2018), where a perennial population of the barrel jellyfish *Rhizostoma pulmo* has been detected since 2014.

*R. pulmo* is a native Rhizostomeae scyphomedusa from the Mediterranean and Black Seas (Leoni et al. 2021a). This scyphomedusa can reach biomasses of 300 tons km<sup>-2</sup> during bloom events (Basso et al. 2019), with dramatic effects on fisheries (Nastav et al. 2013) and potentially on the food web structure (e.g., Brodeur et al., 2002). In Bages Sigean, summer blooms of *R. pulmo* (Leoni et al. 2021b) are a major issue for artisanal fishing due to net clogging, spoiling the commercial value of captured fish and because of the risk of stings (S. Marin pers. comm.). Similar problems have been reported in other ecosystems inhabited by this species, i.e., Mar Menor lagoon (Spain, Fuentes et al. 2011).

The feeding mechanism of *R. pulmo* is peculiar. Instead of a central mouth, such as in *Aurelia* and *Chrysaora*, Rhizostomeae medusae have eight specialized oral arms covered with millimetric mouths where the food is ingested due to micro-currents generated by bell pulsation (Nagata et al., 2016). However, little is known about the diet of this species (Pérez-Ruzafa et al. 2002; Dönmez and Bat 2019).

In this study, we benefited from the large size range of individuals present across the year in Bages Sigean lagoon (Leoni et al. 2021b) to assess *R. pulmo* diet throughout the pelagic stages. Owing to the medusa mouths size (c. 3,000 µm), we hypothesized (H1) a diet mainly composed by a dominance of small prey. In addition, as it is expected that prey encounter rate and micro-currents generated by bell pulsations increase along medusa ontogeny (Nagata et al. 2016), we hypothesized an increase of prey richness (H2) and mobile prey (H3) in the diet along with medusa growth. By means of gut content analysis, we (1) describe prey diversity

and size range during ontogeny, (2) quantify prey relative abundance, (3) examine potential prey-selectivity patterns of the species, and (4) identify the main sources of carbon supply during ontogeny, as well as its predatory impact in the lagoon.

## 4.2 | METHODOLOGY

Biological samples were gathered biweekly between February and November 2019 in Bages Sigeon lagoon (see Figure 1 in Leoni et al., 2021b) between 09:00 and 12:00 AM. The abundances of *R. pulmo* pelagic stages were estimated using two complementary sampling procedures. Young individuals were caught with a 700- $\mu$ m mesh size plankton net fitted with a flowmeter, which was towed horizontally at the sub-surface due to the shallowness of the lagoon. In turn, the abundance of large organisms was estimated with a non-intrusive method of visual counting from the boat (Leoni et al. 2021b). Abundance estimations were expressed as the number of medusae per 100 cubic meters.

### 4.2.1 | Jellyfish gut content analysis

*R. pulmo* medusae size classes were defined based on the absence (juveniles) or presence (adults) of gonads. We used 15 cm as the bell diameter (BD) threshold to distinguish juveniles from adults' specimens, as gonads were present in all individuals with BD >15 cm.

The methodology applied to assess the medusae gut content was based on Nagata & Morandini (2018). Medusa specimens were carefully collected by dip nets from the boat. Only unharmed and active individuals were considered. BD ( $\pm 0.05$  cm) and wet weight (WW  $\pm 0.05$  kg) of the specimens were recorded. Each medusa was stored individually in a plastic jar with formalin 10%. In the laboratory, medusae were singly laid down on a tray and methylene blue was injected into the specimens' gut to facilitate prey visualization (Nagata and Morandini 2018). Later, oral arms were removed by scissors and the cruciform gut was opened. The cavity was rinsed with 0.2  $\mu$ m filtered seawater and the washed content was retained on a 63- $\mu$ m sieve. Consequently, 63- $\mu$ m was the lower size threshold of prey identification. The gut walls were also examined under a Leica stereomicroscope to collect prey eventually retained therein. Both, prey items removed by rinsing and those attached to the gastric cirri were conserved in formalin 4% and included in counts.

Prey items were identified and counted in a Bogorov chamber under a stereomicroscope. When possible, specimens were identified at species or genus level. Otherwise, identification was carried out to the greatest detail possible. Phytoplankton was counted but was not

considered for the analyses as it was probably underestimated due to the minimal size of prey identification. Individual prey measurements were determined from pictures with a camera integrated into the stereomicroscope, using the software Leica Application Suite X (LAS X). Schematic representations of how measurements were taken are presented in Figure S4.1, mainly following Uye (1982).

#### 4.2.2 | Characterization of food availability

To characterize the zooplankton community and to evaluate *R. pulmo* prey selectivity patterns, zooplankton and medusae collections were performed simultaneously. Micro-, meso- and macrozooplankton were collected with 63- $\mu$ m (0.40 m diameter x 1.00 m length), 200- $\mu$ m (0.54 m diameter x 2.50 m length) and 700- $\mu$ m (0.78 m diameter x 2.00 m length) mesh size plankton nets, respectively, each fitted with a flowmeter and towed horizontally in the sub-surface layer. Samples were fixed in formalin 4%. Two samples were taken for meso- and macrozooplankton in the study area at each sampling date, while only one sample was collected for microzooplankton at each date.

Microzooplankton was analyzed with a FlowCam imaging system (Fluid Imaging Inc.; Sieracki et al., 1998) at the Villefranche Oceanography Laboratory, LOV, while the posterior classification was performed in EcoTaxa. Data are available online (<https://ecotaxa.obs-vlfr.fr/prj/3279>). Meso- and macrozooplankton organisms were counted and identified under the stereomicroscope using taxonomic guides (Trégouboff and Rose 1978; Hecq et al. 2014). Zooplankton abundances were estimated from subsamples and expressed as individuals per cubic meter.

#### 4.2.3 | Statistical analysis

To characterize and quantify the diet of *R. pulmo*, each medusa was treated as a sampling unit. In addition, to allow future comparative analyses, we used standard equations and nomenclature employed in trophic indices assessments, as summarized in da Silveira et al. (2020).

##### 4.2.3.1 | Assessing the minimum sample size

A cumulative curve of the number of medusae analyzed against the number of prey taxa in the guts was used to determine adequate sample size, i.e., the minimum number of samples (MNS) to represent the total richness. We used the Chao1 non-parametric estimator ( $S_{Chao1}$ ):

$$S_{Chao1} = S_{obs} + \frac{n_1^2}{2n_2}$$

where  $S_{obs}$  is the observed richness,  $n_1$  is the number of species found once, and  $n_2$  is the number of species found twice (Chao et al. 2009). The sampling effort was considered sufficient when  $S_{obs}$  was equal to 80% of  $S_{Chao1}$  (Jiménez-Valverde and Hortal 2003). This analysis was performed in the software R using the *rarc* function of the 'rich' package (Rossi 2011).

#### 4.2.3.2 | Objective 1. Prey's richness and frequency of occurrence during *R. pulmo* ontogeny

To evaluate whether changes during ontogeny were related to changes in prey's richness, the number of prey taxa found in juvenile and adult medusae was compared using a Kruskal-Wallis test. A significance level of 5% was applied. In addition, the proportion (%) of empty guts ( $G_e$ ) was estimated by month per stage of development.

The frequency of occurrence ( $FO$  in %) of a prey category ( $i$ ) in the gut content of both juvenile and adult medusae was estimated as the number of guts with this food item ( $G_i$ ) over the total number of guts containing food ( $G_f$ ; da Silveira et al. 2020).

#### *Objective 2. Relative abundance of prey on the diet of R. pulmo pelagic life stages*

The percentage of the relative abundance ( $N$ ) of prey was calculated for each prey taxa for all medusae containing food. The average relative abundance was determined by month for both stages of development.  $N$  (%) was estimated as the number of individuals of a prey category ( $N_i$ ) over the total number of prey items found in the medusa gut ( $\sum N_i$ ; Hyslop 1980):

$$\%N = \left( \frac{N_i}{\sum_{x=1}^i N_i} \right) * 100$$

#### 4.2.3.4 | Trophic niche determination

The trophic niche breadth ( $NB$ ) was estimated for juveniles and adults medusae using Levin's standardized index (Krebs 1999):

$$NB_k = \frac{1}{n - (\frac{1}{\sum p_{ik}^2} - 1)}$$

where  $NB_k$  is Levin's standardized index for a predator  $k$ ;  $p_{ik}$  is the proportion of a prey  $i$  in the diet of the predator  $k$ , and  $n$  is the number of prey categories. This index ranges from 0 to 1,

where low values represent a narrow niche breadth or a specialized diet, whilst higher values suggest a generalist diet with a wide niche breadth.

Lastly, we assessed the niche overlap between juveniles and adults when they coexist. This metric was expressed as the percentage of similarity between juveniles' ( $j$ ) and adults' ( $a$ ) diets, and estimated with the simplified Morista's index of similarity ( $NO$ ; Krebs 1999):

$$NO = 2 * \frac{\sum (P_{ij} * P_{ia})}{\sum P_{ij}^2 + \sum P_{ia}^2}$$

Here,  $P_{ij}$  and  $P_{ia}$  are the proportions of the resource  $i$  used respectively by juveniles and adults in relation to the total resources. The values ranged from 0 to 100%, with 0% representing no diet overlap, and 100% identical diets. We followed the criteria of Langton (1982), and determined three categories of niche overlap: low (< 29%), medium (30-60%) and high (> 60%). This index is sensitive to the taxonomic resolution of preys identified. Here, differences at the species level, if they exist, were not considered in the niche overlap evaluation.

#### 4.2.3.5 | Objective 3. Prey selectivity patterns during *R. pulmo* ontogeny

To account for differences in the relative abundance ( $N$ ) of a prey type ( $i$ ) in the gut ( $G_i$ ) vs prey in the environment ( $E_i$ ), we used the linear food selection index ( $LFSI$ ; Strauss 1979). 'Positive selection' was considered when the  $G_i$  was higher than  $E_i$ , and 'negative selection' when  $G_i$  was lower than  $E_i$ .  $LFSI$  was estimated per medusa. Values of  $LFSI$  range from -1 to 1, reflecting the magnitude of prey selection. Null values indicate no selection, positive values suggest some degree of positive selection and negative values have a probable disability to consume the prey, i.e., negative selection. To evaluate whether seasonal and/or ontogenetic changes were related to changes in prey selectivity patterns, a heatmap of  $LFSI$  was performed by month and by medusae size range (BD in cm) for each type of prey. Size classes of 5 cm were set up with juveniles including the classes 0-5, 5-10 and 10-15 cm, and adults the classes 15-20, 20-25, 25-30 and > 30 cm.

#### 4.2.3.6 | Objective 4: Daily Carbon Ration (DCR) assessment and predatory impact

The daily ration ( $DR$ ) was estimated as the number of prey consumed ( $P_c$ ) by medusa per day as:

$$DR = P_c * 24 * DT^{-1}$$



using the digestion time ( $DT$ , in hours) for each prey provided in Larson (1991) (Table S4.1) and corrected by temperature as follows:

$$DT_t = 1 * (DT * Q_{10}^{(t-29)/10})^{-1}$$

where  $t$  is the temperature at each sampling date and  $Q_{10}$  was assumed equal to 2.08 (Purcell 2009). Lastly,  $DR$  was converted to daily carbon ration ( $DCR$ ) by multiplying  $P_c$  by the carbon content ( $C$  in mg) estimated for each prey using specific equations (Table S4.1).  $DCR$  was estimated for prey items found in more than 5% of samples. We used a biometric conversion factor estimating  $C$  as a percentage of *R. pulmo*'s WW:  $C\%WW = 0.34$  (Purcell et al. 2010) to estimate the  $C$  content of each medusa (WW range: 0.25 to 2761g). Quantile regressions (5<sup>th</sup>, 50<sup>th</sup> and 95<sup>th</sup>) were used to evaluate possible changes in carbon sources with medusae size (mgC; Cade and Noon 2003).

Based on medusae abundances, the predatory impact of *R. pulmo* in the lagoon was estimated as  $PI = DR * (D_{pred} * D_{prey}^{-1}) * 100$ , where  $PI$  is the percentage of the prey standing stock consumed by the medusae population per day,  $D_{pred}$  is the abundance of medusae (ind m<sup>-3</sup>) and  $D_{prey}$  the abundance of the prey in the environment (ind m<sup>-3</sup>; Nagata and Morandini 2018).  $PI$  was estimated for juveniles and adults by prey taxa.

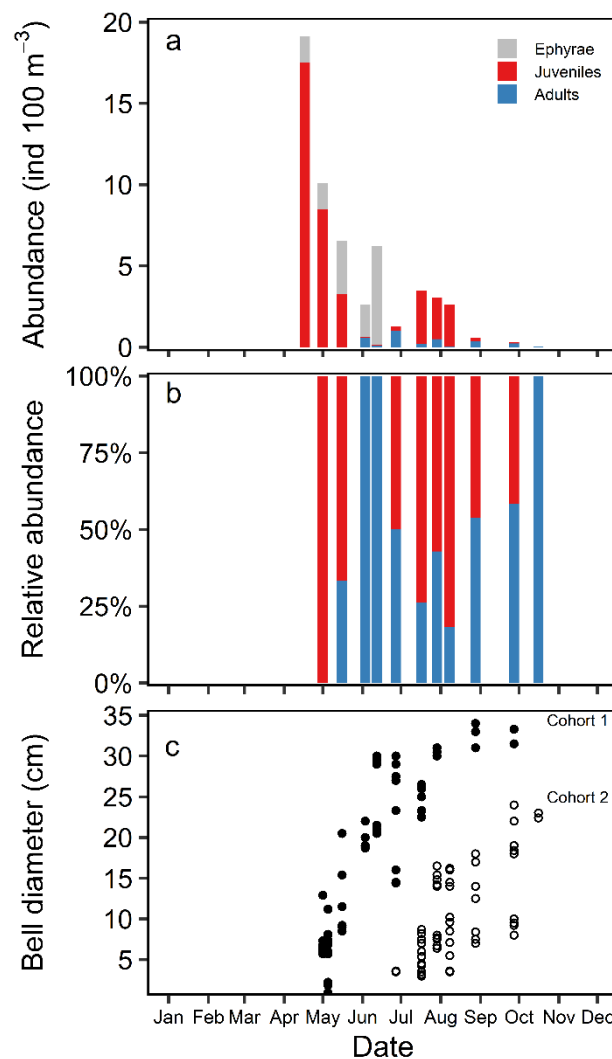
All the analyses were performed using the open source software R 3.6.0 (R Core Team 2020) and plots were created with the 'ggplot2' package (Wickham 2016).

## 4.3 | RESULTS

### 4.3.1 | Jellyfish population dynamics

In total, 16 samplings were performed. Ephyrae and small medusae appeared for the first time in April and the last medusae were observed in October. The seasonal dynamics of *R. pulmo* pelagic stages showed a maximum abundance in April and two smaller peaks in June and July (Fig. 4.1a). Ephyrae occurred from April to June, juveniles from April to September, and adults from May to October. Maximum abundances of ephyrae, juveniles and adults medusae were observed in June (6.1 ind 100 m<sup>-3</sup>), April (17.5 ind 100 m<sup>-3</sup>) and June (1.0 ind 100 m<sup>-3</sup>), respectively. Due to overlapped cohorts, in some months, more than one developmental stage was present. The first cohort developed from April to September, the second cohort from May to October, and the third cohort from June to October. However, as there were not enough individuals collected from the third cohort, only specimens from the two first cohorts were considered for gut content analysis (Fig. 4.1b, c). In total, 127 individuals

were collected (Fig. 4.1b), from May to October, with a BD ranging from 0.95 to 34.00 cm (Fig. 4.1c) and a WW from 0.25 to 2761.00 g.



**FIGURE 4.1.** **a.** Total abundance (ind 100 m<sup>-3</sup>) of the pelagic stage of *Rhizostoma pulmo* estimated during 2019 in Bages Sigean lagoon (France). Abundance for each developmental stage is indicated in colors: ephyrae in grey, juveniles (bell diameter <15 cm) in red and adults (bell diameter >15 cm) in blue. **b.** Relative abundance (%) of juveniles (red) and adults (blue) stages of *R. pulmo* collected for gut content analysis, and **c.** bell diameter (cm) of medusae collected for gut content analysis by sampling date. Full dots are the individuals from the first cohort and empty dots are the individuals from the second cohort.

#### 4.3.2 | Prey richness

A total of 16,239 prey items were counted in the gut contents, with an average prey concentration of  $20 \pm 22$  prey medusa<sup>-1</sup> in juveniles and  $253 \pm 338$  prey medusa<sup>-1</sup> in adults. After screening, 14 taxa were assigned into three different prey categories based on size criteria: (i) microzooplankton (63-200  $\mu$ m) containing: foraminifers (phylum Foraminifera), ciliates

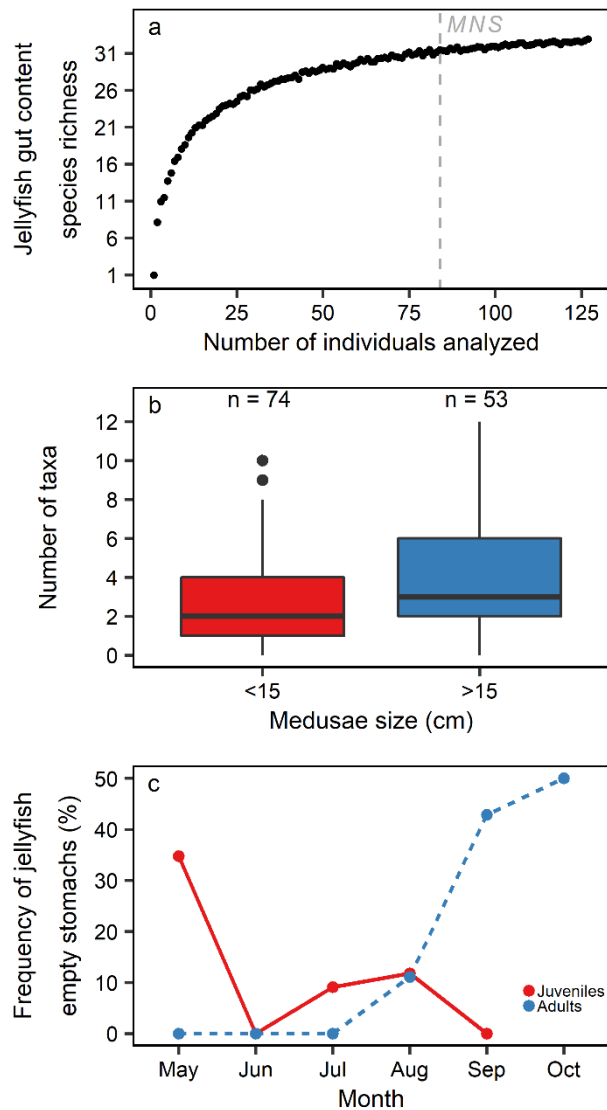
(phylum Ciliophora), bivalve and gastropod veligers (phylum Mollusca), ostracods and copepods' nauplii (phylum Arthropoda), (ii) mesozooplankton (200-700  $\mu\text{m}$ ) composed by: cirripeds' nauplii and harpacticoid, cyclopoid and calanoid copepods (phylum Arthropoda), and (iii) macrozooplankton ( $> 700 \mu\text{m}$ ) including: hydromedusae (phylum Cnidaria), fish eggs (phylum Chordata), crustacean malacostraceans (phylum Arthropoda) and polychaetes (phylum Annelida). Micro- and mesozooplankton specimens were the most recurrent prey, while the predominant group by category was the ciliates (20.8%) and the calanoid copepods (22.8%), respectively. Ciliates were mostly represented by the genus *Codonella*, *Favella*, and *Tintinnopsis*, whilst calanoid copepods were mostly represented by three species: *Acartia clausi* Giesbrecht, 1889, *Paracalanus parvus* (Claus, 1863) and *Pseudocalanus elongatus* (Brady, 1865).

Our sampling size was representative of the prey richness in *R. pulmo*'s guts. Indeed, the Chao1 non-parametric estimator indicated that the sampling effort can be considered sufficient when analyzing 84 specimens (Fig. 4.2a), when  $S_{obs}$  (observed richness = 35) is 80% of the  $S_{Chao1}$  (total richness estimated = 39). The number of taxa identified (14 taxa) showed a significant difference between juveniles and adults ( $df = 1$ ,  $p = 0.007$ ), with more taxa in adults ( $4.2 \pm 2.4$  taxa medusa<sup>-1</sup>) compared to juveniles ( $2.8 \pm 1.9$  taxa medusa<sup>-1</sup>; Fig. 4.2b).

Among the total specimens analyzed, 13% of the medusae guts were judged empty (17 specimens out of 127). Of them, 10 guts had only items of vegetal origin and the remaining 7 were empty. Vegetal structures, including *Pinus* pollen grains and stellate hair of vascular plants (*Elaeagnus* sp.) were observed in 61.2% of the guts analyzed, but were removed from the analyses as they were considered as terrestrial contamination. Thus, only 110 individuals were retained for the analyses: 62 juveniles and 48 adults.  $G_e$  (%) displayed a marked temporal variability (Fig. 4.2c). When *R. pulmo* appeared, more than 30% of juveniles presented empty guts, although no empty guts were observed at the beginning of summer (June), and only a few (~10%) until September. Conversely, all adults presented food in their guts from May to July. From July, an increase in the number of empty guts was noted, up to a maximum in October ( $G_e = 50\%$ ).

#### 4.3.3 | Objective 1. Frequency of occurrence of prey during *R. pulmo* ontogeny

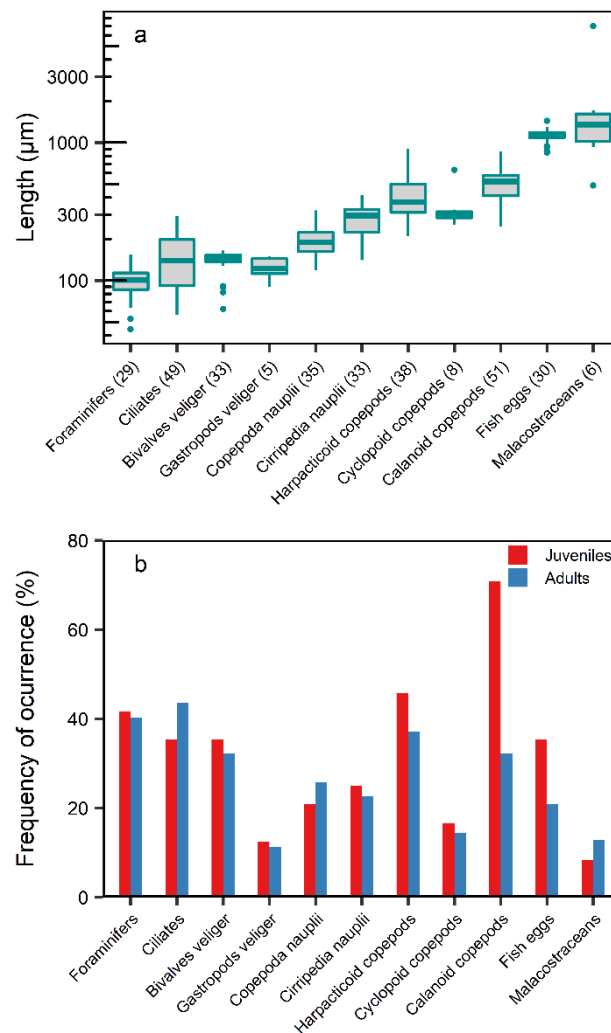
The ingested prey covered a size range from 45 to 9,000  $\mu\text{m}$  (Fig. 4.3a), with most of them (80%) figuring between 165-240  $\mu\text{m}$ . Prey size varied significantly (Kruskal-Wallis,  $df = 1$ ,  $p < 0.001$ ) between juvenile and adult medusae, with juveniles medusae feeding on larger sizes ( $385 \pm 190 \mu\text{m}$ ) than adult medusae ( $136 \pm 60 \mu\text{m}$ ).



**FIGURE 4.2.** **a.** Rarefaction curve for prey species richness indicating the required sampling effort to avoid unbiased *Rhizostoma pulmo* medusa diet determination. In the present study, the minimum number of guts (MNS) to represent prey richness was 84 (grey dashed line). The cumulative curve was calculated using the content of each medusa gut as a sampling unit ( $n = 127$ ). **b.** Number of taxa observed in the gut content of juveniles (bell diameter  $< 15$  cm) and adults (bell diameter  $> 15$  cm) specimens of *R. pulmo* (Kruskal-Wallis  $\chi^2 = 7.38$ ,  $df = 1$ ,  $p = 0.007$ ). **c.** Frequency of medusae empty guts (%) by stage of development (juveniles, represented by a red continuous line, and adults represented by a blue dotted line).

Calanoid and harpacticoid copepods were, together with ciliates, the most frequent prey (Fig. 4.3b). Of them, calanoid copepods doubled their occurrence in juveniles compared to adults, reaching a  $FO = 70\%$  in juveniles. Conversely, ciliates, copepods' nauplii and malacostraceans were slightly more frequent in adults compared to juveniles (Fig. 4.3b). In general, the biggest prey as malacostraceans, were observed with a frequency of occurrence ( $FO$ ) lower than 20%. The less consumed items, i.e., ostracods ( $c. 130 \mu m$ ), hydromedusae ( $c.$

500  $\mu\text{m}$ ) and polychaetes (*c.* 9000  $\mu\text{m}$ ), present in less than 5% of the specimens, were removed for posterior analyses.

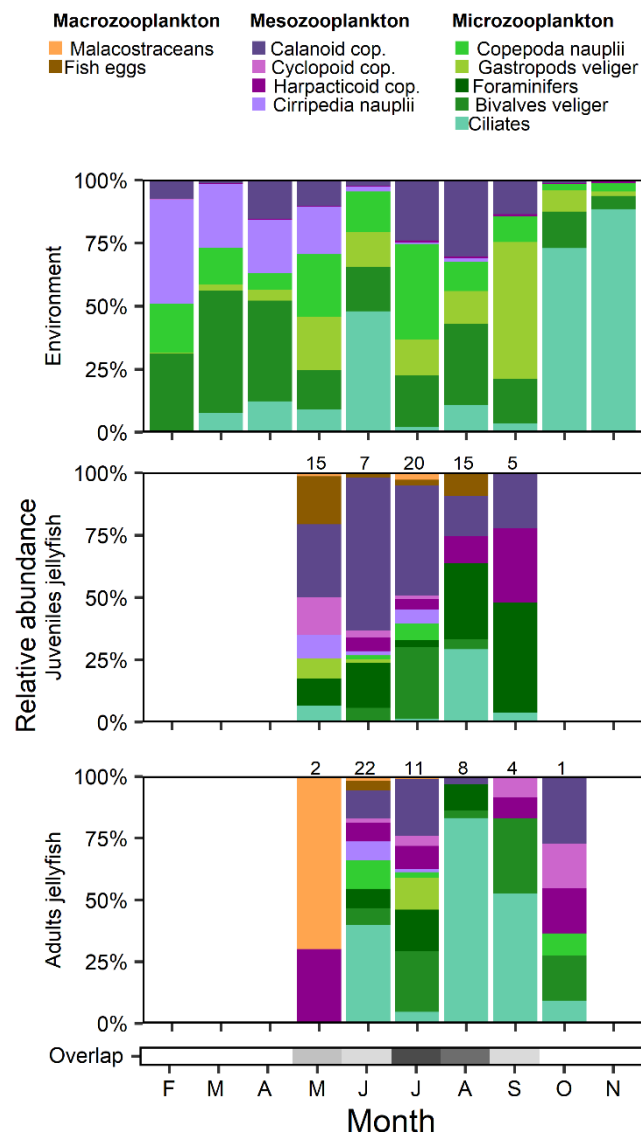


**FIGURE 4.3. a.** Size ( $\mu\text{m}$ ) of the different zooplankton prey items in the gut content of *Rhizostoma pulmo* ( $n = 110$ ) during 2019 in Bages Sigean lagoon (France). Numbers in parenthesis indicate the prey specimens measured. Note that the ‘Y’ axis is represented in a logarithmic scale. **b.** Frequency of occurrence of the different prey items in the gut content of juvenile (bell diameter  $< 15$  cm, in red) and adult (bell diameter  $> 15$  cm, in blue) medusae of *R. pulmo*.

#### 4.3.4 | Objective 2. Relative abundance of prey on the diet of *R. pulmo* pelagic life stages

The relative abundance of prey in the gut contents of the medusae did not follow their seasonal abundance in the environment (Fig. 4.4). From May to July, the diet of juveniles was composed mainly of calanoid copepods ( $N > 25\%$  each month). In August and September, this composition changed to a predominance of foraminifera ( $N > 25\%$ ), matching with the abundance peak of this group (Fig. 4.5), and in lower proportion to ciliates and harpacticoid

copepods. The predation on fish eggs was noticeable during May (*c.* 20%) and August (8%). In contrast, adults showed a different diet composition, with a predominance of ciliates, mainly in June (*c.* 40%), August (*N* > 80%) and September (*c.* 40%), followed by calanoid and harpacticoid copepods, and bivalve veligers.

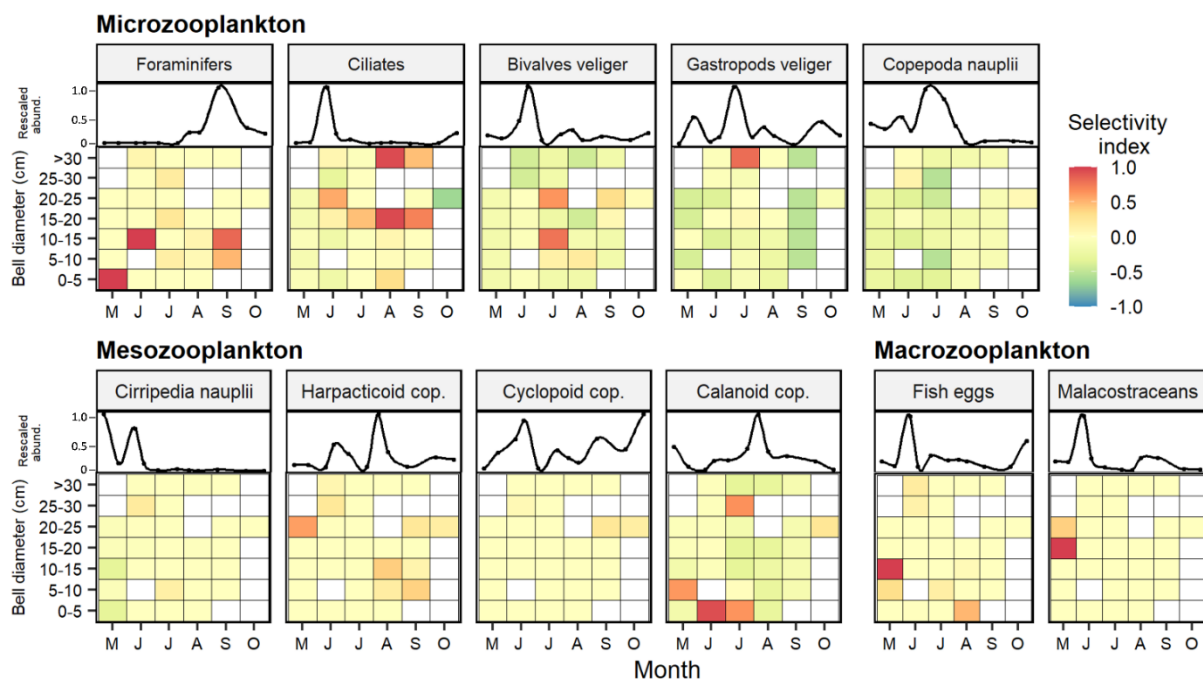


**FIGURE 4.4.** Monthly relative abundance (%) of each taxon observed in Bages Sigeon lagoon (France) (top) from February to November 2019, and in the gut content of *Rhizostoma pulmo* medusae juveniles (center) and adults (bottom) from May to October 2019 for the three size categories: Macrozooplankton (>700  $\mu\text{m}$ , in orange scale: malacostraceans and fish eggs), mesozooplankton (200-700  $\mu\text{m}$ , in purple scale: Calanoid, cyclopoid and harpacticoid copepods, and Cirripedia nauplii) and microzooplankton (63-200  $\mu\text{m}$ , in green scale: Copepoda nauplii, gastropods and bivalves veliger, foraminifers and ciliates). Note the temporal variability in the number of medusae analyzed by month (numbers on top). Niche overlap between juveniles and adults is represented at the bottom, only for months with juveniles and adults coexisting (from May to September). Scale from 0 to 100%, with 0% (white) representing no diet overlap, and 100% (black) identical diets.

Trophic niche breadth suggested a specialist feeding behavior for juvenile and adult medusae with low values in both cases ( $NB_{juveniles}=0.07$ ,  $NB_{adults}=0.08$ ). Most of the time, when juveniles and adults of different cohorts coexist, the niche overlap was low (13% in June and September, and 22% in May), but increased to medium or high in August (54%) and July (68%), respectively (Fig. 4.4). The highest overlap observed in July was caused by the predominance of bivalve veligers and calanoid copepods in the diet of both juveniles and adults.

#### 4.3.5 | Objective 3. Prey selectivity patterns during *R. pulmo* ontogeny

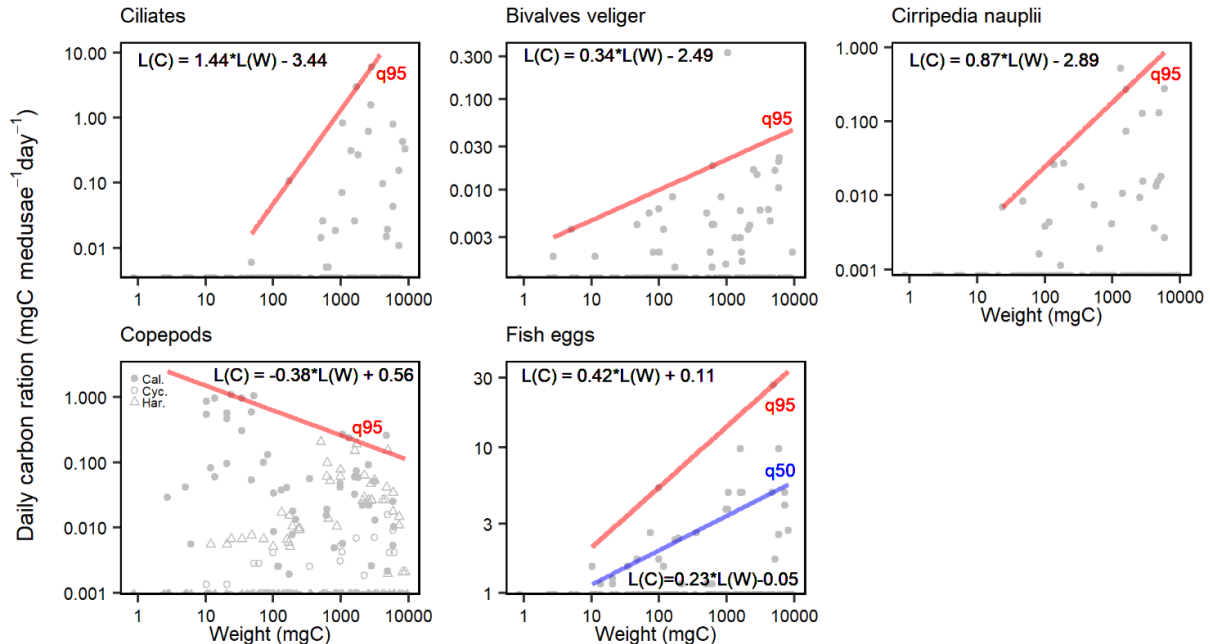
The prey selectivity showed a heterogeneous pattern (Fig. 4.5). Copepods' nauplii and gastropod veligers showed a negative selection most of the time, except for a positive selection of gastropod veligers by the biggest medusae (> 30 cm). Foraminifers, calanoid copepods and fish eggs were positively selected by juvenile medusae during some months. It is worth noticing that calanoid copepods were mostly ingested by the smallest sizes of *R. pulmo* (<10 cm), while ciliates were selected by adult medusae (> 15 cm; Fig. 4.5).



**FIGURE 4.5.** Selectivity index (LFSI) for zooplankton prey per month according to *Rhizostoma pulmo* medusa size. Prey taxa are grouped by size on microzooplankton (63-200  $\mu\text{m}$ ), mesozooplankton (200-700  $\mu\text{m}$ ) and macrozooplankton (> 700  $\mu\text{m}$ ). Positive (orange-red) or negative (green-blue) index values indicate selectivity at a rate above or below environmental concentration, respectively. Yellow indicates that dietary composition was similar to the proportional abundances in the surrounding zooplankton. White areas denote no data. Prey abundance seasonal patterns during 2019 in Bages Sigean lagoon (France), rescaled to 0-1, are shown in the top panel of each plot.

#### 4.3.5 | Objective 4: Daily Carbon Ration assessment and predatory impact

The daily carbon ration (*DCR*, mgC consumed per medusa per day) consumed by the medusae differed between prey types during *R. pulmo* growth (Fig. 4.6). At the smallest sizes of *R. pulmo* (< 34 mgC or < 6 cm of BD), copepods were the most consumed prey, with a *DCR* between *c.* 0.01 to 1 mgC medusa<sup>-1</sup> day<sup>-1</sup>, decreasing their maximum consumption (95<sup>th</sup> quantile) on biggest sizes (Fig. 4.6). Along with medusae growth (from 10 to 2,761g WW, or 34 to 9,387 mgC), prey richness increased. Indeed, 95<sup>th</sup> quantile regression highlighted significant patterns for ciliates, bivalve veligers, cirripeds' nauplii and fish eggs (Fig. 4.6). For all of them, the *DCR* increased from juvenile to adult medusae. Ciliates *DCR* showed a marked increase in the 95<sup>th</sup> quantile, from *c.* 0.01 to 10 mgC medusa<sup>-1</sup> day<sup>-1</sup>. Among mollusks, bivalve veligers contributed significantly more to adult medusae than to juvenile stages *DCR*, while gastropods were an important food resource only for the adults. Finally, fish eggs showed an increase in the mean *DCR* values (50<sup>th</sup> quantile) from *c.* 1 mgC medusa<sup>-1</sup> day<sup>-1</sup> in juvenile medusae to 4 mgC medusa<sup>-1</sup> day<sup>-1</sup> in adults, and with maxima (95<sup>th</sup> quantile) ranging from *c.* 2 to 30 in juvenile and adult medusae, respectively. For *R. pulmo*, the prey that mostly contributed to the *DCR* were copepods for juveniles, and fish eggs and ciliates for adult medusae.



**FIGURE 4.6.** Daily Carbon Ration (mgC consumed medusa<sup>-1</sup> day<sup>-1</sup>) from *Rhizostoma pulmo* gut content in relation with the medusae weight (in mgC). Each point represents one medusa and regression lines the quantile 50% (blue) and 95% (red). Only the statistical significant regressions ( $p < 0.05$ ) are represented. Equations correspond to the quantile regressions between log10 Daily Carbon Ration ( $L(C)$  in mgC medusa<sup>-1</sup> day<sup>-1</sup>) and the log10 medusae weight ( $L(W)$  in mgC). 'X' and 'Y' axis are represented in logarithmic scale. Note that the 'Y' axis scale differs among taxa. Cal.=Calanoid, Cyc=Cyclopoid, Har=Haracticoid.



The predatory impact of *R. pulmo* differs during ontogeny. Juveniles fed on a maximum of 5% of the copepods' standing stock per day, whilst adults showed a consumption of 8% of the ciliates' standing stock per day. Fish eggs (mean diameter  $1170 \pm 126 \mu\text{m}$ ) were consumed with high frequency for juveniles (40%) and adults (20%) with a consumption of approximately 5% of the fish eggs daily standing stock in the lagoon. For the other taxa, the ingestion was lower than 1% of the daily standing stock.

## 4.4 | DISCUSSION

We have assessed the diet composition of *R. pulmo* pelagic stages and identified ontogenetic dietary shifts. In addition, the analysis of two different cohorts allows evaluating the degree of trophic niche breath overlapping between juveniles and adults. The present study, therefore, provides a baseline to understand the trophic role of *R. pulmo* in plankton food webs.

### 4.4.1 | *Rhizostoma pulmo* diet composition

*R. pulmo* fed on different trophic levels, including ciliates, copepods and larger taxa such as fish eggs. These observations are in agreement with the diet reported for this species in the Black Sea (Dönmez & Bat 2019). However, our results contrast with Pérez-Ruzafa et al. (2002) who suggested that *R. pulmo* feed mainly on prey with no active escape ability (e.g., phytoplankton). Such statement is likely biased by the small sample size used ( $n=5$ ). Our results indicate that *R. pulmo* is a selective filter-feeder, although a wide prey species richness is observed, as for other Rhizostomeae (e.g., Kikinger, 1992; Álvarez-Tello et al., 2016; Nagata & Morandini, 2018; Syazwan et al., 2021) that also include phytoplankton, as detected in this study (e.g., diatoms *Bacillaria paxillifer*) and previously documented for *R. pulmo* (Pérez-Ruzafa et al. 2002; Dönmez and Bat 2019) and *R. octopus* (Gmelin, 1791) (Hays et al. 2012).

### 4.4.2 | *R. pulmo* prey size spectrum

Using the only available study to date (Pérez-Ruzafa et al. 2002), Lilley et al. (2009) determined that *R. pulmo* mostly consume ( $> 80\%$ ) small prey ( $< 200 \mu\text{m}$ ). Our results show a wide prey size spectrum, from 45 to 9,000  $\mu\text{m}$ , with 80% of prey belonging to the 165-240  $\mu\text{m}$  window. This size range is expected for the Rhizostomeae diet due to their small mouths size ( $< 3,000 \mu\text{m}$ ). In Semaestomeae species such as *Aurelia* and *Chrysaora*, more than 50% of prey are commonly larger than 800  $\mu\text{m}$  (Lilley et al. 2009). Here, the smaller prey size

identified for *R. pulmo* suggests a probable niche partitioning and different trophic roles between these jellyfish.

#### 4.4.3 | Consequences of ontogenetic dietary shifts on jellyfish

Ontogenetic dietary shifts are widespread in the animal kingdom (Sánchez-Hernández et al. 2019), and there is evidence that jellyfish can modify their diet over their life span (e.g., Graham & Kroutil, 2001). Here, gut content analysis revealed that *R. pulmo* raised prey richness with increasing size of medusae (supporting our H1), but also fed on specific trophic levels during ontogeny. Juvenile stages of *R. pulmo* showed a marked preference for calanoid copepods (FO > 60%), whilst the feeding pressure on this taxon decreased when medusae grew. In contrast, an increasing consumption, i.e., daily carbon ration, was observed mainly on ciliates with medusae growth (see Fig. 4.6). These different prey preferences during ontogeny and the observed niche partitioning of *R. pulmo*, can affect medusae growth and survival, probably with evolutionary advantages for multicohort species. For instance, a niche partitioning between juvenile and adult medusae could reduce competition for food between cohorts, enabling their coexistence in the lagoon.

From a food web perspective, this ontogenetic diet shift might modify the impact and pressure across the plankton food web. In shallow areas of the ocean, lakes or lagoons, the classical food web (large phytoplankton-mesozooplankton-fish) is commonly connected with the microbial food web (bacteria-heterotrophic flagellates-protists) by mesozooplankton species such as copepods (Moore et al. 2019). However, mesocosm experiments have shown that gelatinous zooplankton has a top-down control on both the microbial loop (Turk et al. 2008) and the classic food web (Granéli and Turner 2002). Our results support these observations and further quantify the impact on standing stocks of copepods and ciliates. Juvenile medusae of *R. pulmo* consumed a maximum of 5% of the copepods' daily standing stock, whilst adults showed a consumption of 8% of the ciliates' daily standing stock. These results are close to the reported values for the Rhizostomeae *L. lucerna*, for which a consumption of 6 to 12% of the copepods' daily standing stock was estimated in the southwestern Atlantic coast (Nagata and Morandini 2018), but smaller than the estimations for the giant Japanese Rhizostomeae *Nemopilema nomurai* (24% of mesozooplankton daily standing stocks; Uye 2008). Estimations on Semaestomeae species present a wider interstudy variability, ranging from < 3% of the crustaceans' daily standing stocks consumed by *Aurelia labiata* and *Cyanea capillata* in Alaska (Purcell 2003), to 21% of copepods' daily standing stocks consumed by *Aurelia solida* in Bizerte lagoon (France; Gueroun et al. 2020). Despite these differences, we observed that large

medusae of *R. pulmo* consumed small percentages of copepods' standing stocks when compared to younger stages, as described for *C. capillata* (Purcell 2003). These results highlight that the predatory impact by some jellyfish species on the copepods' community could be relevant only during the first pelagic stages.

#### **4.4.4 | Potential driving mechanisms of ontogenetic diet changes**

The high prey richness we detected in large medusae agrees with reports for other scyphomedusae species (Graham & Kroutil, 2001; Padilla-Serrato et al., 2013; Dönmez & Bat, 2019), and might be related to an increasing encounter rate of unabundant taxa with the predator. This support our hypothesis H2 regarding a diet diversification on adult stages. In contrast, we do reject our hypothesis H3 about an increase of mobile prey, such as copepods, in medusae guts along with medusa growth.

To understand these results, we discuss potential feeding mechanisms below. The food selection of filter-feeder medusae depends on the pre-encounter and post-encounter feeding mechanisms. Pre-encounter rates are dependent on current speeds generated by the medusae, escape capacity of the prey, and encounter rate related to predator-prey abundance and size (Costello and Colin 1994). In this line, our results do not follow the proposed functional model for prey selection of *A. aurita* (Costello & Colin 1995), which hypothesized that the largest medusae might capture more efficiently big mobile prey than juveniles. This explanation is based on the marginal flow speed created by bell pulsation and the increase of encounter rate, which scale with medusae BD (Costello and Colin 1994), as observed also in Rhizostomeae species (Nagata et al., 2016; Graham et al., 2003). Nevertheless, deviations from this pattern have been already reported. The high presence of copepods in the youngest medusae stages of *Rhopilema nomadica* (Kuplik and Angel 2020), *S. meleagris* (Álvarez-Tello et al. 2016), *Pelagia noctiluca* (Rosa et al. 2013), and also in *A. aurita* (Costello & Colin, 1994; Graham & Kroutil, 2001), suggests that other mechanisms, besides size, could take place. For instance, small medusae may not be detected by copepods, which could explain their capture. Conversely, copepods' ability to detect marginal flow speeds created by large medusae (BD >10 cm) would result in a low consumption by medusae in adult stage, limiting their trophic impact (Wagner et al. 2020). Beyond that, a faster metabolism and growth rates observed in the youngest specimens compared to adult stage is a probable explanation for *R. pulmo* (Leoni et al. 2021b), as previously suggested for *P. noctiluca* (Rosa et al. 2013).

Once the contact is established, the ingestion of the prey depend on the physical constrains of the feeding structures (Kuplik and Angel 2020), as well as on the type and amount

of nematocysts (Purcell 1984, 1997, 2003), which suggest that ontogenetic differences partly depend on nematocysts composition (Purcell and Mills 1988; Carr and Pitt 2008; Regula et al. 2009). Broadly, the efficiency of the nematocysts type varies between ‘soft-’ vs ‘hard-bodied’ prey (Purcell 2003) and has been widely described on hydromedusae and siphonophores (e.g., Purcell, 1984; Purcell & Mills, 1988; Damian-Serrano et al., 2021). Also, interspecific variations in the feeding ecology of scyphomedusae with similar bell marginal flow have been correlated with differences in nematocysts composition (Purcell 2003), which have been also observed between stages of development (e.g., planulae, scyphistomeae, ephyrae and medusae) in some Rhizostomeae and Semaestomae species (reviewed in Calder, 1983). However, a shift in nematocysts composition or proportion during medusae ontogeny have been only identified in cubozoan species (*Chironex fleckeri* and *Chiropsalmus quadrigatus*) and related with prey consumption (Carrette et al. 2002; Oba et al. 2004). In both cases, ontogenetic shifts from a crustacean dominant diet (‘hard-bodied’ prey) to a fish diet (‘soft-bodied’ prey) were observed. To our knowledge, only one recent study has analyzed those changes on scyphomedusae (*P. noctiluca*; Ballesteros et al., 2021), while ontogenetic shifts in nematocysts composition remains unknown for *R. pulmo*. In our study, the observations could be related to shifts in hydrodynamics and encounter rates (Costello and Colin 1994), predator-prey behavior (Graham and Kroutil 2001), or to ontogenetic changes of nematocysts composition.

#### **4.4.5 | Recommendations for future jellyfish gut content analysis**

The gut content analysis of a wide range of medusae sizes has provided novel information on the trophic ecology of *R. pulmo* medusae stages. Our suggestion is that jellyfish diet and their influence on the food web should consider all stages of development. Moreover, to identify all potential prey, the use of biochemical markers must be implemented (Milisenda et al. 2018; Marques et al. 2021b). This is particularly important on small prey as phytoplankton, microplankton smaller than 63 µm and detritus, already identified as important food items for some jellyfish species. Despite the limitations of direct gut content analysis, this technique provides a baseline for posterior SI analyses (Pitt and Lucas 2013) and it is the unique approach for which the size of the prey can be measured.

Previous studies have analyzed a limited medusae size range or have only focused on one developmental stage (Costello & Colin, 1994; Álvarez-Tello et al., 2016; Milisenda et al., 2018). Because of this, interspecific comparisons on trophic changes, diet compositions, and selectivity patterns should be made with caution, as a wide variety of methodologies and medusae sizes have been used. We stress the need for a standardization of methods (for

example, Nagata & Morandini, 2018) to assess trophic dietary niches of jellyfish that will allow to identify feeding patterns or latitudinal changes, which are not achievable with current knowledge.

## 4.5 | CONCLUSIONS

Rhizostomeae jellyfish are an important component of the coastal ecosystems, but the dietary niche of most of the species (*c.* 85%) remains unknown and therefore their trophic role in food webs. Here, we identified that medusae of *R. pulmo* do not feed on the same prey during ontogeny, providing evidence that this jellyfish modifies its trophodynamics, as other marine animals such as bony fish (Olson, 1996; Costalago et al., 2012), sharks (Bethea et al. 2007), sea turtles (Vélez-Rubio et al. 2016) and marine mammals (Vales et al. 2014). Since *R. pulmo* appear seasonally on most Mediterranean coasts for approximately 7 months (Leoni et al. 2021a), its predatory impact on the planktonic community should be temporally restricted and variable depending on the stage of development, abundances, and prey densities. Here, we provide the first *in situ* estimations of their predatory impact in natural ecosystems. The inclusion of indirect techniques as SI and FA analyses will help to elucidate if some other prey items are neglected by the visual analysis method. Metabarcoding techniques have also proved to be useful in diet composition identification for marine animals (Berry et al. 2015; Bergmann et al. 2021), and should be considered in future analyses of the diet of Rhizostomeae. Our study provides a baseline for understanding the trophic role of this species, and therefore for its better representation in food web models.

## SUMMARY POINTS

- *R. pulmo* consume a wide diversity of planktonic species in the lagoon, from phytoplankton to micro-, meso- and macrozooplankton.
- The gut content composition of *R. pulmo* differs from the relative abundance of prey in the surrounded environment. This indicates that some degree of selectivity may be operating, as observed in other jellyfish species. More studies on the mechanisms implicated on this selection are needed.
- 80% of the prey belong to the 165-240  $\mu\text{m}$  size window, an expected range for Rhizostomeae species due their small mouths size ( $< 3 \text{ mm}$ ). These prey sizes are smaller than observations in Semaestomeae species, suggesting that a niche partitioning may exist between them.
- The jellyfish pelagic population exerted a total consumption of 0.04-5.5%, 1.04-5.1% and 0.01-8% of the copepods, fish eggs, and ciliates daily standing stocks, respectively. These values are close to estimates on similar species, but lower than others observed in some gelatinous zooplankton.
- Prey preferences varied along ontogeny: Calanoid (70%) and harpacticoid (45.8%) copepods were the most frequent prey and the major carbon contributors for juvenile medusae. In contrast, ciliates (43.5%) were the most frequent prey for adult specimens, which along with fish eggs, represented most of the carbon content in their guts. This indicates an important ontogenetic shift in the trophic role of the species that should be considered in future food web models.
- The predatory pressure shifts with jellyfish ontogeny across different planktonic components, from a maximum consumption of 5% copepods daily standing stock by juvenile medusae, to a consumption of 8% ciliates daily standing stock by adult medusae in the lagoon.

## CHAPTER 5.

# MODELLING A PLANKTONIC FOOD WEB INCLUDING THE POPULATION DYNAMICS OF *RHIZOSTOMA PULMO* UNDER A WARMING OCEAN

Valentina Leoni<sup>1</sup>, Delphine Bonnet<sup>1</sup>, Juan Carlos Molinero<sup>2</sup>, Alejandro Ariza<sup>2</sup>, Lila Beltran<sup>1</sup>, Marie Meffre<sup>1</sup>, Eduardo Ramírez-Romero<sup>3</sup>.

<sup>1</sup> MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Montpellier, France

<sup>2</sup> MARBEC, IRD, CNRS, Ifremer, Université de Montpellier, Sète, France

<sup>3</sup> Instituto de Ciencias Marinas de Andalucía ICMAN-CSIC, Spain





## **Modelling a planktonic food web including the population dynamics of *Rhizostoma pulmo* under a warming ocean**

Among members of pelagic ecosystems, gelatinous zooplankton species are characterized by a high resilience to environmental changes in the ocean. Even further, an increase of these populations in the Mediterranean Sea in recent decades has been associated with anthropogenic alterations in the ecosystems, such as the ocean warming. However, to understand how jellyfish populations will respond to anthropogenic changes, it is necessary to primarily identify what factors are affecting the abundance of the current populations and the mechanisms behind them. Model simulations provide a mechanistic framework to evaluate these responses, but models on rhizostomid species are very limited. Despite they are meant to provide a simplified view of nature, models require a deep knowledge about the biology of the organisms and the ecosystems, including the identification of key components and trophic interactions between them.

Each chapter in this thesis attempted to fill information gaps with different approaches and covering different spatio-temporal scales, using *R. pulmo* as a case study. A comprehensive approach combining this knowledge with other researchers' findings, has allowed us to model its population for the first time. To do so, we used a pelagic trophic model to elucidate the mechanisms shaping the seasonality of *R. pulmo*. On this regard, this last chapter aims to, on one side, evaluate mechanisms behind emergent patterns described in previous chapters. In addition, as an experimental exercise, we explored potential responses under two future scenarios of warming waters predicted by the Intergovernmental Panel on Climate Change (IPCC). We consider modelling approaches as a complementary tool to laboratory experiments and field observations, to respond questions linked to jellyfish blooms, and as a useful tool to generate new hypotheses.

**Keywords:** Planktonic food web • Mechanistic assessment • Warming ocean • Barrell jellyfish



## 5.1 | INTRODUCTION

The Mediterranean Sea has been identified as a primary hotspot of future climate change (Giorgi 2006). Seawater is expected to warm at a faster rate than in the global ocean (Vargas-Yáñez et al. 2008; Adloff et al. 2015), with overall stronger projected impacts on marine communities (Lejeusne et al. 2010; Marbà et al. 2015). By 2100, under a ‘low CO<sub>2</sub> emissions’ scenario (SSP1-2.6) sea surface temperature is predicted to rise between 0.3 and 1.7°C, whilst under a ‘high CO<sub>2</sub> emissions’ scenario (SSP2-4.5) a rise of 2.6 and 4.8°C is projected (IPCC, 2021). Under such scenarios, gelatinous zooplankton are likely to gain competitive advantage over other ecosystem components due to their outstanding resilience to environmental changes (e.g., Purcell 2005; Shoji et al. 2010; Miller and Graham 2012). Indeed, increases of jellyfish populations in the Mediterranean Sea are often associated to anthropogenic stressors such as overfishing (Lynam et al. 2006), habitat modification (Duarte et al. 2013), eutrophication (Haraldsson et al. 2012), but also to ocean warming (Richardson 2008; Leoni et al. 2021a). Contrary to these findings, we also know that new conditions can result in negative impacts on some jellyfish populations. These include an inhibition on larval settlement, a reduction on the capacity of strobilation, an increase of morphological deformities as well as an increase of medusae mortality (Boero et al. 2016; Loveridge et al. 2021a; Enrique-Navarro et al. 2021). Ectotherms, for instance, are dependent on temperature and their distribution is primarily constrained by this environmental factor (Frolova and Miglietta 2020). Such discrepancies illustrate the diversity and complexity of responses of the jellyfish community under climate change.

In fact, little is known about the thermal niche in the majority jellyfish species in the world, despite its paramount importance to project how populations may respond under climate change (Prieto et al. 2010; Purcell et al. 2012b; Frolova and Miglietta 2020). Favorable thermal windows can vary throughout the ontogeny (Marques et al. 2015b; Leoni et al. 2021b), specifically in Medusozoa jellyfish (Cnidaria) which present a complex life cycle with a pelagic sexual and a benthic asexual reproductions (Lucas et al. 2012). For instance, benthic stages of some populations need long winter periods to spawn (Loveridge et al. 2021b), other die under warm temperatures (Lynam et al. 2004), and pelagic stages of some species benefit from warm waters (Purcell 2005). In addition, jellyfish species can experience phenological variations, such as an advance or a delay on bloom formation related to a change in environmental conditions (see review in Leoni et al. 2021a). Species-specific studies are ultimately revealing that jellyfish responses to climate are diverse and difficult to generalize.

A wide variety of efforts have been made to elucidate how the environment affects jellyfish species particularly from *in-vivo* laboratory experiments (e.g., Purcell 2009; Prieto et al. 2010; Purcell et al. 2012; Treible and Condon 2019; Enrique-Navarro et al. 2021) or from model simulations. However, while population dynamics models can provide insightful information about jellyfish responses in their habitat, these simulations are often limited to few iconic species such as the Semaestomeae jellyfish *Aurelia* spp. (Henschke et al. 2018; Hočevár et al. 2018; Ramirez-Romero et al. 2018; Li and Liu 2022), *Pelagia noctiluca* (Malej and Malej 1992; Ramondenc et al. 2020) and the ctenophore *Mnemiopsis leidyi* (Siapatis et al. 2008; Shiganova et al. 2017; Alekseenko et al. 2019). This gap of knowledge becomes more evident when considering that many of coastal bloom-forming scyphomedusae are Rhizostomeae species (Hamner and Dawson 2009). To our knowledge, only two population dynamics models have been developed for this group, on the Mediterranean jellyfish *Cotylorhiza tuberculata* (Ruiz et al. 2012) and the giant jellyfish *Nemopilema nomurai* (Xie et al. 2021).

In the western Mediterranean Sea, *Rhizostoma pulmo* is commonly blooming (Marambio et al. 2021), and together with *C. tuberculata*, *P. noctiluca*, and *Aurelia* spp., is one of the species negatively impacting on fisheries and tourism activities (Mariottini and Pane 2010). Recent studies on its population dynamics have identified a multicohort strategy during a year (Fernández-Alías et al. 2020; Leoni et al. 2021b), supporting laboratory studies where the species did strobilate under a wide range of temperature (Purcell et al. 2012b). The mechanism behind ephyrae liberation has not been elucidated yet, although a temperature shift has been proposed (Fernández-Alías et al. 2020). In addition, food availability has been identified as an important regulator of jellyfish bloom dynamics (Fernández-Alías et al. 2020; Leoni et al. 2021b), and new research shed light on the diet diversification and thermohaline niches variability of the species during ontogeny (Dönmez and Bat 2019; Leoni et al. 2021b, 2022; Fernández-Alías et al. 2021). In recent decades, warming has favored an abundance increase and an earlier occurrence of blooms in *R. pulmo* (Leoni et al. 2021a). This warns on the potential response of this species under projected warming scenarios.

Here we modeled, for the first time, the dynamics of the *R. pulmo* population in a fully coupled way within a planktonic food web. Our model has been developed and validated, by data collected from a regular monitoring of the hydrology and plankton community on one year-round in 2019 in the NW Mediterranean lagoon of Bages Sığan. By using this information, together with the existing literature data, our first aim was to represent the population dynamics of *R. pulmo* within the food web in the lagoon of Bages Sığan. To do so,

a planktonic food web model originally developed for the pelagic stages of *Aurelia aurita* in the Kiel fjord was adapted to *R. pulmo* in Bages Sigean lagoon. As a second aim, we explored the response of the plankton community under two different scenarios of warming projected for the end of the 21<sup>st</sup> century: a moderate increase of 0.3°C and a strong increase of 4.8°C of seawater temperature, following the low (SSP1-2.6) and high (SSP5-8.5) CO<sub>2</sub> emissions scenarios simulated by the Intergovernmental panel on Climate Change (IPCC, 2021). In light of the positive effect of warming in the magnitude of the blooms of *R. pulmo* (Leoni et al. 2021a), we hypothesize an increase in the magnitude of the blooms under both future scenarios.

## 5.2 | METHODOLOGY

### 5.2.1 | Biological and physical data collection

The sampling was performed during 2019 in Bages Sigean, a lagoon located in the Mediterranean French coast (43°05'12.72" N; 3°00'35.3" E). This is a semi-enclosed ecosystem of 38 km<sup>2</sup> with a mean depth of 2 m. Since 2014, a perennial population of *R. pulmo* completes its life cycle therein. Pelagic stages of *R. pulmo* were collected along with macro-, meso-, microzooplankton and water for chlorophyll *a* (Chl *a*) on a bi-weekly basis during 2019. Simultaneously, water temperature and salinity were recorded. A detailed description of the field survey, samples treatment, and population dynamic analyses can be found in Leoni et al. (2021b). The semi-enclosed lagoon of Bages Sigean offered the ideal conditions for simulating a planktonic food web (0D), with minimal advection or displacement of specimens, that usually occur in open waters.

To estimate the carbon content (C) of each zooplankton group, individual measurements were taken. Ephyrae were photographed and their diameter measured with a camera integrated into a Leica stereomicroscope, using the software Leica Application Suite X (LAS X). The initial ephyrae size was fixed at 1.02 mm, the smallest size of ephyrae found in the lagoon, and transformed in C biomass using the diameter (BD in mm) - dry weight (DW in mg) conversion set up for *Aurelia* ephyrae (Ramirez-Romero et al. 2018) as:

$$DW = 0.002 * BD^{2.998} \quad \text{Eq. 1}$$

and considering 1mg DW=70 µg C (Ramirez-Romero et al. 2018). After this stage, ephyrae lips developed into eight oral arms and the individuals converted into medusae. The bell diameters (BD) of juvenile and adult medusae were measured in the field with an ichthyometer (precision ± 0.1 cm) or a digital caliber (precision ± 0.01 cm) for the smallest ones. Medusae

were weighed and measured in the field and immediately frozen at -30°C. Each frozen specimen (n = 27) was lyophilized for 4 to 7 days, depending on its size. Then, the final DW was measured with a balance (precision  $\pm 0.0001$  g). Juvenile medusae started with a size > 1.4 mm. BD was transformed in C biomass using the conversions based on BD and DW as:

$$DW = 0.0056 * BD^{2.82} \quad \text{Eq. 2}$$

and using the biometric conversion C%DW (i.e., the percentage of DW that is made of Carbon) = 5.6, estimated by Purcell et al. (2010) for immature *R. pulmo* medusae from the NW Mediterranean coast of Spain. For the adult medusa stage (BD > 15 cm), when gonads were detected, conversions were made following the equation:

$$DW = 0.0058 * BD^{2.80} \quad \text{Eq. 3}$$

and the conversion factor used was C%DW = 9.6, estimated by Kogovšek et al. (2014) for *R. pulmo* adult specimens from the Adriatic Sea of a mean wet weight (WW) =  $2881 \pm 1407$ g.

Calanoid copepods were the most abundant group of mesozooplankton in the Bages Sigeon lagoon during 2019 (Leoni et al. 2021b). To estimate their C biomass, measurements of body length (L) were taken from individual pictures of specimens collected with a 200- $\mu$ m plankton net. Pictures were taken as for ephyrae, and schematic representations of how measurements were performed are presented in Supplementary Information, Figure S4.1. A mean L value was obtained from 102 copepods, and the individual mean C content was determined from the equation for calanoid copepods estimated in Uye (1982):

$$\log(C) = 3.07 * \log(L) - 8.37 \quad \text{Eq. 4}$$

Microzooplankton in the lagoon was mainly dominated by ciliates (from the genus *Codonella*, *Favella*, *Tintinnopsis*; Leoni et al. 2021b). The individual volume of the lorica ( $\mu\text{m}^3$ ) was estimated following protocols in Ecotaxa. Therein, each picture has an estimated radio and area, from which the biovolume could be calculated considering the most appropriate geometrical shape for these taxa (<https://sites.google.com/view/piqv/piqv-manuals/ecotaxa-manuals>). With this volume, the C content of ciliates was considered as  $0.22 \text{ pgC } \mu\text{m}^{-3}$  (Booth 1993).

Diatoms' initial conditions were obtained from Chl *a* concentration ( $\mu\text{g L}^{-1}$ ) measured *in situ* during 2019. Values were transformed to C using a C: Chl *a* ratio of 44, estimated for green algae (Latasa et al. 2005). Flagellates' initial conditions were obtained from HPLC

analysis, considering Peridinine as the pigment representing this group (Jiang et al. 2012) and transformed to C by a C: Chl *a* ratio of 47 (Latasa 2005). Finally, the initial DIN conditions were set using *in situ* measurements made by Ifremer in 2019 in the lagoon and obtained from their open-access database Surval.

### 5.2.2 | Modeling approach

We have adapt a 0D plankton food web model initially designed for *Aurelia aurita* in the Kiel Fjord (Ramirez-Romero et al. 2018), ranging from nutrients to jellyfish dynamics in the ecosystem. The lower trophic levels were simulated through a classical NPZD model (Fasham et al. 1990; Fennel 2001), coupled to a stage of development resolving model of jellyfish. In the present study, the highest trophic level compartment was represented by three planktonic stages —ephyrae, juvenile medusae, and adult medusae— of the scyphomedusa *R. pulmo*, the main jellyfish inhabiting Bages Sigean lagoon during 2019 (Leoni et al. 2021b). A summary flowchart illustrating the model steps is presented in Figure 5.1 and described below.

### 5.2.3 | Model parametrization

#### 5.2.3.1 | Non-living components

The model is based on Nitrogen as currency, assuming a fixed C:N ratio of 6.6250 (Redfield 1934). Dissolved inorganic nitrogen (DIN) includes nitrates ( $\text{NO}_3^-$ ), nitrites ( $\text{NO}_2^-$ ), and ammonium ( $\text{NH}_4^+$ ). These forms of nitrogen are readily available to phytoplankton and are often a limiting factor controlling the dynamics of the bloom. DIN ( $d\text{DIN}/dt$ ) and detritus D dynamics ( $dD/dt$ ) are described as:

$$\frac{d\text{DIN}}{dt} = -TG_{phy} + \sum(TR_i + TAR) + RT \quad \text{Eq. 5}$$

$$\frac{dD}{dt} = \sum(TM_i) + \sum(TEG_{zoo}) - RT \quad \text{Eq. 6}$$

where the DIN equation (Eq. 5) includes the losses from phytoplankton growth ( $TG_{phy}$ ), and the summary of respiration terms from all living components, both basal respiration ( $TR_i$ ) and active metabolism ( $TAR$ ).  $TAR$  is estimated as a direct portion of ingested food, i.e., the fraction of the ingestion loss by respiration. Finally, a remineralization term ( $RT = R * D$ ) is included and described as a temperature-dependent process linking D to DIN through a remineralization rate as  $R = R_0 * 2.5^{((T-10)/10)}$ , assuming the turnover rate  $R_0 = 0.05 \text{ d}^{-1}$  at  $0^\circ\text{C}$  and  $Q_{10\_R} = 2.5$  (Fennel 2001; Dzierzbicka-Głowacka et al. 2010). In addition, D (Eq. 6) collects natural mortality

losses ( $TM$ ) from all living compartments ( $i$ ) and zooplankton egestion losses ( $TEG_{zoo}$ ) from the sum of the predation processes from the other zooplankton components.

#### 5.2.3.2 | Plankton community

The phytoplankton is represented by two functional groups based on contrasting ecological niches (Ramirez-Romero et al. 2018). The first group represents diatoms, with high affinity for light, i.e., low optimum irradiance ( $I_{opt}$ ) and low affinity for nutrients ( $k_p$ ), low growth rate, and low sensitivity to temperature ( $Q_{10}$ ). Flagellates are represented with high affinity for nutrients and low affinity for light, high growth rate, and sensitivity to temperature ( $Q_{10}$ ) (Table 5.1).

Temporal changes of biomass ( $dBi/dt$ ), including the dynamics of phytoplankton (diatoms and flagellates:  $dPhy/dt$ ), microzooplankton (ciliates:  $dCil/dt$ ) and mesozooplankton (copepods:  $dCop/dt$ ) is described as:

$$\frac{dBi}{dt} = TG_i - (TM_i + TR_i) - \sum(TGRZ) \quad \text{Eq. 7}$$

where  $TG_i$  is the growing term of each group  $i$ , and  $TM_i$  and  $TR_i$  represent the natural mortality and respiration rates, respectively. The last term represents the sum of losses through predation, i.e., grazing rates by predators.  $TG_i$ ,  $TM_i$  and  $TR_i$  are multiplied by C biomasses of each group  $i$ , and  $TGRZ$  by the correspondent predator biomass. For phytoplankton, potential predators include ciliates, copepods and jellyfish, for ciliates the predation by copepods and jellyfish is considered, while for copepods only jellyfish are considered as potential predators. The specific equations corresponding to each planktonic group considered in the model are described below, and parameters considered for each compartment are detailed in Table 5.1.

#### 5.2.3.3 | Phytoplankton

The growth of phytoplankton ( $TG_{phy}$ ) is assessed as follows:

$$TG_{phy} = NF * G_{10} * LF \quad \text{Eq. 8}$$

where  $NF$  is a dimensionless nutrient factor based on a Michaelis–Menten response, represented as:

$$NF = DIN/(K_i + DIN) \quad \text{Eq. 9}$$



with  $K_i$  representing the half-saturation constant for nutrient uptake ( $K_i = 0.5 \cdot \text{Redfield ratio}$ ).  $G_{10}$  is the maximum growth rate ( $G$ ) at  $10^\circ\text{C}$  modified by the effect of the temperature ( $T$ ). In all living compartments, the temperature regulation is included using  $Q_{10\_i}$  for each group (Table 5.1) as:

$$G_{10} = G * Q_{10\_i}^{((T-10)/10)} \quad \text{Eq. 10}$$

Finally, the light limitation factor ( $LF$ ) (Franks 2002) is estimated as:

$$LF = \left( \frac{I}{I_{OR}} \right) * \exp(1 - I/I_{OR}) \quad \text{Eq. 11}$$

Using  $I$  as the averaged irradiance within a water column of a depth  $h = 2$  m (i.e., the average depth of Bages Sigeon lagoon):

$$I = \int_h^0 \frac{I(z)}{h} dz = \int_h^0 \left( \frac{I_0 * e^{-(\lambda * z)}}{h} \right) dz = \frac{I_0}{\lambda} * (1 - e^{(-\lambda)}) \quad \text{Eq. 12}$$

$I_0$  is the daily averaged surface irradiance in the lagoon, and alpha ( $\lambda$ ) is represented as:

$$\lambda = K_w * h + K_s * B_{phy} * h \quad \text{Eq. 13}$$

where  $K_w$  and  $K_s$  are the attenuation coefficient of water ( $K_w = 0.07 \text{ m}^{-1}$ ) and the phytoplankton shelf-shading effect ( $K_s = 0.0095 \text{ m}^2 \text{ mmol N}^{-1}$ ) respectively, and  $B_{phy}$  the biomass of the phytoplankton group.

#### 5.2.3.4 | Micro- and mesozooplankton

The growths of ciliates ( $TG_{cil}$ ) and copepods ( $TG_{cop}$ ) are assessed as follows:

$$TG_i = AE * GRZ_i \quad \text{Eq. 14}$$

where  $AE$  is the assimilation efficiency for each group (Table 5.2) and  $GRZ_i$  represents the food factor for different groups  $i$ , which can be ciliates or copepods. It is assessed as a Michaelis–Menten function with  $F_{x\_i}$  as the available food for ciliates or copepods:

$$GRZ_{i\_x} = F_{x\_i} / (K_i + F_{x\_i}) * G_{10} \quad \text{Eq. 15}$$

Ciliates' prey belong to both diatoms and flagellates phytoplanktonic groups (Table 5.2). In the case of copepods, their prey are ciliates and both phytoplankton groups, with a higher

preference for diatoms (Table 5.2). The total food for a predator,  $F_{x_i}$ , is computed as the sum of prey biomass ( $B_x$ ) by a specific food capture efficiency of each predator for this prey ( $CE_{i_x}$ ), represented by a dimensionless factor from 0 to 1, as:

$$F_{x_i} = \sum(CE_{x_i} * B_x) \quad \text{Eq. 16}$$

#### 5.2.3.5 | *Rhizostoma pulmo* model

The model simulates the pelagic phase of *R. pulmo* life cycle. We considered three stages: ephyrae, juvenile medusae (i.e., medusae with a  $1.4 \text{ cm} < \text{BD} < 15 \text{ cm}$ ), and adult medusae (specimens with gonads and a  $\text{BD} > 15 \text{ cm}$ ). This classification allowed the inclusion of diet changes observed in *R. pulmo* ontogeny as independent parameters (Table 5.2). Overall, juveniles' diet was biased towards a dominance of copepods versus microzooplankton, while adults' diet showed an opposite pattern (Leoni et al. 2022). Accordingly, we used a higher predation efficiency on copepods for juvenile stages and a higher predation efficiency on ciliates for adult stages.

Ephyrae releasing dates were set according to three periods, i.e., three cohorts, identified during one-year field survey in Bages Sigeon (Leoni et al. 2021b), where each cohort represented individuals that were born at the same time. The transition processes ( $T_{j1\_2}$ ) between jellyfish stages ( $j$ ) —from ephyrae to juveniles, and from juveniles to adult medusae— were simulated with the transfer function proposed by Stegert et al. (2007). The transition from ephyrae to juveniles covers a mass range starting from a reference weight  $R_{j1} = 0.15 \text{ } \mu\text{g C}$  (the C content of the initial ephyrae with a  $\text{BD} = 1.02 \text{ mm}$ ) and reaching a maximum weight  $M_{j1\_2} = 0.53 \text{ mgC}$  (the C content for the first medusae stages of a  $\text{BD} = 1.4 \text{ cm}$ ). After the size of  $M_{j1\_2} = 229 \text{ mgC}$  (the first adult medusae of a  $\text{BD} = 15 \text{ cm}$ ), juveniles were converted to adult medusae:

$$T_{j1\_2} = \frac{(W_{j1} - M_{j1\_2})^4}{(W_{j1} - M_{j1\_2})^4 + (R_{j1} - M_{j1\_2})^4}; W_{j1} > M_{j1\_2} \quad \text{Eq. 17}$$

$W_{j1}$  and  $W_{j2}$  are the mean weights for ephyra and juvenile ( $W_j = B_j/A_j$ ) stages, respectively, estimated as the biomass ( $B_j$ ) divided by abundance ( $A_j$ ). The dynamic scheme for *R. pulmo*, for ephyra and both medusa stages, is presented in equations (18) and (19). Compared with ciliates and copepods, *R. pulmo*'s compartment does not have a predation-loss term. Here, the basic equations for biomass ( $B_j$ ,  $\text{mgC m}^{-3}$ ) and abundance ( $A_j$ ,  $\text{individuals m}^{-3}$ ) are:

$$\frac{dB_j}{dt} = T_{j-1,j} + TG_j - (TBR_j + TM_j) - T_{j,j+1} \quad \text{Eq. 18}$$

$$\frac{dA_j}{dt} = T_{j-1,j} - M_j - T_{j,j+1} \quad \text{Eq. 19}$$

In all cases,  $T_{j-1,j}$ ,  $TG_j$ ,  $TBR_j$  (C-specific basal respiration rate),  $M_j$  (mortality rates) and  $T_{j,j+1}$  are multiplied by  $B_j$  in the equation 18 and by  $A_j$  in equation 19. The growth  $TG_i$  ( $d^{-1}$ ) is computed as:

$$TG_i = CR_j * B_j * G_j * F_j / W_j \quad \text{Eq. 20}$$

where  $CR_j$  is the clearance rate per individual ( $m^3 \text{ ind}^{-1} d^{-1}$ ),  $F_j$  the total available food (as Eq. 16), and  $W_j$  the mean weight for the individuals of each stage  $j$  ( $W_j = B_j / A_j$ ). The weight-specific growth rate ( $G_j$ ) is determined from biomass changes of individuals between two time-steps ( $\Delta t = 1 \text{ day}$ ):  $G_j (d^{-1}) = \ln(W_{t+1}/W_t) / \Delta t$  (Ramírez-Romero et al. 2018). Clearance rates ( $CR_j$ ) are defined as a function of *R. pulmo* size (BD) modulated by temperature using a  $Q_{10} = 2.08$ , estimated by Purcell (2009).

CR relationship for *R. pulmo* ephyrae was considered to be similar to *Aurelia*:

$$CR = 0.032 * BD^{2.3} \quad \text{Eq. 21}$$

CR for medusae stages was obtained from previous estimations on the Rhizostomeae *Rhopilema nomadica* in the Mediterranean Sea, as a function of the BD (Kuplik et al. 2021) as:

$$CR = 0.043 * BD^{1.43} \quad \text{Eq. 22}$$

The end of the pelagic stage was set according to the moment when the last adults were observed in Bages Sigeon, and when the bottom of the lagoon was full of dead medusae. All medusae biomass was transformed to detritus (D) at the end of the autumn (21<sup>st</sup> November), the day of the year (doy) = 325 (Leoni et al. 2021b).

## 5.2.4 | Simulations

Initial DIN concentrations were set up to  $0.23 \mu M$ , from field measurements performed in 2019 by Ifremer. Unlike *Aurelia* sp., Rhizostomeae species, including *R. pulmo*, commonly release a small number of ephyrae but develop a bloom by multiple strobilation events during one year (Schiariti et al. 2008). Here, the initial simulation considered a release of  $0.15 \text{ ephyrae m}^{-3}$  on April 17, and liberations of  $0.04$  and  $0.05 \text{ ephyrae } 100m^{-3}$  on May 16 and June 12,

respectively, according to field observations. The first ephyrae release was not observed in the field, but was inferred to capture the first peak of juveniles. The second and third releases were set according to values observed in the field. The simulations of winter months were not considered here due to the absence of planktonic stages of *R. pulmo* in the water column.

**TABLE 5.1.** Summary of parameters used in model simulations of each component from Bages Sigean plankton community.

Parameter	Diatoms	Flagellates	Ciliates	Copepods	Ephyrae	Juvenile medusae	Adult medusae	Units
$G$	2.00	1.20	0.50	0.40	0.70	0.60	0.50	d <sup>-1</sup>
$I_{OR}$	100	200	--	--	--	--	--	W m <sup>-2</sup>
$K_p$	1.00	0.50	--	--	--	--	--	μM
$M$	0.05	0.05	0.03	0.07	0.02	0.03	0.02	d <sup>-1</sup>
$BR$	0.01	0.01	0.05	0.05	0.02	0.02	0.01	d <sup>-1</sup>
$Q_{10}$	2.00	2.50	2.70	2.50	2.08	2.08	2.08	
$E$	--	--	--	--	0.10	0.20	0.30	
$K_f$	--	--	25	50	--	--	--	mgC m <sup>-3</sup>

$G$ =maximum growth rate;  $I_{OR}$ =Irradiance optimum;  $K_p$ =half saturation constant;  $M$ =natural mortality;  $BR$ =basal respiration;  $Q_{10}$ = Temperature coefficient;  $E$ =egestion;  $K_f$ =half saturation constant for grazing.

**TABLE 5.2.** Food preference by taxa considered in the present study.

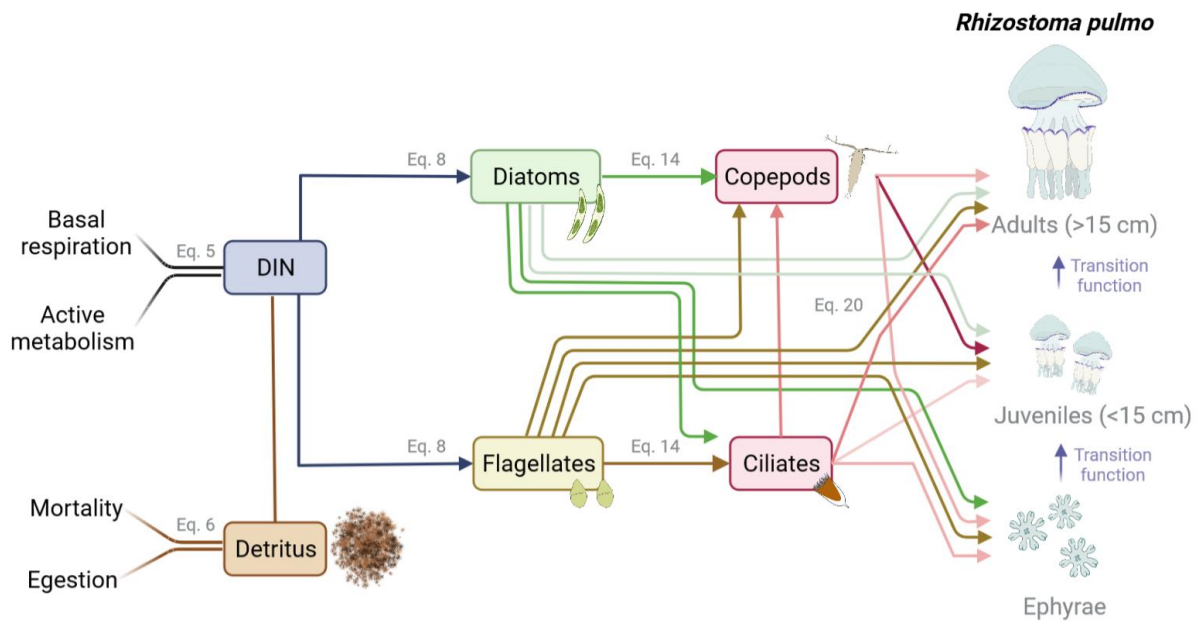
Prey	Predator							
		Diatoms	Flagellates	Ciliates	Copepods	Ephyrae	Juvenile medusae	Adult medusae
	<i>Diatoms</i>	0	0	0.50	0.50	0.90	0.10	0.10
	<i>Flagellates</i>	0	0	0.25	0.30	0.90	0.90	0.90
	<i>Ciliates</i>	0	0	0	0.90	0.60	0.60	1.00
	<i>Copepods</i>	0	0	0	0	0.30	1.00	0.50

## 5.2.5 | Future scenarios

By 2100, under the ‘low CO<sub>2</sub> emissions’ scenario (SSP1-2.6), sea surface temperature (SST) is predicted to rise between 0.3°C to 1.7°C, whilst under the ‘high CO<sub>2</sub> emissions’ scenario (SSP5-8.5, IPCC) SST is predicted to rise between 2.6 and 4.8°C. Here, we assess the possible consequences of these two scenarios of warming, a moderate and a strong increase. *R. pulmo* is a multicohort species with a wide thermal range for polyps’ strobilation from 14 to 28 °C (observed under laboratory conditions, Purcell et al. 2012). In natural conditions in Bages Sigean, we identified the thermal window of the ephyrae to be between 13.9 to 21.8°C. In the simulations we assumed that (i) the species will conserve three cohorts per year of the same magnitude and (ii) a constant ephyrae thermal window. To do so, ephyrae release was set on a

thermal range between 13.9 to 21.8°C in both future scenarios (Purcell et al. 2012b; Fernández-Alías et al. 2020; Leoni et al. 2021b). Finally, as under the scenario of high temperature increase winter temperature never drops under 10°C, the death of medusae was not fixed due to their capacity to overwinter under those conditions (Fuentes et al. 2011).

To identify potential phenological changes in future scenarios compared on *in situ* observations, the peak of the bloom was considered as the first day when the adult medusae rise their maximum abundance (Leoni et al. 2021a).



**FIGURE 5.1.** Conceptual diagram of the proposed simplified planktonic food web in Bages Sigean lagoon (France). Arrows represent the flow between the compartments. Equations (Eq.) representing the main processes between components are indicated. DIN = dissolved inorganic nitrogen. Transition functions represent equation 17.

## 5.2.6 | Validation

To assess the skill of the model, we computed the bias and root mean square difference (RMSD) comparing *in situ* observations and simulations. We computed these metrics and plotted them in targeted diagrams (Jolliff et al. 2009; Salon et al. 2019) for the simulated biomasses (diatoms, flagellates, ciliates, copepods, and jellyfish).

### 5.2.7 | Niche estimations

We estimate the thermal niche under both scenarios using a nonparametric test of association between temperature and the abundance of ephyra, juvenile and adult stages of *R. pulmo*. The approach encompasses a cumulative frequency method and a Monte Carlo randomization (Paramo et al. 2003). It is based on the maximum absolute difference between the cumulative frequency distribution (CFD) of temperature and the abundance weighted CFD of the temperature. First, the relative CFD for temperature was calculated and then was weighted by the abundance of each *R. pulmo* pelagic stage. The comparison of unweighted and weighted CFD indicates the association of the population with the temperature (Molinero et al. 2009). This allows testing, by a randomization procedure, the degree of association between the species abundance and temperature. It was finally compared with their current thermal niches (Leoni et al. 2021b).

### 5.2.8 | Code availability

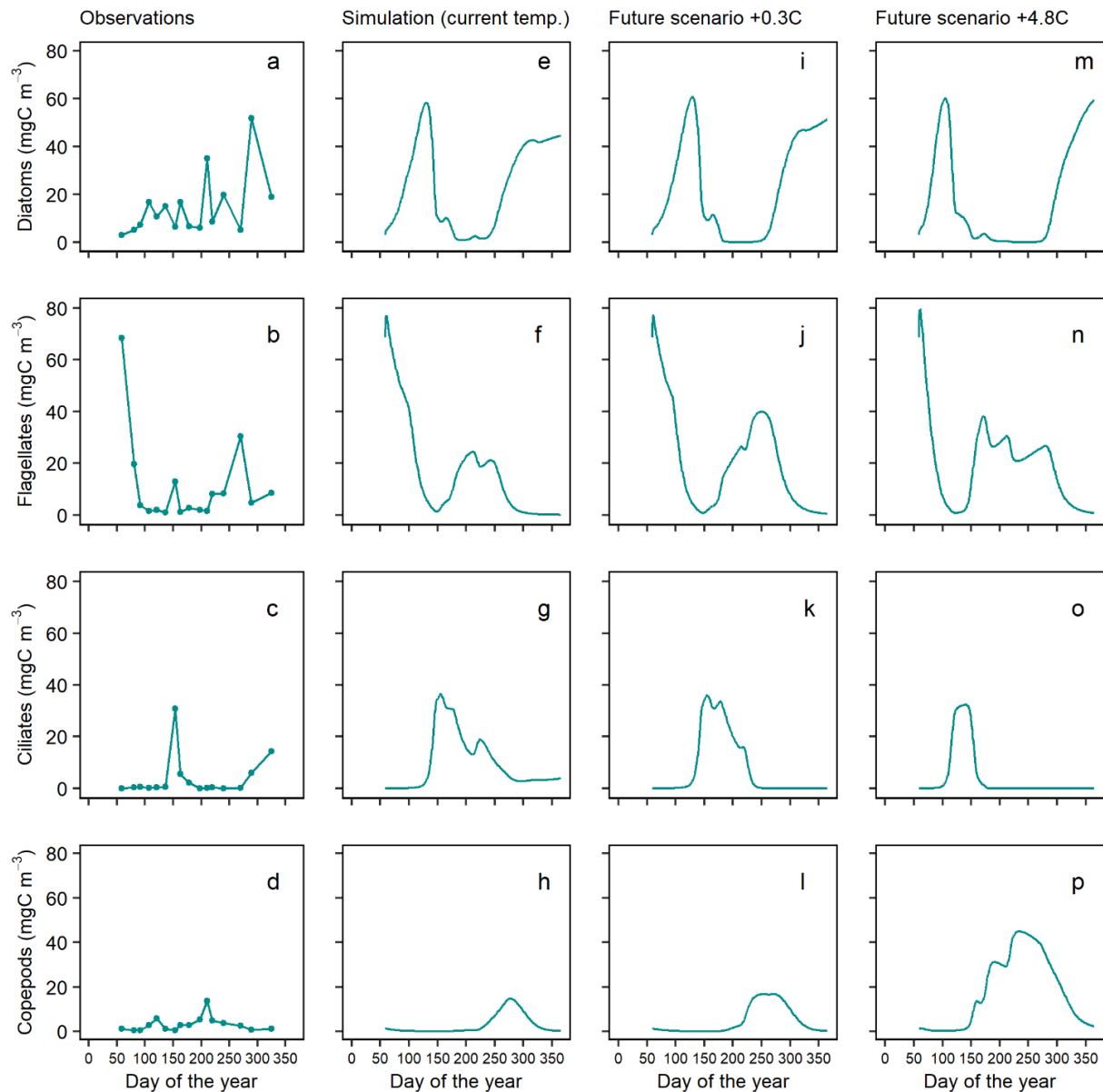
The code was written in the open-source software R and is available in the platform GitHub (<https://github.com/valentina-leoni/npzdj>). Initial values used to run simulations in the present research, as well as temperature, for Bages Sigean lagoon during 2019 are also provided for reproducibility and testing purposes.

## 5.3 | RESULTS

### 5.3.1 | Plankton community in Bages Sigean lagoon

#### 5.3.1.1 | Seasonal planktonic succession under current temperature conditions

Overall, the magnitude and the number of biomass peaks throughout the year were comparable between observations (Fig. 5.2a-d) and simulations (Fig. 5.2e-h). The diatom compartment was the group showing the most remarkable differences in the biomass magnitude, with a marked overestimation in spring, and underestimations during summer months (Fig. 5.2a, e). On the other hand, flagellates' dynamics presented similar temporal patterns and values between observations (Fig. 5.2b) and simulations (Fig. 5.2f). The sharp spring peak observed *in situ* in ciliates dynamics (Fig. 5.2c) was captured in the simulations (Fig. 5.2g), whereas the magnitude of the highest peak of copepods' biomass was captured on the simulation, although with a time delay observed to some extent (Fig. 5.2d, h).



**FIGURE 5.2.** Field data (**a-d**) and model simulations under temperature conditions measured in Bages Sigean lagoon during 2019 (**e-h**) and under scenarios of low (**i-l**) and high (**m-p**) temperature increases.

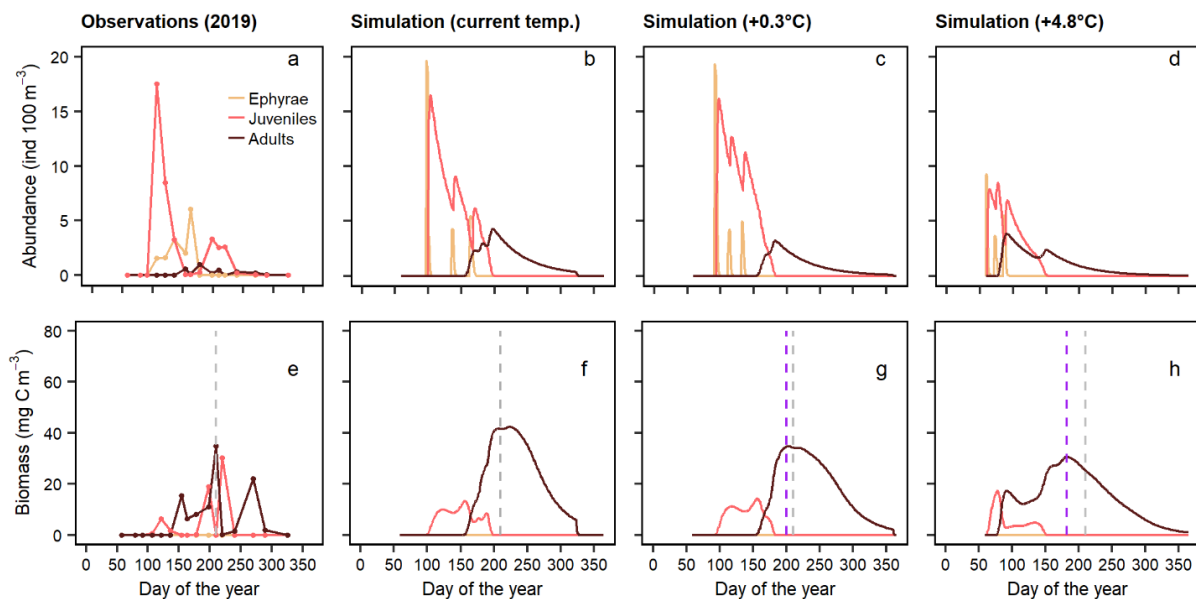
### 5.3.1.2 | Future scenarios simulations

The comparison between simulations under projected scenarios (Fig. 5.2i-p), suggested a marked positive effect on copepods' biomass (Fig. 5.2l, p), mainly under +4.8°C scenario. Copepods doubled their magnitude of the second peak in autumn, followed by a decline when diatoms started to rise, exceeding  $40 \text{ mgC m}^{-3}$  at the end of the year. Flagellates were the second group showing a marked positive response to the +4.8°C scenario, with an overall increase of abundances (Fig. 5.2n).

### 5.3.2 | *R. pulmo* population dynamics in Bages Sigean lagoon

#### 5.3.2.1 | Seasonality under current temperature conditions

The development of *R. pulmo* medusae occurs during spring-summer and disappears in autumn (Fig. 5.3a, e). Field data showed a maximum abundance of 17.5 ind. 100m<sup>-3</sup> for juveniles and 1.0 ind. 100m<sup>-3</sup> for adult medusae (Fig. 5.3a). In the simulation, released ephyrae started to grow rapidly and reached the medusa stage in a few days (Fig. 5.3c). Maximum abundances reached similar values in the simulation and in field observations for juveniles (c. 15 ind. 100m<sup>-3</sup>), whilst higher values were observed for adults (3.5 ind. 100m<sup>-3</sup>). In the model, the overlap of cohorts observed *in situ* was simulated. Jellyfish biomass peak in the lagoon (34.8 mgC m<sup>-3</sup>) occurred in August (Julian day 210). In the simulations, the peak of biomass occurred at the same time, in the same order of magnitude, rising 35.1 mgC m<sup>-3</sup>. Despite the sharp peaks of biomass observed throughout the year were not captured in the simulation, the adult stages started around day 150, the peak at day 210 and the bloom finished around day 300 both *in situ* (Fig. 5.3e) and in the simulations (Fig. 5.3f). These differences were expected due to the fluctuating dynamics of organisms in the natural environment.



**FIGURE 5.3.** Abundance and biomass dynamics observations (a-b) and simulations of three pelagic stages of *Rhizostoma pulmo* under 2019 conditions (c-d), and under temperature predicted in a low (SSP1-2.6) (e-f) and high (SSP5-8.5) CO<sub>2</sub> emissions scenarios (IPCC, 2021) (g-h). The vertical grey dashed line indicates the peak of bloom (biomass) of simulations under original conditions in 2019. The vertical purple dashed line indicates the peak of the bloom under future temperature conditions. An advance in the peak of the bloom is observed under a temperature increase of +0.3°C and +4.8°C.

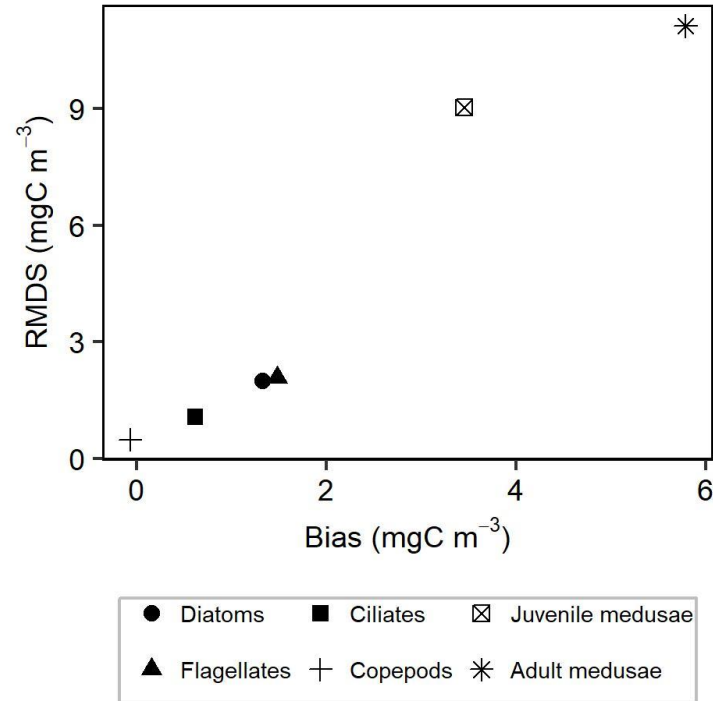


### 5.3.2.2 | *R. pulmo* dynamics under future scenarios

In both warming scenarios, the simulations showed an earlier peak of the bloom. In the moderate increase of temperature scenario, biomass peak occurs 10 days before, when comparing with scenario of 2019, and 28 days before (approximately one month) under +4.8°C (Fig. 5.3.c-d, g-h). However, this advance was not followed by higher abundances. On the contrary, maximum abundance decreased, since ephyrae stage, to values lower than 10 ind. 100m<sup>-3</sup> caused by a mortality increment. In addition, the peak of jellyfish biomass decreased with a successive increase of temperature (Fig. 5.3g, h), achieving a minimum of 25.5 mgC m<sup>-3</sup> in the warmest scenario. This earlier occurrence of jellyfish bloom, together with a reduction of biomass, could promote the increase of copepod abundances in the lagoon (Fig. 5.2p) as a consequence of a reduction of predation pressure during the year.

### 5.3.3 | Validation

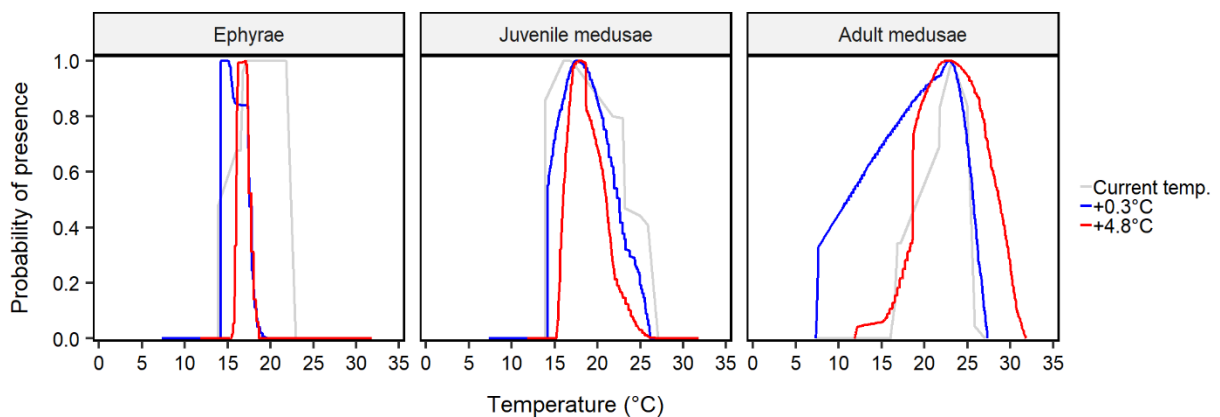
Overall, the model captured the dynamics of the planktonic community in the lagoon (Fig. 5.2a-h and 5.3a-b, e-f) and showed a good agreement with *in situ* dynamics for all groups of prey (Fig. 5.4). The most accurate results were the simulations of copepods' biomass, followed by ciliates. Both phytoplankton groups considered here, diatoms and flagellates, have a similar accuracy and bias. All of them showed an acceptable performance. Juvenile and adult jellyfish biomasses, both presented the highest RMDS, probably due to the strong variability in jellyfish biomass estimations (Fig. 5.3e) related with their heterogeneous and patched distribution of medusae in the environment. Model simulations capture the seasonality of *R. pulmo*, with the maximum peak abundances and biomasses in the same period, but with a smoothest pattern (Fig. 5.3f) and overestimated biomasses (positive *Bias* values, Fig. 5.4).



**FIGURE 5.4.** Target diagram between model simulations and plankton dynamics for the different groups (shapes). The X-axis indicates the bias and the y-axis how accurate are the estimations of the model simulations regarding *in situ* observations.

### 5.3.4 | Niche estimations

Estimations of the thermal niches (Fig. 5.5) showed a narrowing both for ephyrae and juvenile medusae under scenarios of warming waters. The optimum temperature for ephyrae was displaced to values close to 15°C, whilst the optimum for juveniles was within the same optimal range estimated in 2019. By contrast, adults' thermal range showed the same optimum but an overall expansion in both projected scenarios.



**FIGURE 5.5.** Thermal niches of ephyra, juvenile and adult medusa of *Rhizostoma pulmo* in Bages Sigean lagoon (France) during 2019 (grey), and under a low (blue) and high (red) temperature increase.

## 5.4 | DISCUSSION

In this chapter, we addressed the issue of modeling jellyfish population dynamics in a fully coupled way within a plankton food web of a shallow ecosystem, which is crucial to understand marine ecosystems dynamics and underlying drivers of jellyfish abundance. As already proposed on harvested fish species (Faugeras and Maury 2007), a future scenario of rising jellyfish abundance, and consequently jelly-fisheries increase, places modelling as a required and useful tool to reach sustainable catch levels.

### 5.4.1 | Taking a step forward in understanding the ecology of *R. pulmo* from a mechanistic perspective

In recent years, the uncertainties about the effects of climate change on jellyfish populations have been highlighted (e.g, Morandini 2022). Most of the insights on this regard have been based on correlations between abundance and environmental factors (Pitt et al. 2018), lacking a mechanistic understanding to reconcile the correlations with causality, which will ultimately allow the generation of more realistic projections. Major obstacles must be overcome to link physiological process, population dynamics and functional role of the species at the community level to find a unique mechanistic framework (Maury and Poggiale 2013).

Compared with other taxa, modelling jellyfish populations is challenging due to the lack of estimations of basic parameters for many species, such as diet preferences, growth rates and thermal niches, but also due to the complex life cycles and reproductive plasticity of jellyfish. Since benthic and pelagic stages differ so greatly—one millimetre stage fixed to a substrate, and another in the water column capable of reaching individual biomasses of kilograms—only a few studies have investigated both at once (e.g., Willcox et al. 2008; Malej et al. 2012; Marques et al. 2019). Most of the available information is for the well-known *Aurelia* spp., which has enabled modeling both its pelagic and benthic phases (Henschke et al. 2018; Ramirez-Romero et al. 2018). However, the accuracy of simulations on the benthic stages has not been validated so far due to the lack of knowledge on the dynamics of scyphistomae at this time (Henschke 2019). Here, to understand jellyfish seasonality, we proposed the implementation of a food web model linked with the dynamics of *R. pulmo* pelagic stages.

Food availability and temperature were used as main triggers of the seasonal dynamics of *R. pulmo* in Bages Sigeon lagoon during 2019. In particular, the temperature shaped the

planktonic food web dynamics, by timing jellyfish blooms. A decrease of growth rate between the first two cohorts was observed in the field, with maximum value for the former (Leoni et al. 2021b). A synergy of both temperature and food abundance seems to modify the growth rate of cohorts, as both parameters define the growth term of the model (Eq. 20) and the same variability was identified in the model. Simulations showed the key role of food availability in the seasonality of jellyfish biomass and bloom formation. This might explain previous field observations in *R. pulmo* (Leoni et al. 2021b), also identified in *Aurelia* spp. (Lucas 1996; Marques et al. 2015b), *Chrysaora hysoscella* (Buecher et al. 2001), *P. noctiluca* (Rosa et al. 2013), for which food was the main driver of their population dynamics in nature.

Here, the ontogenetic changes in jellyfish trophic preferences were considered, not only between ephyrae and medusae stages, but also throughout medusa stages. The diet diversification during ontogeny (Leoni et al. 2022) enabled the coexistence of juveniles and adults in the lagoon avoiding competition, and the success of the bloom. Furthermore, the multiple strobilation pattern was simulated by means of several ephyrae release events. This explained at a certain point *in situ* observations (Chapter 3 and 4), as well as other biological traits such as the estimated jellyfish biomass in the lagoon (Leoni et al. 2021b). Through this modelling approach, we have established a baseline to explore the underlying mechanisms driving the dynamics of *R. pulmo*, which help to elucidate the ecological role of this species in the Mediterranean Sea.

The high values obtained in the root mean square difference for jellyfish biomasses (Fig. 5.4) could be explained by the sensitivity of this metric to extreme values. *In situ* biomass estimations of large jellyfish organisms suffer from the patchy distribution of these blooms, which gives a discontinuous pattern during the year. The improvement of sampling techniques, such as counting by drones covering all the lagoon could help in this regard (Fuentes et al. 2011; Schaub et al. 2018). Despite this, the accuracy on the maximum biomass values during summer months indicates that prey items considered here are a good representation of the most relevant food sources for the species.

#### **5.4.2 | Response of *R. pulmo* under a warming ocean**

Predicting species responses to warming is a major issue in contemporary ecology. In the Mediterranean Sea, warming conditions are resulting in the spatial redistribution of species (Moullec et al. 2022), abundance changes (Lejeusne et al. 2010) and shifts in the timing of biological events (Marbà et al. 2015), with major consequences on the structure and functioning of the ecosystems. Most of these warming impacts on Mediterranean biota have been reported

on fish and cnidarian species and were concentrated in the NW Mediterranean Sea and the Adriatic Sea (Marbà et al. 2015).

A compilation on the sensitivity of Mediterranean species identified that the impacts on cnidarians for the period 1950–2011 were observed when temperature anomalies were relatively high (5°C; Marbà et al. 2015), highlighting the resistance of this taxa to environmental changes. The main impacts of warming on *R. pulmo* detected by our simulations were an advance in the timing of the annual peak, and contrary to expectations, a reduction of maximum biomass values, mostly under +4.8°C. An advance on jellyfish blooms has been previously forecasted in the Bering Sea by the end of the 21<sup>st</sup> century (Hermann et al. 2021). It was mainly related to an earlier phytoplankton bloom, but also to the effect of water temperature on jellyfish growth rates. The observed advance on the timing of *R. pulmo* bloom might be due to an earlier ephyrae liberation, but also to an effect of temperature on their physiology, for example increased growth rates (Widmer 2005).

If the main effect of the ocean warming on this jellyfish is a phenological change, the potential shifts in the trophic web are more complex than expected (Edwards and Richardson 2004). Currently, strobilation takes place in spring, and the bloom development of *R. pulmo* occurs in summer months. During spring, the lagoon presents favorable conditions for juvenile fishes of commercial interest (<http://www.aude.gouv.fr>). Gut content analysis identified fish eggs as a secondary but important food resource mainly for largest medusae. Probably due to the low abundance of fish eggs during summer months in the field, jellyfish predatory impact on this group was low (Leoni et al. 2022). Our results showed that under warming conditions, whilst in lower abundances, adult medusae appear one month earlier. If fish spawning continuous to occur during spring, an advance of the bloom could match with the period of high fish eggs abundance. Previous studies on rhizostomid species (Nagata and Morandini 2018) suggested that predation pressure on fish eggs could increase if these prey are more available in the environment, putting jellyfish as a potential threat for local fisheries.

Contrary to expectations, the biomass of the jellyfish bloom showed lower values under both conditions of temperature increase. It is probable that a slight increase of sea surface temperature promotes higher blooms of *R. pulmo* (Purcell et al. 2012b; Leoni et al. 2021a). However, intense warming (here +4.8°C) could reduce the survival rate of these organisms in the early stages and decrease the bloom size if they are unable to move to areas with optimal temperatures. Nevertheless, changes in environmental conditions may affect phenotypic plasticity of jellyfish in ways that will enable them to adapt to climate change conditions in the future. Since jellyfish are known to be quite tolerant of fluctuating environmental conditions,

mainly those adapted to a temperate ecosystem, a gradual acclimation to future warming conditions is possible. In addition, the species' capacity to consume a wide variety of prey (Leoni et al. 2022) could allow them to adapt their diet based on the availability of prey (Milisenda et al. 2018).

#### 5.4.3 | Model's limitations, assumptions and suggestions of improvements

By simplification ecological interactions through a set of interrelated mathematical equations, we can evaluate ecological drivers and test different forcing scenarios. To keep as simple as possible, strong assumptions have however to be made since information gaps on *R. pulmo* remain. In this section, we will discuss these assumptions and the limits of our model, in the frame of future research directions. These assumptions are:

(I) *Constant strobilation events and same liberated ephyrae number.* In the model simulating current conditions, the lack of information on the timing of strobilation and the abundance of polyps *in situ* forced us to give a specific input of ephyrae based on field observations. Up to date, strobilation process has been only assessed in laboratory experiments (Purcell et al. 2012) as most polyps of Rhizostomeae species have not yet been found in nature. On *R. pulmo*, a laboratory temperature shock seems to drive the strobilation (Anaïs Courtet, Paris Aquarium, pers. comm.). When future temperature conditions were projected, both the number of ephyrae and strobilation events were conserved, as the response in produced ephyrae strongly depends on the past conditions experienced by the polyps, for which we have no information. The next step in *R. pulmo* modelling is the incorporation of benthic stage dynamics, as strobilation has been demonstrated to be a key factor on bloom development (Henschke et al. 2018; Marques et al. 2019). Joint efforts using approaches already generated for example in benthic stages of similar species such as *C. tuberculata* (Ruiz et al. 2012) will allow modelling the complete life-cycle once field data will be obtained.

(II) *Lack of acclimatization by 2100.* As discussed in the previous section, this has hampered the interpretation of results when exposing jellyfish to future conditions in laboratory experiments (Enrique-Navarro et al. 2021). Nevertheless, as temperature could affect also the amount of ephyrae liberated (Purcell et al. 2012b), and probably cohort numbers (Fernández-Alías et al. 2020; Leoni et al. 2021b), future laboratory experiments should evaluate these scenarios on *R. pulmo* (Prieto et al. 2010), which should be incorporated in model simulations.

(III) *Equal initial conditions in the lagoon in projected scenarios.* In order to assess the effects of temperature on the food web, the initial conditions of the model were the same in all scenarios. Nevertheless, as it is expected that warming conditions promote eutrophication in

coastal ecosystems but also a decrease in precipitation (Bugnot et al. 2020), future forecast analyses on bloom development should evaluate the combined effect of warming and different levels of nutrient inputs.

(IV) *Forced bloom collapse*. In addition to assumption on bloom formation (strobilation), the mechanism behind the jellyfish bloom collapse has not been elucidated yet. Post-spawning mortality, temperature stress or food limitation have been suggested as potential causes (e.g., Lucas 1996; Bonnet et al. 2012). Also, *in situ* observations on *A. coerulea* scyphistomae and ephyrae predation highlight the role of top down control in bloom regulation and jellyfish mortality (Marques et al. 2016). The predatory impact of the fish community from Bages Sigeon on *R. pulmo* should be analyzed.

## 5.5 | CONCLUSIONS

To be useful, a model must mimic the reality with some degrees of precision, but also should include variables that are easy to obtain in the field. Here, a different diet for each stage was included, based on mesoplankton in juvenile medusae and more on small plankton in adult medusae, capturing the avoidance of competition between stages and potential trophic cascades. Thermal forcing and dependence of the jellyfish life cycle on food availability produce coherent results with the seasonal observations of *R. pulmo* in a semi-closed natural environment.

This study provides evidences that *R. pulmo*'s population dynamics is mainly driven by seasonal temperature variability and prey dynamics. Moreover, we hypothesized that jellyfish will modify their seasonality due to climate change in the coming decades. However, our model predicted an increase of mortality rate at ephyrae stage and a subsequent reduction of *R. pulmo* abundances in Bages Sigeon. While the underlying mechanisms are just starting to be understood, our model combined with climate projections indicates that a warming of Mediterranean waters could result in significant jellyfish phenological changes by the end of the century. Nevertheless, it is important to highlight that our results rely on the assumption that thermal conditions for strobilation stay unaltered, something that probably will change due to the adaptation and acclimatization capacities of this group.

## SUMMARY POINTS

- Overall, the model captures the dynamics of the planktonic community in the lagoon and shows a good agreement with *in situ* dynamics for all groups of prey.
- Temperature and resources availability seem to shape *R. pulmo* the population dynamics in the lagoon, by timing the start of the bloom and regulating its magnitude.
- The main differences between observations and simulations were detected for the seasonal peaks of jellyfish biomasses. The improvement of *in situ* sampling techniques, such as counting by drones or submersible towed cameras in all the lagoon could help obtaining more accurate biomass estimations of jellyfish blooms with a patchy distribution.
- Contrary to expectations, the biomass of the jellyfish shows lower values under both conditions of temperature increase. It is probable that a slight increase of sea surface temperature promotes higher blooms of *R. pulmo*, whilst intense warming could reduce the survival rate of these organisms in the early stages and therefore decrease the bloom size if they are unable to move to areas with optimal temperatures.



## CHAPTER 6.

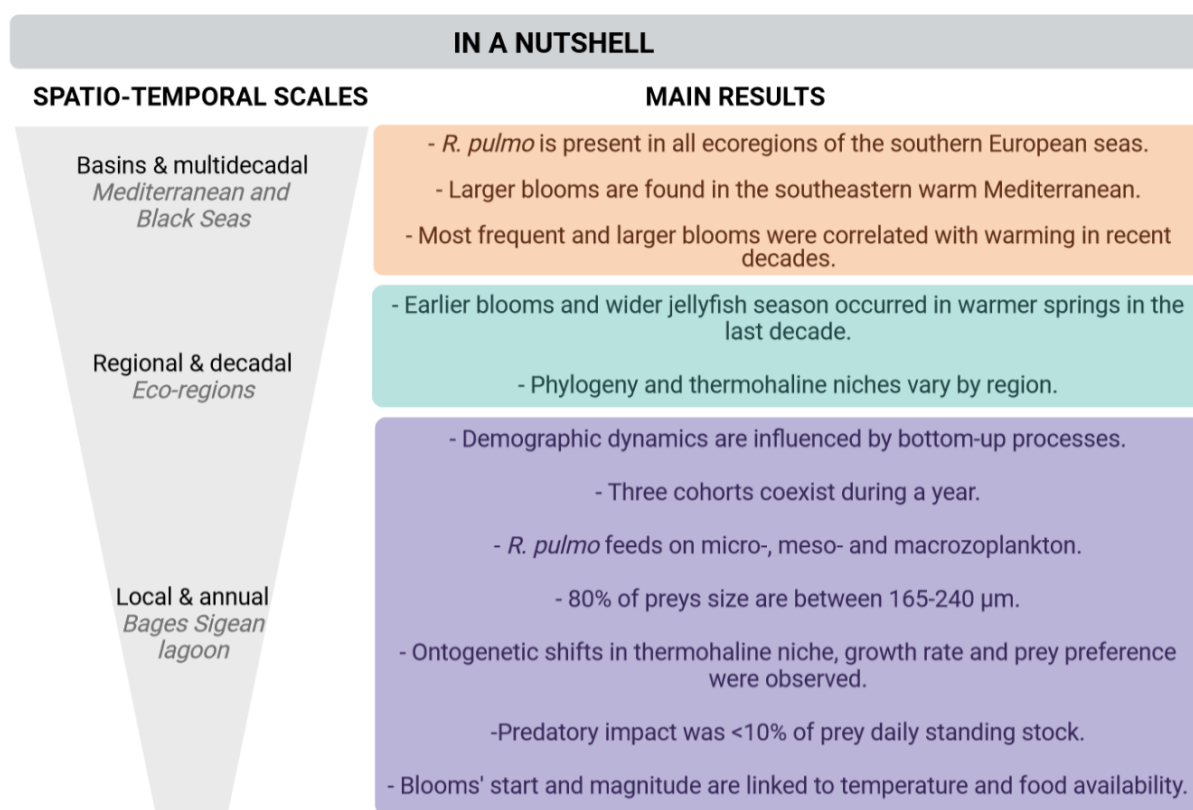
# GENERAL DISCUSSION AND FUTURE DIRECTIONS



## 6.1 | UNDERSTANDING JELLYFISH BLOOMS REQUIRES A MULTISCALE APPROACH

One of the most burning issues in jellyfish ecology is to identify the environmental conditions that trigger and maintain bloom episodes. When it comes to elucidate the drivers governing jellyfish blooms, two approaches are generally found in literature: large-scale assessments on taxonomically broad categories (Lilley et al. 2011; Condon et al. 2013; Lucas et al. 2014) or regional-scale assessments on specific species (Daly Yahia et al. 2010; Marambio et al. 2021; Violić et al. 2022). However, to our knowledge, only one prior study had compiled the entire information on one coastal macro-medusa, *Pelagia noctiluca*, throughout its full range of distribution (Goy et al. 1989), elevating the current study to the first extensive one on *R. pulmo* within the southern European seas.

Our strategy provides a novel and comprehensive view of a so far understudied species. Each of the four topics addressed in this Ph.D. has involved the application of diverse observational approaches, laboratory tools and analyses to assess patterns and processes occurring at different spatio-temporal scales (Fig. 6.1).



**FIGURE 6.1.** Summary of the results obtained on *Rhizostoma pulmo* in the different axis of the thesis. On the left side the temporal and spatial scale are indicated, and on the right side the main results obtained from large scale (orange and green sections) to local scale (purple section).

## 6.2 | MULTIPLE RESPONSES IN A CHANGING OCEAN

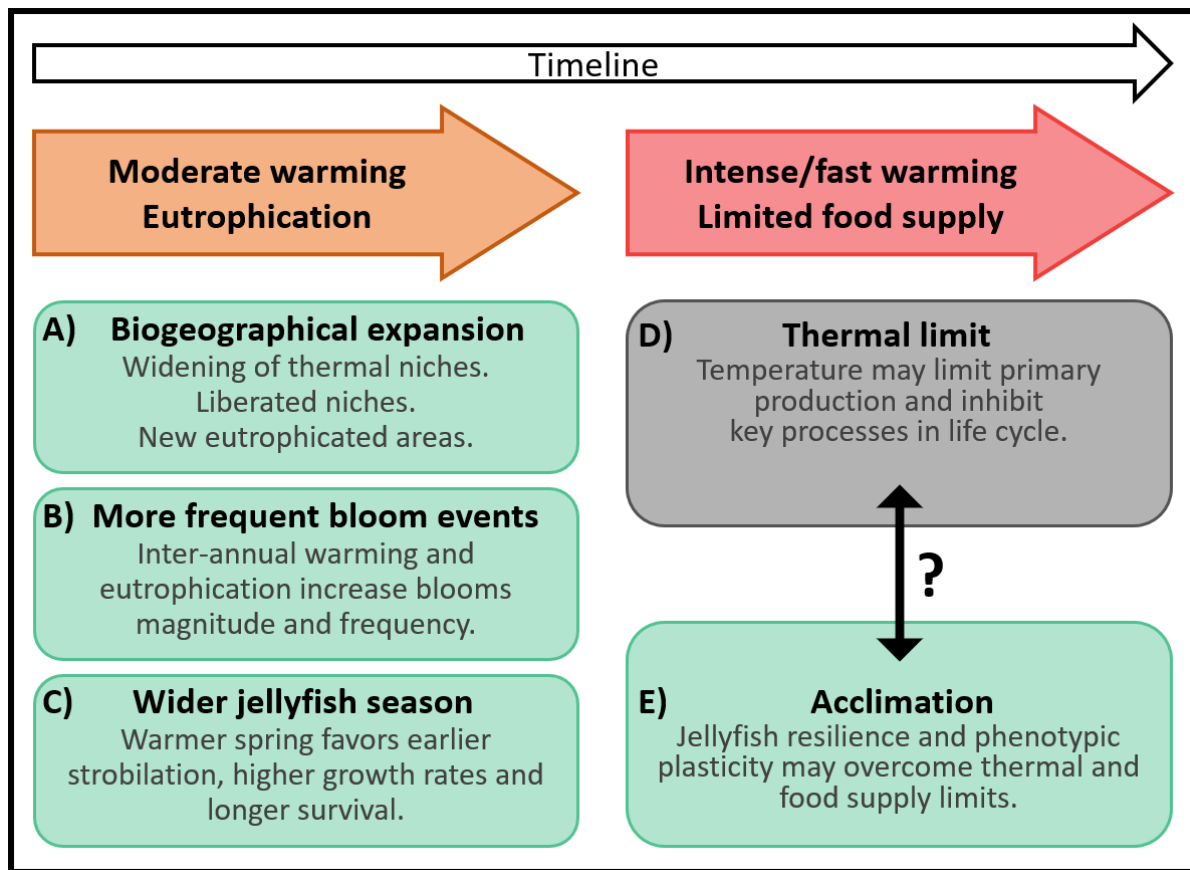
Using the approaches listed above, this thesis contributes to basic knowledge on the ecology of *R. pulmo* and provides key insights about the future of this species in the Mediterranean Sea. Whether jellyfish blooms will increase or decrease is complex as it is species-specific and depends on a wide variety of ecological processes operated at various stages of the life cycle. Despite these difficulties, we discuss here on possible future scenarios for *R. pulmo*, based on our findings and previous knowledge from literature.

**Biogeographical expansion.** Bloom events, for instance, were more intense in the southeastern warm Mediterranean than in colder waters in the northwest (Chapter 2). These findings warn about a potential increase of *R. pulmo* bloom events towards the northwest, as it is where the Mediterranean will warm with more intensity in the years to come (Salat and Pascual 2002; Lejeusne et al. 2010). If that is the case, the geographical expansion of large *R. pulmo* blooms would follow the same direction as other Mediterranean rhizostomids such as *Cotylorhiza tuberculata* (Prieto et al. 2010). Other habitats modifications may operate in conjunction with warming and might accelerate the expansion of large jellyfish blooms. For example eutrophication, which is significantly more intense in the northwest Mediterranean (Karydis and Kitsiou 2012) and numerous studies have already documented the affinity of *R. pulmo* for these nutrient-rich waters (Pérez-Ruzafa et al. 2002; Lilley et al. 2009; Marambio et al. 2021). In fact, those increasing opportunities for settlement and survival have already been observed in other rhizostomids, such as the Lessepsian species *Rhopilema nomadica* (Edelist et al. 2020). All these signs show that the forecasted tropicalization of the Mediterranean (Moschella 2008) is already a reality for rhizostomids. As the Mediterranean temperature continues to rise, *R. pulmo* large blooms may hence keep expanding (Fig. 6.2a).

**More frequent and intense bloom events.** The scenario of continuous warming in the Mediterranean (Lejeusne et al. 2010) also suggests that *R. pulmo* populations will rise in the future (Fig. 6.2b). Indeed, we documented an increase in the intensity and frequency of blooms in the Mediterranean from the early 2000s' to 2019 in relation to positive anomalies of sea surface temperature (Chapter 2). Similar increasing abundances of jellyfish have also been punctually reported in several locations of the Mediterranean (e.g., in the Adriatic Sea, French coast, or the Gulf of Tunis, Spain, Daly Yahia et al. 2010; Condon et al. 2013; Aouititen et al. 2019; Violić et al. 2019; Edelist et al. 2020; Bellido et al. 2020) and around the world linked

to warming events (Girón-Nava et al. 2015; Quiñones et al. 2015; Boero et al. 2016). The northwest Mediterranean Sea has also experienced temperature-related increases of other planktonic cnidarians in the past, such for siphonophores and hydromedusae species (Molinero et al. 2008; Guerrero et al. 2018). All these clues bring the question of the mechanisms through which warming may favor jellyfish populations and the development of blooms. So far, laboratory experiments suggest that warmer temperatures increase asexual reproduction rates of the scyphistomae benthic stage producing more buds and ephyrae (Purcell et al. 2012b). Another environmental factor that might favour jellyfish bloom events is the water eutrophication. This has been already observed in the Chesapeake Bay and the Adriatic Sea for the scyphomedusae *Chrysaora quinquecirrha* and *P. noctiluca*, respectively (Purcell et al. 1999). Even though we did not find a relationship between primary production and the magnitude of the blooms, we identified food availability as a main determinant of bloom development (Chapter 3, 4 and 5).

**Larger jellyfish seasons.** Typically, the pelagic stages of *R. pulmo* appear in spring (April) and occur in the water column until autumn (October), with maximum abundances observed during summer months (July-August, Chapter 3). In years of warmer springs, however, the jellyfish season seems to start earlier and last longer. Indeed, in a 10-year period (2008-2018), our calculations suggest that *R. pulmo* season begins two months earlier and lasts two months more (Chapter 2). One plausible explanation for the former is an earlier and longer strobilation under warming waters, as observed for *Aurelia* spp. (Purcell et al. 2007), *C. tuberculata* (Kikinger 1992), *N. nomurai* (Feng et al. 2020) and for *R. pulmo* under experimental conditions (Purcell et al. 2012b). Warming may also increase growth rates of pelagic stages, which together with an earlier strobilation, have been suggested as plausible explanations of the early apparition of *Discomedusa lobata* and *Chrysaora hysoscella* under warmer years in the Adriatic Sea (Violić et al. 2019). Warmer waters could, therefore, benefit *R. pulmo* by promoting a higher recruitment and a faster development of pelagic stages in the future (Widmer 2005; Van Walraven et al. 2015; Violić et al. 2019, Fig. 6.2c). Additionally, pelagic stages will likely survive for longer if temperature is kept within their tolerance ranges over longer periods (Daly Yahia et al. 2010; Violić et al. 2019; Marques et al. 2021a). This might even allow jellyfish to overwinter to next season (Purcell 2005).



**FIGURE 6.2.** Synthesis on potential responses of *Rhizostoma pulmo* in a future warmer ocean. On the left side, present observed trends are enumerated, in relation to warming and eutrophication of the Mediterranean Sea. On the right side, these trends might be interrupted or continued under more intense warming and limited primary production, depending on physiological thresholds and acclimation capacity of *R. pulmo*.

**Thermal limit vs. Acclimation.** While in principle, warming seems to favor jellyfish reproduction and survival, some studies suggest that this situation may be reversed if certain thresholds are exceeded (Benovic et al. 2000; Klein et al. 2017; Marques et al. 2019; Enrique-Navarro et al. 2021). The first limit is not related to jellyfish thermal tolerance but to the decrease in primary production, and therefore, to jellyfish food availability in a future ocean. This however is still a matter of debate in Earth system model projections (Kwiatkowski et al. 2020) and difficult to interpret in the context of semi-enclosed areas where eutrophication is intense. In regard to thermal tolerance, there are critical points in the life cycle of jellyfish where warming could have negative impacts. For example, species living in warm waters may not be able to tolerate further warming, and their distribution could shift toward cooler areas, and active seasons could be shortened (Purcell 2005). Other scyphomedusae inhabiting the same latitudinal range than *R. pulmo* are expecting to reduce the size of their population under warming conditions. This is the case of the scyphomedusae *Aurelia coerulea* (Bonnet et al.

2016; Marques et al. 2019). For this species, dry and warm summers are expected to promote massive mortality in scyphistomae inducing reduction in ephyrae production (Marques et al. 2019). In other species, such as *C. tuberculata*, despite the positive effect of warming waters in their populations (Prieto et al. 2010), a future with softened thermal oscillations due to warmer winters is expected to reduce the temperature activation threshold needed for strobilation, and consequently a reduction of the number of ephyrae liberated (Enrique-Navarro et al. 2021). Indirect negative effects of warming have also been observed in the hydromedusae community of the Adriatic Sea. For these populations, a drastic reduction was detected due to the decrease of oxygen levels in the area (Benovic et al. 2000). Hence, if our model predictions hold true, summer *R. pulmo* blooms will occur in the future but with an earlier apparition and at lower abundances in some coastal areas (Fig. 6.2d).

Despite these experiences, one might argue that those thermal inhibitions or detriments of key life cycle processes occurred under extreme or fast warming experiments. These scenarios, however, did not consider the great adaptability to changing environments that characterize cnidarians (Bakun and Weeks 2006; Purcell et al. 2007). The fluctuating environmental conditions to which temperate species are often exposed may influence the phenotypic plasticity of polyps making them more tolerant to climate change and, therefore they will be more predisposed to withstand future climate conditions by acclimation (Sunday et al. 2011; Dam 2013). For instance, the transgenerational acclimation to warming observed on *Aurelia aurita* showed to be advantageous to mitigate negative effects that the new environmental conditions may have on the offspring (Lu et al. 2020). In addition, the multicohort feature of some species — such as *R. pulmo* — suggests a wide plasticity of benthic stages, capable to strobilate under a large range of conditions (Purcell et al. 2012b). It has been observed that jellyfish can also adapt their life cycle with environmental conditions, changing their reproduction strategies according to external factors. For instance, instead of the classical strobilation, polyps of some species such as *Aurelia relicta* and *C. tuberculata* could completely develop into a new ephyrae. This reproductive plasticity could contribute to jellyfish success throughout the varied conditions of future oceans (D'Ambra et al. 2021). To survive in a new environment, the species needs also to be able to adapt their diet. Several examples in other scyphomedusae species provided insights on the adaptive potential of this group to a new food resource. For instance, *Stomolophus meleagris* varies its diet between regions from the Pacific to the Atlantic coasts of North America (Larson 1991; Padilla-Serrato et al. 2013; Álvarez-Tello et al. 2016), whilst *Phyllorhiza punctata* presents different feeding preferences worldwide (Fancett 1988; Graham et al. 2003; Peach and Pitt 2005). For *R. pulmo*,

we identified mesozooplankton as a fundamental resource for young medusae stages, and microzooplankton as the most important prey for larger ones (Chapter 4). This raises the question of how the response of the plankton community to climate change will influence *R. pulmo* populations. Therefore, plasticity of *R. pulmo* in obtaining resources under new conditions will determine, at this point, whether the species will benefit from the expected structural changes in the plankton community (Mitchell et al. 2021).

### 6.3 | UNRESOLVED QUESTIONS AND WAYS FORWARD

**The benthic phase, elusive, but critical to understand jellyfish bloom dynamics.** Polyps are by far the most unknown jellyfish stage in nature. Most of the unresolved questions in this thesis relate, to some extent, to the lack of observations of this fundamental stage in natural conditions. For example, the factor driving the start of the blooms, the initial size of the benthic population and its thermal window. This is not an isolated problem for *R. pulmo*, but a common gap in jellyfish research. To our knowledge, only *Aurelia* sp. has been monitored in nature, considering both the polyp and medusae stages at the same time (Marques et al. 2015b, 2019). We therefore recommend the establishment of specific polyps sampling programs in the Bages Sigean lagoon, to shed light on the environmental factors regulating the observed population dynamics in the lagoon.

**Experimentation to establish tolerance limits.** Besides the need of the *in situ* identification of polyps, tolerance limits and resilience of these organisms are necessary to better understand their response to a warming ocean. Therefore, complementary laboratory experiments should be conducted on all stages of the life cycle to analyze *R. pulmo* acclimation potential. In particular, transgenerational phenological plasticity (Byrne et al. 2020) emerges as one of the most important questions to decipher the role of jellyfish in a changing ocean. The interaction of temperature with other factors such as acidification and low oxygen concentrations, and substrates preference of planulae are also a priority for future *in vivo* experiments in *R. pulmo*, along with studies to elucidate mechanisms behind diet preferences. Indeed, these experiments will allow to depict the synergism and antagonism effects of the climate change among multiple stressors. We then recommend conducting these experiments in order to provide valuable physiological parameters for improving mathematical models and future predictions on *R. pulmo* population dynamics.



### Long-term observations and their incorporation in scientific surveys.

Despite the utility of our research to fill gaps on many unknown aspects of the biology and ecology *R. pulmo*, our one-year monitoring constitutes a snapshot in time. If we want to understand the evolution of the coastal ecosystem exposed to heavy human activities, high-resolution surveys programs sustained on time should be implemented on strategic points of the Mediterranean Sea. This may include coastal lagoons under protection such as Bages Sigeon, and more human-impacted areas such as the Mar Menor lagoon. The semi-closed natural condition of these areas will allow us to answer questions such as what drives gelatinous zooplankton composition and to explain the seasonal and inter-annual variability of the species in the ecosystems. We therefore recommend including the survey of these populations in the regular monitoring performed by diverse institutions, to validate the predictions obtain in our models but also to obtain valuable information for users of the lagoons such as fishermen, tourists and local people.

The need for continued local studies is only part of the picture; large areas must be covered as well. Jellyfish have been, however, historically neglected in national and international marine scientific surveys, often displaced between the economic importance of commercial fish species and the cost-effective and relatively simple sampling of smaller zooplankton. Despite these programs are increasingly multidisciplinary and allegedly follow an ecosystemic approach, ship time is uncommonly dedicated to specific jellyfish sampling, specimens are mainly collected from the by-catch of other samplers, and specialists are rarely on board to sample, identify and preserve the jellyfish. Considering the increasing societal and scientific importance of jellyfish, we advocate to include them in national and international sampling programs and consider them as an essential ocean sentinel (Lynam et al. 2011; Miloslavich et al. 2018; Prieto 2018). This should be achieved through the implementation of specific sampling approaches more suitable to study jellyfish, such as Drones, environmental DNA samplings, slower and shorted net sampling to prevent deterioration of samples (Magalhães et al. 2021; Minamoto et al. 2017; Schaub et al. 2018). Additionally, citizen science programs represent a great opportunity to cover larger areas of the coast that scientific projects can not achieve (Edelist et al. 2022). We then recommend to sustain these programs in time and to not confine them to summer seasons and short-term projects.

## 6.4 | CONCLUSION

Throughout this thesis, we showed the diversity of responses and factors affecting the ecology of a jellyfish species at different scales. Overall, temperature has been identified as a key factor affecting the distribution, magnitude and frequency of *R. pulmo* blooms, as well as the timing of the jellyfish season. Food availability appear to be a key factor in the development of blooms, and the coexistence of multiple cohorts during one year appears to be favored by the ontogenetic dietary shifts *R. pulmo* experienced. Although the species seems to thrive in warmer conditions, intense and fast climate changes may be detrimental for the species. Its success will ultimately be determined by how quickly the species adapts to warmer waters as well as its flexibility in acquiring food in highly eutrophic or stratified waters. The complexity observed in a single species emphasizes the need of conducting species-specific research to identify which species could increase their abundances in the future, and where. By doing so, more accurate information about the evolution of jellyfish bloom episodes will be obtained, supporting the development of mitigation measures to reduce their future impacts.

## SUPPLEMENTARY INFORMATION

**TABLE S1.1.** Number of species of Medusozoa (excluding the benthic Stauromedusae) affecting human activities. The percentage of the total valid species is indicated in parenthesis. The number of valid species is based on Jarms and Morandini (2019) for Semaestomeae, Rhizostomeae and Cubozoa, and on Gibbons et al. (2010) for Hydrozoa (excluding the exclusively benthic species). The number of blooming species is based on Hamner and Dawson (2009). The number of species interfering with fisheries and aquaculture activities is based on the reviews of Purcell et al. (2007) and Bosch-Belmar et al. (2021), and those affecting tourism activities, power plants and the invasive species are based on the review of Purcell et al. (2007). Species considered as fishery resource were obtained from Brotz (2016). <sup>a</sup>Note that 31 of the 35 blooming Semaestomeae belong to genus *Aurelia* and *Chrysaora*.

Class	Valid species	Bloom-forming species*	Negative effects on					Food resource
			Fisheries	Aquaculture	Tourism	Power plants	Invasions	
Semaestomeae	74	35 <sup>a</sup> (47.3%)	8 (10.8%)	5 (6.8%)	4 (5.4%)	4 (5.4%)	2 (2.7%)	8 (10.8%)
Rhizostomeae	89	49 (55.1%)	8 (8.9%)	0	4 (4.5%)	2 (2.2%)	3 (3.4%)	28 (31.5%)
Cubozoa	47	4** (8.5%)	2 (4.3%)	0	5 (10.6%)	0	0	3 (6.4%)
Hydrozoa	978	<10 (<1.5%)	6 (0.6%)	14 (1.4%)	8 (0.8%)	0	4 (0.4%)	0
<b>Total</b>	1188		44 (3.7%)	19 (1.6%)	21 (1.8%)	6 (0.5%)	9 (0.8%)	39 (3.3%)

\*Number of blooming species is the maximum, probably overestimated, as Hamner and Dawson (2009) considered all the species of a genus to bloom or not bloom, while many exceptions exist on this pattern.

\*\*Cubozoan species are not commonly blooming, here are indicated the number of species capable of mass aggregations or accumulations.

**TABLE S2.1.** Historical records from published scientific literature of *Rhizostoma pulmo* medusae from the Southern European Seas by ecoregion. Numbers of ecoregions correspond to the map of the Figure 2.2a in the main text.

Peer-review literature				
Ecoregion		Reference	Period	Observations
<b>1</b>	Alboran Sea	Mills et al. (1996)	1991	Scuba diving sampling
		Kienberger & Prieto (2018)	1993, 1997-1998, 2011-2012	Photos
<b>2</b>	Western Mediterranean	Péron & Lesueur (1810)	1810	Descriptive study
		Morand & Dallot (1985)	1898-1914	Sightings
		Carli (1991)	1984-1986	Sightings
		Pérez-Ruzafa et al. (2002)	1988, 1997	Visual census from boat and towed nets
		Carli et al. (1995)	1990-1992	Sightings
		Lilley et al. (2009)	1993, 2003, 2005-2006	Sightings live and stranded individuals
		Boero et al. (2016)	2009-2015	Sightings from citizen science
		Fuentes et al. (2011)	1996, 2003-2004, 2007-2009	Sampling monitors (plankton nets, video, coastal sightings)

3	Adriatic Sea	Kogovšek et al. (2010)	1875, 1883, 1899, 1900-1903, 1908-1911, 1914, 1921, 1976-1992, 1994, 1996-1998, 2000-2009	Literature review and scientific sightings
		Malej & Vukovic (1983)	1983	Sightings
		Avian et al. (1991)	1988	Collect of individuals for nematocyst analysis
		Babić (1913)	1902-1903, 1911	Descriptive study
		Nastav et al. (2013)	2004-2005	Monthly sampling from commercial fishing vessels
		Boero et al. (2016)	2009-2015	Sightings from citizen science
		Palmieri et al. (2014)	2012	Questionnaires to fishermen
		Violić et al. (2019)	2017	Monthly sightings from shore, vessels, dives, and fishermen reports.
4	Ionian Sea	Scalera-Liaci (1991)	1987	Sightings from citizen science
		Basso et al. (2019)	2016	Scuba diving collection to study the microbial community
5	Tunisian Plateau	Daly Yahia et al. (2003)	1993-1995	Monthly sampling with plankton nets and manual collections
		Addad et al. (2008)	2004	Bimonthly manual collection
		Touzri et al. (2012)	2004-2005	Counts from a boat
		Ben Faleh et al. (2017)	2013	Collections for genetic analysis
		Gueroun (2016)	2013-2014	Counts from a boat
6	Aegean Sea	Forbes (1843)	1842	Report
		Alpaslan (2001)	1885, 2000	Scoop net
		Öztürk & Topaloğlu (2011)	2008-2009	Snorkelling and scuba diving
		Alpaslan et al. (2011)	2009-2010	Scuba diving
7	Levantine Sea	Galil et al. (1990)	1935, 1965, 1971, 1974, 1977, 1983, 1988-1989	Literature review
		Lakkis (1971)	1969	Plankton nets
		Lakkis & Zeidane (1985)	1970-1982	Plankton nets
		Lakkis (1991)	1986	Bongo plankton net
		Bingel et al. (1991)	1986	Biweekly sampling with plankton net
		Çiçek (2011)	2008-2001	Underwater visual census
		Killi et al. (2018)	2015	Questionnaires to fishermen, local people, divers

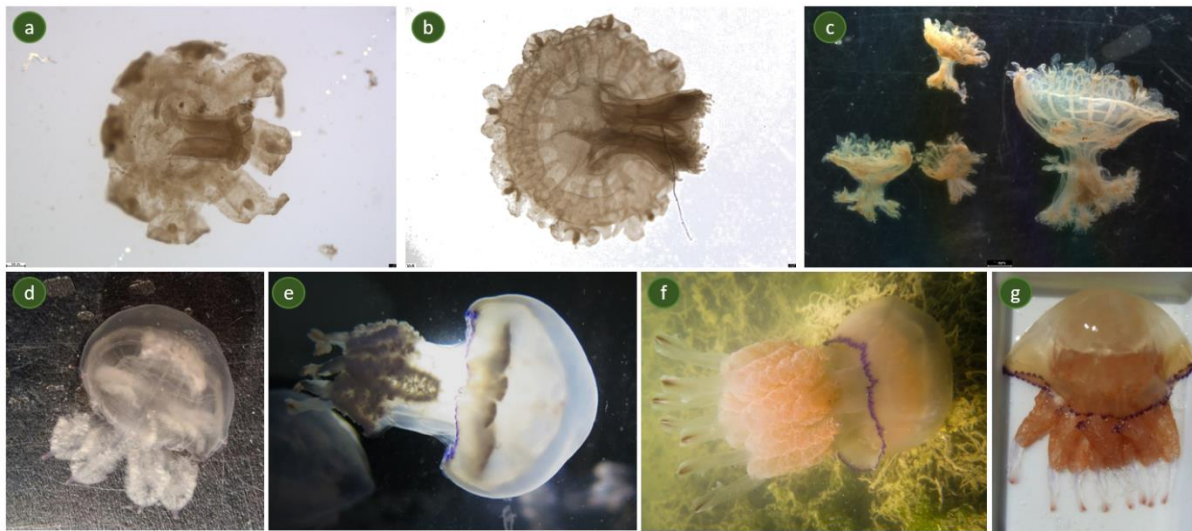
8	Black Sea	Zaitsev & Mamaev (1997)	1960-1970, 1973-1974	Sightings
		Mutlu (2009)	2006-2007	Sightings
		Dönmez & Bat (2019)	2008-2010	Plankton net collections for gut content analysis
	Atlantic Ocean	Kienberger & Prieto (2018)	1993, 1997-1998, 2011-2012	Photos

**TABLE S2.2.** Historical records of *Rhizostoma pulmo* medusae from citizen reports or scientific initiatives from the Southern European Seas by ecoregion. Numbers of ecoregions correspond to the map of the Figure 2.2a in the main text.

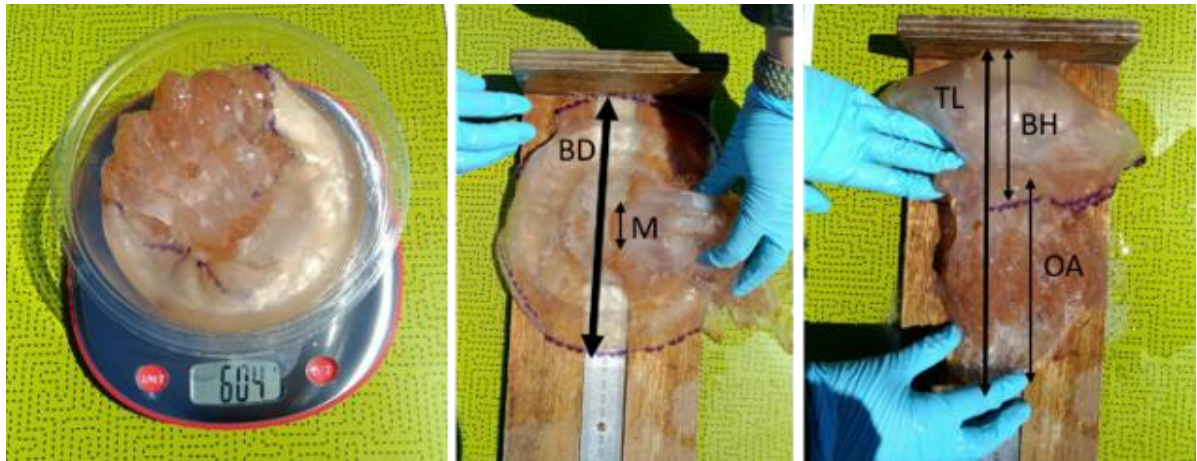
Citizen reports			
Ecoregion		Reference	Year
2	Western Mediterranean	<i>JellyWatch</i> (2020)	2013-2018
		<i>PERSEUS</i> (2020)	2013-2015
		<i>MedusApp 1.0</i> (2020)	2016, 2018-2019
		D. Bonnet <i>per. obs.</i>	2010-2011, 2014, 2018-2019
		<i>GBIF</i> (2020)	1898-1917, 1973, 1998, 2001-2005, 2007, 2009-2019
		Boero et al. (2019)	2009-2017
3	Adriatic Sea	<i>GBIF</i> (2020)	1898-1917, 1973, 1998, 2001-2005, 2007, 2009-2019
		<i>MedusApp 1.0</i> (2020)	2016, 2018-2019
		Condon et al. (2015)	1790, 1830, 1837-1838, 1843, 1874-1875, 1879-1880, 1883-1884, 1895-1896, 1899-1903, 1907-1911, 1913-1914, 1921, 1922, 1937, 1962, 1993, 1995, 1999-2009
		<i>JellyWatch</i> (2020)	2013-2018
		<i>PERSEUS</i> (2020)	2013-2015
		Boero et al. (2019)	2009-2017
4	Ionian Sea	<i>JellyWatch</i> (2020)	2013-2018
5	Tunisian Plateau	<i>PERSEUS</i> (2020)	2013-2015
		<i>JellyWatch</i> (2020)	2013-2018
		<i>GBIF</i> (2020)	1898-1917, 1973, 1998, 2001-2005, 2007, 2009-2019
6	Aegean Sea	<i>JellyWatch</i> (2020)	2013-2018
		<i>GBIF</i> (2020)	1898-1917, 1973, 1998, 2001-2005, 2007, 2009-2019
7	Levantine Sea	<i>JellyWatch</i> (2020)	2013-2018
		Condon et al. (2015)	2011
		<i>GBIF</i> (2020)	1898-1917, 1973, 1998, 2001-2005, 2007, 2009-2019
8	Black Sea	<i>PERSEUS</i> (2020)	2013-2015
		<i>GBIF</i> (2020)	1898-1917, 1973, 1998, 2001-2005, 2007, 2009-2019
		<i>JellyWatch</i> (2020)	2013-2018

**TABLE S2.3.** Detail information on the data collected in the different sources, and how they were included in each category of the abundance Index (N indicates the number of records on each category). The limit of the number of individuals per m<sup>3</sup> or m<sup>2</sup> was define based on personal field observation of the *Rhizostoma pulmo* population dynamics.

Abundance Index	Category	Data	N
0	Absence	0 absence	200
1	Presence in low abundance	1 to 10 individuals 0.0000001 to 0.3 ind/m <sup>3</sup> < 10 ind/m <sup>2</sup> Presence/ very rare/ scarce/ rare/ low/ single/ low abundances/ common / fewer medusae than normal	4617
2	Bloom	> 10 individuals > 1 ind/m <sup>3</sup> > 10ind/m <sup>2</sup> Many/ bloom/ big aggregations/ abundant /very abundant/ several/ high abundance/ large numbers	2542



**FIGURE S3.1.** Pelagic stages of *Rhizostoma pulmo* observed in Bages Sigean lagoon during 2019. **a.** Ephyrae. **b-c.** Metaephyrae stages. **d-g.** Medusae stages, from juvenile (**d-e**) to adult medusae (**f-g**). Photos by: Sandrine Crochemore (a, b), Valentina Leoni (c, d, g), Marie Meffre (e) and Raquel Marques (f).



**FIGURE S3.2.** Morphological measurements taken on living specimens of *Rhizostoma pulmo*. Regarding the measurement technique, we recommend handling this species in ventilated rooms or open places. During field surveys we detected that the stress caused by the handling during the measurements triggered the generation of mucus (as previously described in *L. lucerna* Nagata 2015), which would release volatile substances in the air that produced allergic responses. In particular, we experienced excessive sneezing and allergic reactions in the eyes (the latter treated with corticoids), both of them accompanied by headaches. This has already been previously described by Kokelj and Plozzer (2002).

Microzooplankton		Meso zooplankton		Macrozooplankton
Foraminifers	Ciliates	Cirripedia nauplii	Calanoid cop.	Fish eggs
Gastropods veliger	Bivalves veliger	Cyclopoid cop.	Harpacticoid cop.	Malacostraceans
Copepoda nauplii				Polychaetes

**FIGURE S4.1.** Schematic representation of the main taxa observed in the gut content of *Rhizostoma pulmo* medusae in Bages Sigeon lagoon (France) during 2019. Arrows denote the axis used for size measurements, following the same axes as Uye (1982) for copepods (cop.), Cirripedia nauplii, Bivalves veliger, Polychaeta, and Malacostraca (represented here by a Cumacea). Illustration by Justine Courboulès.



**TABLE S4.1.** Carbon content (C) equations used in the present study (Nassogne 1972; Uye 1982; Martinussen and Båmstedt 1995; Mauchline 1998; Loret et al. 2000; Ara 2001; Torniainen and Lehtiniemi 2008; Wukovits et al. 2018). For Foraminifera, Ciliates, Bivalvia veliger and fish eggs, a mean value of C per specimen was used. The digestion time values (hours) were obtained from Larson (1991).

Taxa	Carbon content (µg)	Reference	Digestion time (h)
Microzooplankton (63-200 µm)			
Foraminifers	0.068	Wukovits et al. (2018)	4 <sup>a</sup>
Ciliates	0.055	Loret et al. (2000)	1.5
Gastropods veliger	$C=57*L^{2.362}*k$	Nassogne (1972)	2
Bivalves veliger	0.2	Martinussen & Båmstedt(1995)	4
Copepoda nauplii	$C=10^{1.33*\log L-4.13}*k$	Mauchline (1998)	1.5
Mesozooplankton (200-700 µm)			
Cirripedia nauplii	$\log C = 3.72*\log L-9.66$	Uye (1982)	2
Calanoid cop.	$\log C=3.08*\log L -8.51$	Uye (1982)	1.5
Cyclopoid cop.	$\log C = 1.13*\log L-3.90$	Uye (1982)	1.5
Harpacticoid cop.	$C=8.148*10^{-8}*L^{2.74}*0.46$	Ara (2001)	2
Macrozooplankton (>700 µm)			
Fish eggs	125	Torniainen & Lehtiniemi (2008)	3

C = carbon content; L = organism length (µm); k = 0.41 (coefficient to convert WW to C). Cop. = Copepoda. For Foraminifers<sup>a</sup>, digestion times were considered the same as for Bivalves veliger



## REFERENCES

- Abed-Navandi D, Kikinger R (2007) First record of the tropical scyphomedusa *Phyllorhiza punctata* von Lendenfeld, 1884 (Cnidaria: Rhizostomeae) in the Central Mediterranean Sea. *AI* 2:391–394. doi: 10.3391/ai.2007.2.4.7
- Acevedo MJ, Fuentes V, Olariaga A, Canepa A, Belmar MB, Bordehore C, Calbet A (2013) Maintenance, feeding and growth of *Carybdea marsupialis* (Cnidaria: Cubozoa) in the laboratory. *J Exp Mar Biol Ecol* 439:84–91. doi: 10.1016/j.jembe.2012.10.007
- Acuña JL, Lopez-Urrutia A, Colin S (2011) Faking giants: The evolution of high prey clearance rates in jellyfishes. *Science* 333:1627–1629. doi: 10.1126/science.1205134
- Addad S, Yahia MND, Belghith H, Zamamouch S, Goy J (2008) Analyse taxonomique, écologique et caractérisation biochimique des scyphoméduses de la Baie de Bizerte et de Tunis (juillet-décembre 2004). *Bull de la Soc Zool de France* 133:33–41.
- Adloff F, Somot S, Sevault F, Jordà G, Aznar R, Déqué M, Herrmann M, Marcos M, Dubois C, Padorno E, Alvarez-Fanjul E, Gomis D (2015) Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. *Clim Dyn* 45:2775–2802. doi: 10.1007/s00382-015-2507-3
- Alekseenko E, Baklouti M, Carlotti F (2019) Main factors favoring *Mnemiopsis leidyi* individuals growth and population outbreaks: A modelling approach. *J Mar Syst* 196:14–35. doi: 10.1016/j.jmarsys.2019.01.001
- Álvarez-Tello FJ, López-Martínez J, Lluch-Cota DB (2016) Trophic spectrum and feeding pattern of cannonball jellyfish *Stomolophus meleagris* (Agassiz, 1862) from central Gulf of California. *J Mar Biol Ass* 96:1217–1227. doi: 10.1017/S0025315415001605
- Aouititen M, Bekkali R, Nachit D, Luan X, Mrhraoui M (2019) Predicting jellyfish strandings in the Moroccan North-West Mediterranean coastline. *ESJ*. doi: 10.19044/esj.2019.v15n2p72
- Ara K (2001) Length-weight relationships and chemical content of the planktonic copepods in the Cananeia Lagoon estuarine system, Sao Paulo, Brazil. *Plankton Biol Ecol* 48:121–127.
- Arai MN (1997) *A Functional Biology of Scyphozoa*. Springer Netherlands, Dordrecht
- Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proc Natl Acad Sci USA* 112:E4065–E4074. doi: 10.1073/pnas.1421946112
- Astorga D, Ruiz J, Prieto L (2012) Ecological aspects of early life stages of *Cotylorhiza tuberculata* (Scyphozoa: Rhizostomae) affecting its pelagic population success. *Hydrobiologia* 690:141–155. doi: 10.1007/s10750-012-1036-x
- Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103. doi: 10.1038/nature02996
- Atkinson D, Sibly RM (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol Evol* 12:235–239. doi: 10.1016/S0169-5347(97)01058-6
- Augustine S, Rosa S, Kooijman SALM, Carlotti F, Poggiale J-C (2014) Modeling the eco-physiology of the purple mauve stinger, *Pelagia noctiluca* using Dynamic Energy Budget theory. *J Sea Res* 94:52–64. doi: 10.1016/j.seares.2014.06.007
- Avian M (1986) Temperature influence on *in vitro* reproduction and development of *Pelagia noctiluca* (Forskål). *Ital J Zool* 53:385–391. doi: 10.1080/11250008609355528

- Bakun A, Weeks SJ (2006) Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? *Fish Fish* 7:316–333. doi: 10.1111/j.1467-2979.2006.00229.x
- Ballesteros A, Östman C, Santín A, Marambio M, Narda M, Gili J-M (2021) Cnidome and morphological features of *Pelagia noctiluca* (Cnidaria: Scyphozoa) throughout the different life cycle stages. *Front Mar Sci* 8:714503. doi: 10.3389/fmars.2021.714503
- Båmstedt U, Martinussen MB (2000) Estimating digestion rate and the problem of individual variability, exemplified by a scyphozoan jellyfish. *J Exp Mar Biol Ecol* 251:1–15. doi: 10.1016/S0022-0981(00)00182-9
- Barnes DKA (2002) Invasions by marine life on plastic debris. *Nature* 416:808–809. doi: <https://doi.org/10.1038/416808a>
- Bar-On YM, Phillips R, Milo R (2018) The biomass distribution on Earth. *Proc Natl Acad Sci USA* 115:6506–6511. doi: 10.1073/pnas.1711842115
- Basso L, Rizzo L, Marzano M, Intraruovo M, Fosso B, Pesole G, Piraino S, Stabili L (2019) Jellyfish summer outbreaks as bacterial vectors and potential hazards for marine animals and humans health? The case of *Rhizostoma pulmo* (Scyphozoa, Cnidaria). *Sci Total Environ* 692:305–318. doi: 10.1016/j.scitotenv.2019.07.155
- Baty F, Ritz C, Charles S, Brutsche M, Flandrois J-P, Delignette-Muller M-L (2015) A toolbox for nonlinear regression in R: The package nlstools. *J Stat Softw* 66:1–21.
- Beaugrand G, Luczak C, Edwards M (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob Change Biol* 15:1790–1803. doi: 10.1111/j.1365-2486.2009.01848.x
- Beaumont NJ, Austen MC, Mangi SC, Townsend M (2008) Economic valuation for the conservation of marine biodiversity. *Mar Pollut Bull* 56:386–396. doi: 10.1016/j.marpolbul.2007.11.013
- Bellido JJ, Báez JC, Souviron-Priego L, Ferri-Yañez F, Salas C, López JA, Real R (2020) Atmospheric indices allow anticipating the incidence of jellyfish coastal swarms. *Medit Mar Sci*. doi: 10.12681/mms.20983
- Ben Faleh A, Allaya H, Armani A, Shahin A (2017) Significant genetic differentiation among meroplanktonic barrel jellyfish *Rhizostoma pulmo* (Cnidaria: Scyphozoa) in the Mediterranean Sea. *Afr J Mar Sci* 39:1–8. doi: 10.2989/1814232X.2017.1303395
- Benedetti F, Vogt M, Elizondo UH, Righetti D, Zimmermann NE, Gruber N (2021) Major restructuring of marine plankton assemblages under global warming. *Nat Commun* 12:5226. doi: 10.1038/s41467-021-25385-x
- Benovic A, Lucic D, Onofri V (2000) Does change in an Adriatic hydromedusan fauna indicate an early phase of marine ecosystem destruction? *Mar Ecol* 21:221–231. doi: 10.1046/j.1439-0485.2000.00712.x
- Bergmann MPM van Z, Postaire BD, Gastrich K, Heithaus MR, Hoopes LA, Lyons K, Papastamatiou YP, Schneider EVC, Strickland BA, Talwar BS, Chapman DD, Bakker J (2021) Elucidating shark diets with DNA metabarcoding from cloacal swabs. *Mol* 21:1056–1067. doi: 10.1111/1755-0998.13315
- Berline L, Rammou A-M, Doglioli A, Molcard A, Petrenko A (2014) A connectivity-based eco-regionalization method of the Mediterranean Sea. *PLoS ONE* 9:e111978. doi: 10.1371/journal.pone.0111978
- Berry O, Bulman C, Bunce M, Coghlan M, Murray DC, Ward RD (2015) Comparison of morphological and DNA metabarcoding analyses of diets in exploited marine fishes. *Mar Ecol Prog Ser* 540:167–181. doi: 10.3354/meps11524

- Bethea DM, Hale L, Carlson JK, Cortés E, Manire CA, Gelsleichter J (2007) Geographic and ontogenetic variation in the diet and daily ration of the bonnethead shark, *Sphyrna tiburo*, from the eastern Gulf of Mexico. *Mar Biol* 152:1009–1020. doi: 10.1007/s00227-007-0728-7
- Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. *Fish Inv ser* 14:1–533.
- Bhaud M, Cha JH, Duchêne JC, Nozais C (1995) Influence of temperature on the marine fauna: What can be expected from a climatic change. *J Therm Biol* 20:91–104. doi: 10.1016/0306-4565(94)00031-D
- Bianchi CN, Morri C (2000) Marine biodiversity of the Mediterranean Sea: Situation, problems and prospects for future research. *Mar Pollut Bull* 40:10. doi: [https://doi.org/10.1016/S0025-326X\(00\)00027-8](https://doi.org/10.1016/S0025-326X(00)00027-8)
- Boero F (2014) Review of jellyfish blooms in the Mediterranean and Black Sea. *Mar Biol Res* 10:1038–1039. doi: 10.1080/17451000.2014.880790
- Boero F, Bouillon J, Gravili C, Miglietta M, Parsons T, Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Mar Ecol Prog Ser* 356:299–310. doi: 10.3354/meps07368
- Boero F, Brotz L, Gibbons MJ, Piraino S, Zampardi S (2016) 3.10 Impacts and effects of ocean warming on jellyfish. In: Laffoley D, Baxter JM (eds) *Explaining ocean warming: Causes, scale, effects and consequences*. IUCN, Gland, Switzerland, pp 213–237
- Bone Q (2005) Gelatinous animals and physiology. *J Mar Biol Ass* 85:641–653. doi: 10.1017/S0025315405011574
- Bonnet D (2013) Etude du plancton gélatineux sur la façade Méditerranéenne- GELAMED- Programme Liteau (189)- rapport d'activités.
- Bonnet D, Molinero JC, Schohn T, Yahia MND (2012) Seasonal changes in the population dynamics of *Aurelia aurita* in Thau lagoon. *Cah Biol Mar* 53:343–347.
- Bonnet D, Molinero J-C, Batistic M, Boero F, Daly N, Deidun A, Golo R, Gueroun SKM, Hervé A, Isinibilir M, Kienberger K, Kogovšek T, Lučić D, Malej A, Marques R, Miloslavić M, Pascual M, Piraino S, Prieto L, Yilmaz IN, Zampardi S, Zervoudaki S (2016) *Aurelia* spp. Ecology in the Mediterranean Sea.
- Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, Gehlen M, Halloran P, Heinze C, Ilyina T, Séférian R, Tjiputra J, Vichi M (2013) Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* 10:6225–6245. doi: 10.5194/bg-10-6225-2013
- Borsa P, Blanquer A, Berrebi P (1997) Genetic structure of the flounders *Platichthys flesus* and *P. stellatus* at different geographic scales. *Mar Biol* 129:233–246. doi: 10.1007/s002270050164
- Bosch-Belmar M, Azzurro E, Pulis K, Milisenda G, Fuentes V, Kéfi-Daly Yahia O, Micallef A, Deidun A, Piraino S (2017) Jellyfish blooms perception in Mediterranean finfish aquaculture. *Mar Policy* 76:1–7. doi: 10.1016/j.marpol.2016.11.005
- Bosch-Belmar M, Milisenda G, Basso L, Doyle TK, Leone A, Piraino S (2021) Jellyfish impacts on marine aquaculture and fisheries. *Rev Fish Sci Aquac* 29:242–259. doi: 10.1080/23308249.2020.1806201
- Brewer RH (1989) The annual pattern of feeding, growth, and sexual reproduction in *Cyanea* (Cnidaria: Scyphozoa) in the Niantic River Estuary, Connecticut. *Biol Bull* 176:272–281. doi: 10.2307/1541985
- Briggs JC (ed) (1995) Chapter 13 Species diversity: land and sea. In: *Developments in Palaeontology and Stratigraphy*. Elsevier, pp 371–389
- Brodeur R, Sugisaki H, Hunt G (2002) Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Mar Ecol Prog Ser* 233:89–103. doi: 10.3354/meps233089

- Brotz L (2016) Jellyfish fisheries of the world. The University of British Columbia
- Brotz L, Pauly D (2012) Jellyfish populations in the Mediterranean Sea. *Acta Adriat* 19.
- Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. *Hydrobiologia* 690:3–20. doi: 10.1007/s10750-012-1039-7
- Brotz L, Schiariti A, López-Martínez J, Álvarez-Tello J, Peggy Hsieh Y-H, Jones RP, Quiñones J, Dong Z, Morandini AC, Preciado M, Laaz E, Mianzan H (2017) Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds. *Rev Fish Biol Fisheries* 27:1–29. doi: 10.1007/s11160-016-9445-y
- Brown CJ, O'Connor MI, Poloczanska ES, Schoeman DS, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Pandolfi JM, Parmesan C, Richardson AJ (2016) Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Glob Change Biol* 22:1548–1560. doi: 10.1111/gcb.13184
- Brown CW, Hood RR, Long W, Jacobs J, Ramers DL, Wazniak C, Wiggert JD, Wood R, Xu J (2013) Ecological forecasting in Chesapeake Bay: Using a mechanistic–empirical modeling approach. *J Mar Syst* 125:113–125. doi: 10.1016/j.jmarsys.2012.12.007
- Bryndum-Buchholz A, Tittensor DP, Blanchard JL, Cheung WWL, Coll M, Galbraith ED, Jennings S, Maury O, Lotze HK (2019) Twenty-first-century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. *Glob Change Biol* 25:459–472. doi: 10.1111/gcb.14512
- Buecher E, Sparks C, Brierley A, Boyer H, Gibbons M (2001) Biometry and size distribution of *Chrysaora hysoscella* (Cnidaria, Scyphozoa) and *Aequorea aequorea* (Cnidaria, Hydrozoa) off Namibia with some notes on their parasite *Hyperia medusarum*. *J Plankton Res* 23:1073–1080. doi: 10.1093/plankt/23.10.1073
- Bugnot AB, Mayer-Pinto M, Airolidi L, Heery EC, Johnston EL, Critchley LP, Strain EMA, Morris RL, Loke LHL, Bishop MJ, Sheehan EV, Coleman RA, Dafforn KA (2020) Current and projected global extent of marine built structures. *Nat Sustain* 10. doi: <https://doi.org/10.1038/s41893-020-00595-1>
- Bulleri F, Chapman MG (2010) The introduction of coastal infrastructure as a driver of change in marine environments. *J Appl Ecol* 47:26–35. doi: 10.1111/j.1365-2664.2009.01751.x
- Byrne M, Foo SA, Ross PM, Putnam HM (2020) Limitations of cross- and multigenerational plasticity for marine invertebrates faced with global climate change. *Glob Change Biol* 26:80–102. doi: 10.1111/gcb.14882
- Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. *Front Ecol Environ* 1:412–420.
- Caisey X (2009) *Rhizostoma octopus*. In: Ifremer. <https://image.ifremer.fr/data/00677/78940/>.
- Calder DR (1982) Life history of the cannonball jellyfish, *Stomolophus meleagris* L. Agassiz, 1860 (Scyphozoa, Rhizostomida). *Biol Bull* 162:149–162. doi: 10.2307/1540810
- Calder DR (1983) Nematocysts of stages in the life cycle of *Stomotophus meleagris*, with keys to scyphistomae and ephyrae of some western Atlantic Scyphozoa. *Can J Zool* 61:1185–1192.
- Canepa A, Fuentes V, Bosch-Belmar M, Acevedo M, Toledo-Guedes K, Ortiz A, Durá E, Bordehore C, Gili J-M (2017) Environmental factors influencing the spatio-temporal distribution of *Carybdea marsupialis* (Lineo, 1978, Cubozoa) in South-Western Mediterranean coasts. *PLoS ONE* 12:e0181611. doi: 10.1371/journal.pone.0181611
- Carr EF, Pitt KA (2008) Behavioural responses of zooplankton to the presence of predatory jellyfish. *J Exp Mar Biol Ecol* 354:101–110. doi: 10.1016/j.jembe.2007.10.012

- Carrette T, Alderslade P, Seymour J (2002) Nematocyst ratio and prey in two Australian cubomedusans, *Chironex fleckeri* and *Chiropsalmus* sp. *Toxicon* 40:1547–1551. doi: 10.1016/S0041-0101(02)00168-X
- Cataudella S, Crosetti D, Massa F (2015) Mediterranean coastal lagoons: sustainable management and interactions among aquaculture, capture fisheries and the environment. FAO, Rome
- Ceh J, Gonzalez J, Pacheco AS, Riascos JM (2015) The elusive life cycle of scyphozoan jellyfish – metagenesis revisited. *Sci Rep* 5:12037. doi: 10.1038/srep12037
- Cesmat L, Dusserre K, Fiandrino A, Benau L (2012) Etude hydrologique de l'étang de Bages-Sigean. Impact de différents scénarii d'aménagement et de gestion sur les variations de salinité. Agence de l'eau, Conservatoire des Espaces Naturels du Languedoc-Roussillon, Parc Naturel Régional de la Narbonnaise en Méditerranée, Ifremer, France
- Chao A, Colwell RK, Lin C-W, Gotelli NJ (2009) Sufficient sampling for asymptotic minimum species richness estimators. *Ecol* 90:1125–1133. doi: <https://doi.org/10.1890/07-2147.1>
- Chapman DG, Robson DS (1960) The analysis of a catch curve. *Biometrics* 16:354–368.
- CIESM (2014) JellyWatch - CIESM the Mediterranean Science Commission. <http://www.ciesm.org/gis/JW/build/JellyBlooms.php>. Accessed 27 Feb 2020
- Cimino MA, Patris S, Ucharm G, Bell LJ, Terrill E (2018) Jellyfish distribution and abundance in relation to the physical habitat of Jellyfish Lake, Palau. *J Trop Ecol* 34:17–31. doi: 10.1017/S0266467418000044
- CMEMS (2019) Copernicus Marine Service. <http://marine.copernicus.eu/>.
- Cohen JM, Lajeunesse MJ, Rohr JR (2018) A global synthesis of animal phenological responses to climate change. *Nature Clim Change* 8:224–228. doi: 10.1038/s41558-018-0067-3
- Coll M, Piroddi C, Steenbeek J, Kaschner K, Ben Rais Lasram F, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T, Danovaro R, Estrada M, Frogia C, Galil BS, Gasol JM, Gertwagen R, Gil J, Guilhaumon F, Kesner-Reyes K, Kitsos M-S, Koukouras A, Lampadariou N, Laxamana E, López-Fé de la Cuadra CM, Lotze HK, Martin D, Mouillot D, Oro D, Raicevich S, Rius-Barile J, Saiz-Salinas JI, San Vicente C, Somot S, Templado J, Turon X, Vafidis D, Villanueva R, Voultsiadou E (2010) The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. *PLoS ONE* 5:e11842. doi: 10.1371/journal.pone.0011842
- Coll M, Piroddi C, Albouy C, Lasram FBR, Cheung WWL, Christensen V, Karpouzi VS, Guilhaumon F, Mouillot D, Paleczny M, Palomares ML, Steenbeek J, Trujillo P, Watson R, Pauly D (2012) The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Glob Ecol Biogeogr* 21:465–480. doi: 10.1111/j.1466-8238.2011.00697.x
- Collingridge K, van der Molen J, Pitois S (2014) Modelling risk areas in the North Sea for blooms of the invasive comb jelly *Mnemiopsis leidyi* A. Agassiz, 1865. *AI* 9:21–36. doi: 10.3391/ai.2014.9.1.02
- Coma R, Ribes M, Serrano E, Jiménez E, Salat J, Pascual J (2009) Global warming-enhanced stratification and mass mortality events in the Mediterranean. *PNAS* 106:6176–6181. doi: 10.1073/pnas.0805801106
- Condon RH, Graham WM, Duarte CM, Pitt KA, Lucas CH, Haddock SHD, Sutherland KR, Robinson KL, Dawson MN, Decker MB, Mills CE, Purcell JE, Malej A, Mianzan H, Uye S, Gelcich S, Madin LP (2012) Questioning the rise of gelatinous zooplankton in the World's Oceans. *BioScience* 62:160–169. doi: 10.1525/bio.2012.62.2.9
- Condon RH, Duarte CM, Pitt KA, Robinson KL, Lucas CH, Sutherland KR, Mianzan HW, Boggeberg M, Purcell JE, Decker MB, Uye SI, Madin LP, Brodeur RD, Haddock SHD, Malej A, Parry GD, Eriksen E, Quinones J,

- Acha M, Harvey M, Arthur JM, Graham WM (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *PNAS* 110:1000–1005. doi: 10.1073/pnas.1210920110
- Condon RH, Lucas CH, Duarte CM, Pitt KA, Haddock SHD, Madin LP, Brodeur RD, Sutherland KR, Mianzan HW, Purcell JE, Decker MB, Uye S-I, Malej A, Borgeberg M, Everett JT, Gibbons M, Gonzalez H, Hay S, Hensche N, Hobson RJ, Kingsford MJ, Kremer P, Lehtiniemi M, Ohman M, Rissik D, Sheard K, Suthers I, Coleman N, Costello JH, Gershwin LA, Graham WM, Robinson KL, Richardson TM, Giesecke R, Gorsky G, Greve W, Halsband-Lenk C, Hays G, Hobson V, Klein D, Lebrato M, Loveridge J, Martens P, Milos C, Perry G, Stemmann L, Sullivan B, Walker T, Schildhauer M, Regetz J (2015) JeDI: Jellyfish Database Initiative. doi: 10.1575/1912/7191
- Costalago D, Navarro J, Álvarez-Calleja I, Palomera I (2012) Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. *Mar Ecol Prog Ser* 460:169–181. doi: 10.3354/meps09751
- Costello JH, Colin SP (1994) Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. *Mar Biol* 121:327–334. doi: 10.1007/BF00346741
- Costello JH, Colin SP (1995) Flow and feeding by swimming scyphomedusae. *Mar Biol* 124:399–406. doi: 10.1007/BF00363913
- Crist E, Mora C, Engelman R (2017) The interaction of human population, food production, and biodiversity protection. *Science* 356:260–264. doi: 10.1126/science.aal2011
- CSIC (2021) La Mar de Medusas. <https://www.csic.es/es/investigacion/proyectos-de-investigacion/la-mar-de-medusas>.
- Cury P, Shin Y, Planque B, Durant J, Fromentin J, Kramerschadt S, Stenseth N, Travers M, Grimm V (2008) Ecosystem oceanography for global change in fisheries. *Trends Ecol Evol* 23:338–346. doi: 10.1016/j.tree.2008.02.005
- da Silveira EL, Semmar N, Cartes JE, Tuset VM, Lombarte A, Ballester ELC, Vaz-dos-Santos AM (2020) Methods for trophic ecology assessment in fishes: A critical review of stomach analyses. *Rev Fish Sci Aquac* 28:71–106. doi: 10.1080/23308249.2019.1678013
- Daly Yahia MN, Goy J, Daly Yahia-Kéfi O (2003) Distribution et écologie des méduses (Cnidaria) du golfe de Tunis (Méditerranée sud occidentale). *Acta Oceanol* 26:645–655. doi: 10.1016/j.oceact.2003.05.002
- Daly Yahia MN, Batistic M, Lucic D, Fernandez de Puelles ML, Licandro P, Malej A, Molinero JC, Siokou-Frangou I, Zervoudaki S, Prieto L, Goy J, Daly Yahia-Kéfi O (2010) Are the outbreaks of *Pelagia noctiluca* (Forsskål, 1775) more frequent in the Mediterranean basin? In: Gislason A, Gorsky G (eds) Proceedings on the “Joint ICES/CIESM workshop to compare zooplankton ecology and methodologies between the Mediterranean and the North Atlantic (WKZEM).” ICES / CIEM, pp 8–14
- Dam HG (2013) Evolutionary adaptation of marine zooplankton to global change. *Annu Rev Mar Sci* 5:349–370. doi: 10.1146/annurev-marine-121211-172229
- D’Ambra I, Merquiol L, Graham WM, Costello JH (2021) “Indirect development” increases reproductive plasticity and contributes to the success of scyphozoan jellyfish in the oceans. *Sci Rep* 11:18653. doi: 10.1038/s41598-021-98171-w
- D’Ambrosio M, Molinero JC, Azeiteiro UM, Pardal MA, Primo AL, Nyitrai D, Marques SC (2016) Interannual abundance changes of gelatinous carnivore zooplankton unveil climate-driven hydrographic variations in the Iberian Peninsula, Portugal. *Mar Environ Res* 120:103–110. doi: 10.1016/j.marenvres.2016.07.012

- Damian-Serrano A, Haddock SHD, Dunn CW (2021) The evolution of siphonophore tentilla for specialized prey capture in the open ocean. *PNAS* 118:1–9. doi: 10.1073/pnas.2005063118
- David C, Vaz S, Loots C, Antajan E, van der Molen J, Travers-Trolet M (2015) Understanding winter distribution and transport pathways of the invasive ctenophore *Mnemiopsis leidyi* in the North Sea: coupling habitat and dispersal modelling approaches. *Biol Invasions* 17:2605–2619. doi: 10.1007/s10530-015-0899-y
- Dawson MN, Hamner WM (2009) A character-based analysis of the evolution of jellyfish blooms: adaptation and exaptation. *Hydrobiologia* 616:193–215. doi: 10.1007/s10750-008-9591-x
- Dawson MN, Martin LE, Penland LK (2001) Jellyfish swarms, tourists, and the Christ-child. In: Purcell JE, Graham WM, Dumont HJ (eds) *Jellyfish Blooms: Ecological and Societal Importance*. Springer, Dordrecht,
- Dawson MN, Cieciel K, Decker MB, Hays GC, Lucas CH, Pitt KA (2015) Population-level perspectives on global change: genetic and demographic analyses indicate various scales, timing, and causes of scyphozoan jellyfish blooms. *Biol Invasions* 17:851–867. doi: 10.1007/s10530-014-0732-z
- De Domenico S, De Rinaldis G, Paulmery M, Piraino S, Leone A (2019) Barrel jellyfish (*Rhizostoma pulmo*) as source of antioxidant peptides. *Mar Drugs* 17:134. doi: 10.3390/md17020134
- Deidun A, Sciberras A (2017) Unearthing marine biodiversity through citizen science - the Spot the Jellyfish and the Spot the Alien Fish campaign case studies from the Maltese Islands (Central Mediterranean). *Bulletin of the Entomological Society of Malta* 9:3.
- Deli T, Kalkan E, Karhan SÜ, Uzunova S, Keikhosravi A, Bilgin R, Schubart CD (2018) Parapatric genetic divergence among deep evolutionary lineages in the Mediterranean green crab, *Carcinus aestuarii* (Brachyura, Portunoidea, Carcinidae), accounts for a sharp phylogeographic break in the Eastern Mediterranean. *BMC Evol Biol* 18:53. doi: 10.1186/s12862-018-1167-4
- Deutsch C, Penn JL, Seibel B (2020) Metabolic trait diversity shapes marine biogeography. *Nature* 585:557–562. doi: 10.1038/s41586-020-2721-y
- Di Camillo CG, Betti F, Bo M, Martinelli M, Puce S, Bavestrello G (2010) Contribution to the understanding of seasonal cycle of *Aurelia aurita* (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. *J Mar Biol Assoc* 90:1105–1110. doi: 10.1017/S0025315409000848
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–929. doi: 10.1126/science.1156401
- Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: The other CO<sub>2</sub> problem. *Annu Rev Mar Sci* 1:169–192. doi: 10.1146/annurev.marine.010908.163834
- Dong Z, Liu D, Keesing JK (2010) Jellyfish blooms in China: Dominant species, causes and consequences. *Mar Pollut Bull* 60:954–963. doi: 10.1016/j.marpolbul.2010.04.022
- Dönmez MA, Bat L (2019) Detection of feeding dietary *Rhizostoma pulmo* (Macri, 1778) in Samsun coasts of the Black Sea, Turkey. *EgeJFAS* 36:135–144. doi: 10.12714/egejfas.2019.36.2.0
- Duarte CM, Pitt KA, Lucas CH, Purcell JE, Uye S, Robinson K, Brotz L, Decker MB, Sutherland KR, Malej A, Madin L, Mianzan H, Gili JM, Fuentes V, Atienza D, Pagés F, Breitbart D, Malek J, Graham WM, Condon RH (2013) Is global ocean sprawl a cause of jellyfish blooms? *Front Ecol Environ* 11:91–97. doi: 10.1890/110246
- Durgham H (2011) First records of *Phyllorhiza punctata* von Lendenfeld, 1884 (Cnidaria: Rhizostomeae) from the Mediterranean Coast of Syria. *Int J Oceans Oceanogr* 5:153–155.

- Dzierzbicka-Głowacka L, Kuliński K, Maciejewska A, Jakacki J, Pempkowiak J (2010) Particulate organic carbon in the southern Baltic Sea: numerical simulations and experimental data. *Oceanologia* 52:621–648. doi: 10.5697/oc.52-4.621
- Edelist D, Guy-Haim T, Kuplik Z, Zuckerman N, Nemoy P, Angel DL (2020) Phenological shift in swarming patterns of *Rhopilema nomadica* in the Eastern Mediterranean Sea. *J Plankton Res* 1–9. doi: 10.1093/plankt/fbaa008
- Edelist D, Knutsen Ø, Ellingsen I, Majaneva S, Aberle N, Dror H, Angel DL (2022) Tracking jellyfish swarm origins using a combined oceanographic-genetic-citizen science approach. *Front Mar Sci* 9:869619. doi: 10.3389/fmars.2022.869619
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884. doi: 10.1038/nature02808
- EEA (ed) (2006) The changing faces of Europe’s coastal areas. European Environment Agency; Office for Official Publications of the European Communities, Copenhagen, Denmark : Luxembourg
- Enrique-Navarro A, Huertas IE, León Cobo MJ, Prieto L (2021) Impact of ocean warming and ocean acidification on asexual reproduction and statolith formation of the symbiotic jellyfish *Cotylorhiza tuberculata*. *PLoS ONE* 16:e0254983. doi: 10.1371/journal.pone.0254983
- Fancett MS (1988) Diet and prey selectivity of scyphomedusae from Port Phillip Bay, Australia. *Mar Biol* 98:503–509. doi: 10.1007/BF00391541
- Fasham MJR, Ducklow HW, McKelvie SM (1990) A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J Mar Res* 48:591–639. doi: 10.1357/002224090784984678
- Faugeras B, Maury O (2007) Modeling fish population movements: From an individual-based representation to an advection–diffusion equation. *J Theor Biol* 247:837–848. doi: 10.1016/j.jtbi.2007.04.012
- Feng S, Lin J, Sun S, Zhang F, Li C, Xian W (2020) Combined effects of seasonal warming and hyposalinity on strobilation of *Nemopilema nomurai* polyps. *J Exp Mar Biol Ecol* 524:151316. doi: 10.1016/j.jembe.2020.151316
- Fennel W (2001) Modeling of copepods with links to circulation models. *J Plankton Res* 1217–1232. doi: https://doi.org/10.1093/plankt/23.11.1217
- Fenner PJ, Hadok JC (2002) Fatal envenomation by jellyfish causing Irukandji syndrome. *MJA* 177:2.
- Fernández-Alías A, Marcos C, Quispe JI, Sabah S, Pérez-Ruzafa A (2020) Population dynamics and growth in three scyphozoan jellyfishes, and their relationship with environmental conditions in a coastal lagoon. *Estuar Coast Shelf Sci* 243:106901. doi: 10.1016/j.ecss.2020.106901
- Fernández-Alías A, Marcos C, Pérez-Ruzafa A (2021) Larger scyphozoan species dwelling in temperate, shallow waters show higher blooming potential. *Mar Pollut Bull* 173:113100. doi: 10.1016/j.marpolbul.2021.113100
- Ferrer L, Pastor A (2017) The Portuguese man-of-war: Gone with the wind. *Reg Stud Mar* 14:53–62. doi: 10.1016/j.rsma.2017.05.004
- Fiandrino A, Ouisse V, Dumas F, Lagarde F, Pete R, Malet N, Le Noc S, de Wit R (2017) Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. *Mar Pollut Bull* 119:132–144. doi: 10.1016/j.marpolbul.2017.03.006
- Firth LB, Knights AM, Bridger D, Evans AJ, Mieszkowska N, Moore P, O’ Connor NE, Sheehan E, Thompson RC, Hawkins SJ (2016) Ocean sprawl: challenges and opportunities for biodiversity management in a changing



- world. CRC Press, Taylor & Francis Group, 6000 Broken Sound Parkway NW, Suite 300, Boca Raton, FL 33487-2742
- Fleming NEC, Harrod C, Newton J, Houghton JDR (2015) Not all jellyfish are equal: isotopic evidence for inter- and intraspecific variation in jellyfish trophic ecology. *PeerJ* 3:1–21. doi: 10.7717/peerj.1110
- Folino-Rorem NC, Reid M, Peard T (2016) Culturing the freshwater hydromedusa, *Craspedacusta sowerbii* under controlled laboratory conditions. *Invertebr Reprod Dev* 60:17–27. doi: 10.1080/07924259.2015.1114040
- Ford DF, Plants-Paris ED, Ford NB (2020) Comparison of Louisiana Pigtoe (*Pleurobema riddellii*, Mollusca, Unionidae) growth at three different locations in the Neches River Basin of East Texas. *Hydrobiologia* 847:2021–2033. doi: 10.1007/s10750-020-04228-8
- Fossette S, Katija K, Goldbogen JA, Bograd S, Patry W, Howard MJ, Knowles T, Haddock SHD, Bedell L, Hazen EL, Robison BH, Mooney TA, Shorter KA, Bastian T, Gleiss AC (2016) How to tag a jellyfish? A methodological review and guidelines to successful jellyfish tagging. *J Plankton Res* 1–17. doi: 10.1093/plankt/fbw073
- Franks PJS (2002) NPZ models of plankton dynamics: Their constructions, coupling to physics, and application. *J Oceanogr* 58:379–387. doi: 10.1023/A:1015874028196
- Frolova A, Miglietta MP (2020) Insights on bloom forming jellyfish (Class: Scyphozoa) in the Gulf of Mexico: Environmental tolerance ranges and limits suggest differences in habitat preference and resistance to climate change among congeners. *Front Mar Sci* 7:93. doi: 10.3389/fmars.2020.00093
- Fu F, Tatters A, Hutchins D (2012) Global change and the future of harmful algal blooms in the ocean. *Mar Ecol Prog Ser* 470:207–233. doi: 10.3354/meps10047
- Fuchs B, Wang W, Graspentner S, Li Y, Insua S, Herbst E-M, Dirksen P, Böhm A-M, Hemmrich G, Sommer F, Domazet-Lošo T, Klostermeier UC, Anton-Erxleben F, Rosenstiel P, Bosch TCG, Khalturin K (2014) Regulation of polyp-to-jellyfish transition in *Aurelia aurita*. *Curr Biol* 24:263–273. doi: 10.1016/j.cub.2013.12.003
- Fuentes V, Straehler-Pohl I, Atienza D, Franco I, Tilves U, Gentile M, Acevedo M, Olariaga A, Gili JM (2011) Life cycle of the jellyfish *Rhizostoma pulmo* (Scyphozoa: Rhizostomeae) and its distribution, seasonality and inter-annual variability along the Catalan coast and the Mar Menor (Spain, NW Mediterranean). *Mar Biol* 158:2247–2266. doi: 10.1007/s00227-011-1730-7
- Galil BS (2000) A sea under siege – alien species in the Mediterranean. *Biol Invasions* 2:177–186.
- Garcia J (1990) Population dynamics and production of *Phyllorhiza punctata* (Cnidaria: Scyphozoa) in Laguna Joyuda, Puerto Rico. *Mar Ecol Prog Ser* 64:243–251. doi: 10.3354/meps064243
- GelAvista (2021) GelAvista. In: GelAvista. <https://gelavista.ipma.pt/>.
- Getino Mamet LN, Gómez Daglio L, García-De León FJ (2019) High genetic differentiation in the edible cannonball jellyfish (Cnidaria: Scyphozoa: *Stomolophus* spp.) from the Gulf of California, Mexico. *Fish Res* 219:105328. doi: 10.1016/j.fishres.2019.105328
- Ghermandi A, Galil B, Gowdy J, Nunes PALD (2015) Jellyfish outbreak impacts on recreation in the Mediterranean Sea: welfare estimates from a socioeconomic pilot survey in Israel. *Ecosyst Serv* 11:140–147. doi: 10.1016/j.ecoser.2014.12.004
- Gibbons MJ, Janson LA, Ismail A, Samaai T (2010) Life cycle strategy, species richness and distribution in marine Hydrozoa (Cnidaria: Medusozoa). *J Biogeogr* 37:441–448. doi: 10.1111/j.1365-2699.2009.02226.x

- Gilbert AL, Lattanzio MS (2016) Ontogenetic variation in the thermal biology of yarrow's spiny lizard, *Sceloporus jarrovi*. PLOS ONE 11:e0146904. doi: 10.1371/journal.pone.0146904
- Giorgi F (2006) Climate change hot-spots. Geophys Res Lett. doi: 10.1029/2006GL025734
- Girón-Nava A, López-Sagástegui C, Aburto-Oropeza O (2015) On the conditions of the 2012 cannonball jellyfish (*Stomolophus meleagris*) bloom in Golfo de Santa Clara: a fishery opportunity? Fish Manag Ecol 22:261–264. doi: 10.1111/fme.12115
- Glasby TM, Connell SD, Holloway MG, Hewitt CL (2007) Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? Mar Biol 151:887–895. doi: 10.1007/s00227-006-0552-5
- Glynn F, Houghton JDR, Provan J (2015) Population genetic analyses reveal distinct geographical blooms of the jellyfish *Rhizostoma octopus* (Scyphozoa). Biol J Linn Soc 116:582–592. doi: 10.1111/bij.12614
- Goffart A, Hecq J, Legendre L (2002) Changes in the development of the winter-spring phytoplankton bloom in the Bay of Calvi (NW Mediterranean) over the last two decades: a response to changing climate? Mar Ecol Prog Ser 236:45–60. doi: 10.3354/meps236045
- Golani D (1998) Impact of Red Sea fish migrants through the Suez Canal on the aquatic environment of the eastern Mediterranean. Bulletin Series Yale School of Forestry and Environmental Studies 103:375–387.
- Goldstein J, Riisgård HU (2016) Population dynamics and factors controlling somatic degrowth of the common jellyfish, *Aurelia aurita*, in a temperate semi-enclosed cove (Kertinge Nor, Denmark). Mar Biol 163:33. doi: 10.1007/s00227-015-2802-x
- González MT, Sepúlveda FA, Zárate PM, Baeza JA (2020) Regional population genetics and global phylogeography of the endangered highly migratory shark *Lamna nasus*: Implications for fishery management and conservation. Aquatic Conserv: Mar Freshw Ecosyst. doi: <https://doi.org/10.1002/aqc.3455>
- Gordon M, Seymour J (2012) Growth, development and temporal variation in the onset of six *Chironex fleckeri* medusae seasons: A contribution to understanding jellyfish ecology. PLoS ONE 7:e31277. doi: 10.1371/journal.pone.0031277
- Gordon M, Hatcher C, Seymour J (2004) Growth and age determination of the tropical Australian cubozoan *Chiropsalmus* sp. Hydrobiologia 530/531:339–345.
- Gotoh RO, Chang S-J, Qu X, Ito C, Okuizumi K, Yoon WD, Iizumi H, Hanzawa N (2017) Distribution and dispersal of the giant jellyfish *Nemopilema nomurai* (Scyphozoa, Cnidaria) inferred from its genetic population structure. Biogeography 93–100.
- Goy J, Morand P, Etienne M (1989) Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. Deep-Sea Res 36:269–279. doi: 10.1016/0198-0149(89)90138-6
- Graham WM, Bayha KM (2007) Biological invasions by marine jellyfish. In: Nentwig W (ed) Biological Invasions. Springer, Berlin, Heidelberg, pp 239–255
- Graham WM, Kroutil RM (2001) Size-based prey selectivity and dietary shifts in the jellyfish, *Aurelia aurita*. J Plankton Res 23:67–74. doi: 10.1093/plankt/23.1.67
- Graham WM, Martin DL, Felder DL, Asper VL, Perry HM (2003) Ecological and economic implications of a tropical jellyfish invader in the Gulf of Mexico. Biol Invasions 53–69. doi: 10.1007/978-94-010-0169-4\_6
- Graham WM, Gelcich S, Robinson KL, Duarte CM, Brotz L, Purcell JE, Madin LP, Mianzan H, Sutherland KR, Uye S, Pitt KA, Lucas CH, Bøgeberg M, Brodeur RD, Condon RH (2014) Linking human well-being and

- jellyfish: ecosystem services, impacts, and societal responses. *Front Ecol Environ* 12:515–523. doi: 10.1890/130298
- Granéli E, Turner J (2002) Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study. *Mar Ecol Prog Ser* 239:57–68. doi: 10.3354/meps239057
- Greve W, Prinage S, Zidowitz H, Nast J, Reiners F (2005) On the phenology of North Sea ichthyoplankton. *ICES Journal of Marine Science* 62:1216–1223. doi: 10.1016/j.icesjms.2005.03.011
- Gueroun SKM (2016) Dynamique des populations et écologie trophique des scyphoméduses du bassin sud méditerranéen: Etude *in situ* et expérimentales de l'impact de la prédation d'*Aurelia* sp.8 et de *Pelagia noctiluca* sur le réseau trophique pélagique. Université de Carthage
- Gueroun SKM, Molinero JC, Piraino S, Yahia MND (2020) Population dynamics and predatory impact of the alien jellyfish *Aurelia solida* (Cnidaria, Scyphozoa) in the Bizerte Lagoon (southwestern Mediterranean Sea). *Mediterr Mar Sci* 21:22–35. doi: 10.12681/mms.17358
- Gueroun SKM, Torres TM, Santos AD, Vasco-Rodrigues N, Canning-Clode J, Andrade C (2021) *Catostylus tagi* (Class: Scyphozoa, Order: Discomedusae, Suborder: Rhizostomida, Family: Catostylidae) life cycle and first insight into its ecology. *PeerJ* 9:e12056. doi: 10.7717/peerj.12056
- Guerrero E, Gili J-M, Maynou F, Sabatés A (2018) Diversity and mesoscale spatial changes in the planktonic cnidarian community under extreme warm summer conditions. *J Plankton Res* 40:178–196. doi: 10.1093/plankt/fby001
- Guest WC (1959) The occurrence of the jellyfish *Chiropsalmus quadrumanus* in Matagorda Bay, Texas. *Bull Mar Sci* 79–33.
- Guinder V, Molinero J (2013) Climate change effects on marine phytoplankton. In: Menendez M (ed) *Marine Ecology in a Changing World*. CRC Press, pp 68–90
- Haddock SHD (2004) A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia* 530/531:549–556.
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. *Science* 319:948–952. doi: 10.1126/science.1149345
- Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, O'Hara C, Scarborough C, Selkoe KA (2019) Recent pace of change in human impact on the world's ocean. *Sci Rep* 9:11609. doi: 10.1038/s41598-019-47201-9
- Hamner WM, Dawson MN (2009) A review and synthesis on the systematics and evolution of jellyfish blooms: advantageous aggregations and adaptive assemblages. *Hydrobiologia* 616:161–191. doi: 10.1007/s10750-008-9620-9
- Han C-H, Uye S (2010) Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* s.l. *Plankton Benthos Res* 5:98–105. doi: 10.3800/pbr.5.98
- Haraldsson M, Tönnesson K, Tiselius P, Thingstad TF, Aksnes DL (2012) Relationship between fish and jellyfish as a function of eutrophication and water clarity. *Mar Ecol Prog Ser* 471:73–85. doi: 10.3354/meps10036
- Hardinge G (2019) The macroecology of globally-distributed deep-sea jellyfish. University of Southampton

- Harrison A-L, Costa DP, Winship AJ, Benson SR, Bograd SJ, Antolos M, Carlisle AB, Dewar H, Dutton PH, Jorgensen SJ, Kohin S, Mate BR, Robinson PW, Schaefer KM, Shaffer SA, Shillinger GL, Simmons SE, Weng KC, Gjerde KM, Block BA (2018) The political biogeography of migratory marine predators. *Nat Ecol Evol* 2:1571–1578. doi: 10.1038/s41559-018-0646-8
- Hastings A (2013) Population Dynamics. In: *Encyclopedia of Biodiversity*. Elsevier, pp 175–181
- Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW (2012) High activity and Levy searches: jellyfish can search the water column like fish. *Proc R Soc B: Biol Sci* 279:465–473. doi: 10.1098/rspb.2011.0978
- Hays GC, Doyle TK, Houghton JDR (2018) A paradigm shift in the trophic importance of jellyfish? *Trends Ecol Evol* 33:874–884. doi: 10.1016/j.tree.2018.09.001
- Hecq JH, Collignon A, Goffart A (2014) Atlas du zooplancton des eaux côtières corses. Travail de synthèse réalisé à la demande de l'Agence de l'Eau RMC, France
- Heisler J, Glibert PM, Burkholder JM, Anderson DM, Cochlan W, Dennison WC, Dortch Q, Gobler CJ, Heil CA, Humphries E, Lewitus A, Magnien R, Marshall HG, Sellner K, Stockwell DA, Stoecker DK, Suddleson M (2008) Eutrophication and harmful algal blooms: A scientific consensus. *Harmful Algae* 8:3–13. doi: 10.1016/j.hal.2008.08.006
- Helaouët P, Beaugrand G, Reid PC (2011) Macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Prog Oceanogr* 91:217–228. doi: 10.1016/j.pocean.2010.11.003
- Henschke N (2019) Jellyfishes in a changing ocean. In: *Predicting Future Oceans*. Elsevier, pp 137–148
- Henschke N, Stock C, Sarmiento J (2018) Modeling population dynamics of scyphozoan jellyfish (*Aurelia* spp.) in the Gulf of Mexico. *Mar Ecol Prog Ser* 591:167–183. doi: 10.3354/meps12255
- Hermann AJ, Kearney K, Cheng W, Pilcher D, Aydin K, Holsman KK, Hollowed AB (2021) Coupled modes of projected regional change in the Bering Sea from a dynamically downscaling model under CMIP6 forcing. *Deep Sea Research Part II: Topical Studies in Oceanography* 194:104974. doi: 10.1016/j.dsr2.2021.104974
- Hočevár S, Malej A, Boldin B, Purcell J (2018) Seasonal fluctuations in population dynamics of *Aurelia aurita* polyps in situ with a modelling perspective. *Mar Ecol Prog Ser* 591:155–166. doi: 10.3354/meps12387
- Hoegh-Guldberg O, Bruno JF (2010) The impact of Climate Change on the world's marine ecosystems. *Science* 328:1523–1528. doi: 10.1126/science.1189930
- Holst S (2012) Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. *Hydrobiologia* 690:127–140. doi: 10.1007/s10750-012-1043-y
- Holst S, Sötje I, Tiemann H, Jarms G (2007) Life cycle of the rhizostome jellyfish *Rhizostoma octopus* (L.) (Scyphozoa, Rhizostomeae), with studies on cnidocysts and statoliths. *Mar Biol* 151:1695–1710. doi: 10.1007/s00227-006-0594-8
- Hoover R, Hoover D, Miller M, Landry M, DeCarlo E, Mackenzie F (2006) Zooplankton response to storm runoff in a tropical estuary: bottom-up and top-down controls. *Mar Ecol Prog Ser* 318:187–201. doi: 10.3354/meps318187
- Houghton J, Doyle T, Davenport J, Hays G (2006) Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. *Mar Ecol Prog Ser* 314:159–170. doi: 10.3354/meps314159

- Houghton JDR, Doyle TK, Davenport J, Lilley MKS, Wilson RP, Hays GC (2007) Stranding events provide indirect insights into the seasonality and persistence of jellyfish medusae (Cnidaria: Scyphozoa). *Hydrobiologia* 589:1–13. doi: 10.1007/s10750-007-0572-2
- Hutchinson GE (1957) *A Treatise on Limnology*. John Wiley & Sons, New York
- Hyslop JF (1980) Stomach content analysis-a review on methods and their application. *J Fish Biol* 17:411–429.
- iMedJelly (2019) In: iMedJelly. <http://www.medjelly.com/>.
- Indarjo A, Salim G, Zein M (2020) Characteristics of Von Bertalanffy growth, allometric, condition index and mortality of *Periophthalmus barbarus* in Mangrove and Bekantan Conservation Area (KKMB), Tarakan, North Kalimantan. *IJMS* 25:31–38.
- IPCC (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press
- Jarms G, Morandini AC (2019) *World Atlas of Jellyfish*. Dölling und Galitz Verlag
- Javidpour J, Molinero J, Ramírez-Romero E, Roberts P, Larsen T (2020) Cannibalism makes invasive comb jelly, *Mnemiopsis leidyi*, resilient to unfavourable conditions. *Commun Biol* 3:212. doi: 10.1038/s42003-020-0940-2
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. In: *Advances in Marine Biology*. Elsevier, pp 201–352
- Jiang J, Zhang H, Kang Y, Bina D, Lo CS, Blankenship RE (2012) Characterization of the peridinin-chlorophyll a-protein complex in the dinoflagellate *Symbiodinium*. *Biochim Biophys Acta* 1817:983–989. doi: 10.1016/j.bbabi.2012.03.027
- Jiménez-Valverde A, Hortal J (2003) Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Revista Ibérica de Aracnología* 8:151–161.
- Jolliff JK, Kindle JC, Shulman I, Penta B, Friedrichs MAM, Helber R, Arnone RA (2009) Summary diagrams for coupled hydrodynamic-ecosystem model skill assessment. *J Marine Syst* 76:64–82. doi: 10.1016/j.jmarsys.2008.05.014
- Kamburska L, Fonda-Umani S (2006) Long-term copepod dynamics in the Gulf of Trieste (Northern Adriatic Sea): recent changes and trends. *Clim Res* 31:195–203. doi: 10.3354/cr031195
- Karydis M, Kitsiou D (2012) Eutrophication and environmental policy in the Mediterranean Sea: a review. *Environ Monit Assess* 184:4931–4984. doi: 10.1007/s10661-011-2313-2
- Katsanevakis S, Coll M, Piroddi C, Steenbeek J, Ben Rais Lasram F, Zenetos A, Cardoso AC (2014) Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Front Mar Sci* 1:32. doi: 10.3389/fmars.2014.00032
- Kawahara M, Uye S, Burnett J, Mianzan H (2006a) Stings of edible jellyfish (*Rhopilema hispidum*, *Rhopilema esculentum* and *Nemopilema nomurai*) in Japanese waters. *Toxicon* 48:713–716. doi: 10.1016/j.toxicon.2006.06.015
- Kawahara M, Uye S, Ohtsu K, Iizumi H (2006b) Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. *Mar Ecol Prog Ser* 307:161–173. doi: 10.3354/meps307161
- Kienberger K, Prieto L (2018) The jellyfish *Rhizostoma luteum* (Quoy & Gaimard, 1827): not such a rare species after all. *Mar Biodiv* 48:1455–1462. doi: 10.1007/s12526-017-0637-z

- Kienberger K, Riera-Buch M, Schönemann AM, Bartsch V, Halbauer R, Prieto L (2018) First description of the life cycle of the jellyfish *Rhizostoma luteum* (Scyphozoa: Rhizostomeae). PLoS ONE 13:e0202093. doi: 10.1371/journal.pone.0202093
- Kikinger R (1992) *Cotylorhiza tuberculata* (Cnidaria: Scyphozoa) - Life history of a stationary population. Mar Ecol 13:333–362. doi: 10.1111/j.1439-0485.1992.tb00359.x
- Kim D-H, Seo J-N, Yoon W-D, Suh Y-S (2012) Estimating the economic damage caused by jellyfish to fisheries in Korea. Fish Sci 78:1147–1152. doi: 10.1007/s12562-012-0533-1
- Kingsford J, Pitt A, Gillanders M (2000) Management of jellyfish fisheries, with special reference to the Order Rhizostomeae. Oceanogr Mar Biol 85–156.
- Kjørboe T (2013) Zooplankton body composition. Limnol Oceanogr 58:1843–1850. doi: 10.4319/lo.2013.58.5.1843
- Klein SG, Pitt KA, Carroll AR (2017) Pre-exposure to simultaneous, but not individual, climate change stressors limits acclimation capacity of Irukandji jellyfish polyps to predicted climate scenarios. Coral Reefs 36:987–1000. doi: 10.1007/s00338-017-1590-9
- Kogovšek T, Bogunović B, Malej A (2010) Recurrence of bloom-forming scyphomedusae: wavelet analysis of a 200-year time series. Hydrobiologia 645:81–96. doi: 10.1007/s10750-010-0217-8
- Kogovšek T, Tinta T, Klun K, Malej A (2014) Jellyfish biochemical composition: importance of standardised sample processing. Mar Ecol Prog Ser 510:275–288. doi: 10.3354/meps10959
- Kokelj F, Plozzer C (2002) Irritant contact dermatitis from the jellyfish *Rhizostoma pulmo*. Contact Dermatitis 46:179–180. doi: 10.1034/j.1600-0536.2002.460313.x
- Krebs CJ (1999) Ecological methodology, 2nd edn. Benjamin Cummings, New York
- Kremer P (1976) Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In: Wiley M (ed) Estuarine Processes. Academic Press, pp 197–215
- Kremer P, Reeve MR (1989) Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. II. Carbon budgets and growth model. J Plankton Res 11:553–574. doi: 10.1093/plankt/11.3.553
- Krüger F (1968) Stoffwechsel und Wachstum bei Scyphomedusan. Helgoländer wissenschaftliche Meeresuntersungen 18:367–383.
- Kuplik Z, Angel DL (2020) Diet composition and some observations on the feeding ecology of the rhizostome *Rhopilema nomadica* in Israeli coastal waters. J Mar Biol Ass 100:681–689. doi: 10.1017/S0025315420000697
- Kuplik Z, Kerem D, Angel DL (2021) Respiration rates, metabolic demands and feeding of ephyrae and young medusae of the Rhizostome *Rhopilema nomadica*. Diversity 13:320. doi: 10.3390/d13070320
- Kwiatkowski L, Torres O, Bopp L, Aumont O, Chamberlain M, Christian JR, Dunne JP, Gehlen M, Ilyina T, John JG, Lenton A, Li H, Lovenduski NS, Orr JC, Palmieri J, Santana-Falcón Y, Schwinger J, Séférian R, Stock CA, Tagliabue A, Takano Y, Tjiputra J, Toyama K, Tsujino H, Watanabe M, Yamamoto A, Yool A, Ziehn T (2020) Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. Biogeosciences 17:3439–3470. doi: 10.5194/bg-17-3439-2020
- Lamb PD, Hunter E, Pinnegar JK, Doyle TK, Creer S, Taylor MI (2019) Inclusion of jellyfish in 30+ years of Ecopath with Ecosim models. ICES Journal of Marine Science 76:1941–1950. doi: 10.1093/icesjms/fsz165

- Langton RW (1982) Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish. *Fish Bull* 80:16.
- Larson RJ (1991) Diet, prey selection and daily ration of *Stomolophus meleagris*, a filter-feeding scyphomedusa from the NE Gulf of Mexico. *Estuar Coast Shelf Sci* 32:511–525. doi: 10.1016/0272-7714(91)90038-D
- Latasa M, Morán XAG, Scharek R, Estrada M (2005) Estimating the carbon flux through main phytoplankton groups in the northwestern Mediterranean. *Limnology and Oceanography* 50:1447–1458. doi: 10.4319/lo.2005.50.5.1447
- Lawley JW, Carroll AR, McDougall C (2021) Rhizostomins: A Novel Pigment Family From Rhizostome Jellyfish (Cnidaria, Scyphozoa). *Front Mar Sci* 8:752949. doi: 10.3389/fmars.2021.752949
- Lebrato M, Pitt KA, Sweetman AK, Jones DOB, Cartes JE, Oschlies A, Condon RH, Molinero JC, Adler L, Gaillard C, Lloris D, Billett DSM (2012) Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia* 690:227–245. doi: 10.1007/s10750-012-1046-8
- Lebrato M, Pahlow M, Frost JR, Küter M, Jesus Mendes P, Molinero J, Oschlies A (2019) Sinking of gelatinous zooplankton biomass increases deep carbon transfer efficiency globally. *Global Biogeochem Cycles* 33:1764–1783. doi: 10.1029/2019GB006265
- Lechable M, Jan A, Duchene A, Uveira J, Weissbourd B, Gissat L, Collet S, Gilletta L, Chevalier S, Leclère L, Peron S, Barreau C, Lasbleiz R, Houliston E, Momose T (2020) An improved whole life cycle culture protocol for the hydrozoan genetic model *Clytia hemisphaerica*. *Biol Open* 9:1–13. doi: 10.1242/bio.051268
- Lee PLM, Dawson MN, Neill SP, Robins PE, Houghton JDR, Doyle TK, Hays GC (2013) Identification of genetically and oceanographically distinct blooms of jellyfish. *J R Soc Interface* 10:20120920–20120920. doi: 10.1098/rsif.2012.0920
- Legendre P, Legendre L (1998) *Numerical Ecology*, 2nd English Edition. Elsevier, Amsterdam
- Lejeusne C, Chevaldonné P, Pergent-Martini C, Boudouresque CF, Pérez T (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends Ecol Evol* 25:250–260. doi: 10.1016/j.tree.2009.10.009
- Lenoir J, Svenning J-C (2015) Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography* 38:15–28. doi: 10.1111/ecog.00967
- Leone A, Lecci RM, Milisenda G, Piraino S (2019) Mediterranean jellyfish as novel food: effects of thermal processing on antioxidant, phenolic, and protein contents. *Eur Food Res Technol* 245:1611–1627. doi: 10.1007/s00217-019-03248-6
- Leoni V, Bonnet D, Ramírez-Romero E, Molinero JC (2021a) Biogeography and phenology of the jellyfish *Rhizostoma pulmo* (Cnidaria: Scyphozoa) in southern European seas. *Global Ecol Biogeogr* 30:622–639. doi: <https://doi.org/10.1111/geb.13241>
- Leoni V, Molinero JC, Meffre M, Bonnet D (2021b) Variability of growth rates and thermohaline niches of *Rhizostoma pulmo*'s pelagic stages (Cnidaria: Scyphozoa). *Mar Biol* 168:107. doi: 10.1007/s00227-021-03914-y
- Leoni V, Molinero JC, Crochemore S, Meffre M, Bonnet D (2022) Ontogenetic dietary shifts of the medusa *Rhizostoma pulmo* (Cnidaria: Scyphozoa). under review 849:2933–2948. doi: <https://doi.org/10.1007/s10750-022-04903-y>

- Li C, Liu H (2022) Exploring cosmopolitan jellyfish (*Aurelia* spp.) bloom dynamics and ecological implications in subtropical waters with mechanistic dynamic modeling. *J Mar Syst* 228:103705. doi: 10.1016/j.jmarsys.2022.103705
- Lilley MKS, Houghton JDR, Hays GC (2009) Distribution, extent of inter-annual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. *J Mar Biol* 89:39. doi: 10.1017/S0025315408002439
- Lilley MKS, Beggs SE, Doyle TK, Hobson VJ, Stromberg KHP, Hays GC (2011) Global patterns of epipelagic gelatinous zooplankton biomass. *Mar Biol* 158:2429–2436. doi: 10.1007/s00227-011-1744-1
- Link JS, Watson RA (2019) Global ecosystem overfishing: Clear delineation within real limits to production. *Sci Adv* 5:eaav0474. doi: 10.1126/sciadv.aav0474
- Lodi L, Tardin R (2018) Citizen science contributes to the understanding of the occurrence and distribution of cetaceans in southeastern Brazil – A case study. *Ocean Coast Manag* 158:45–55. doi: 10.1016/j.ocecoaman.2018.03.029
- López-Martínez J, Arzola-Sotelo EA, Nevárez-Martínez MO, Álvarez-Tello FJ, Morales-Bojórquez E (2020) Modeling growth on the cannonball jellyfish *Stomolophus meleagris* based on a multi-model inference approach. *Hydrobiologia* 847:1399–1422. doi: 10.1007/s10750-020-04182-5
- Loret P, Le Gall S, Dupuy C, Blanchot J, Pastoureaud A, Delesalle B, Caisey X, Jonquière G (2000) Heterotrophic protists as a trophic link between picocyanobacteria and the pearl oyster *Pinctada margaritifera* in the Takapoto lagoon (Tuamotu Archipelago, French Polynesia). *Aquat Microb Ecol* 22:215–226. doi: 10.3354/ame022215
- Lotan A, Fine M, Ben-Hillel R (1994) Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. *Mar Ecol Prog Ser* 109:59–65. doi: 10.3354/meps109059
- Lotze HK, Tittensor DP, Bryndum-Buchholz A, Eddy TD, Cheung WWL, Galbraith ED, Barange M, Barrier N, Bianchi D, Blanchard JL, Bopp L, Büchner M, Bulman CM, Carozza DA, Christensen V, Coll M, Dunne JP, Fulton EA, Jennings S, Jones MC, Mackinson S, Maury O, Niiranen S, Oliveros-Ramos R, Roy T, Fernandes JA, Schewe J, Shin Y-J, Silva TAM, Steenbeek J, Stock CA, Verley P, Volkholz J, Walker ND, Worm B (2019) Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc Natl Acad Sci USA* 116:12907–12912. doi: 10.1073/pnas.1900194116
- Loveridge A, Pitt KA, Lucas CH, Warnken J (2021a) Extreme changes in salinity drive population dynamics of *Catostylus mosaicus* medusae in a modified estuary. *Mar Environ Res* 168:105306. doi: 10.1016/j.marenvres.2021.105306
- Loveridge A, Lucas CH, Pitt KA (2021b) Shorter, warmer winters may inhibit production of ephyrae in a population of the moon jellyfish *Aurelia aurita*. *Hydrobiologia* 848:739–749. doi: 10.1007/s10750-020-04483-9
- Lu Y, Lucas C, Loveridge A (2020) Transgenerational acclimation influences asexual reproduction in *Aurelia aurita* jellyfish polyps in response to temperature. *Mar Ecol Prog Ser* 656:35–50. doi: 10.3354/meps13517
- Lucas CH (1996) Population dynamics of *Aurelia aurita* (Scyphozoa) from an isolated brackish lake, with particular reference to sexual reproduction. *J Plankton Res* 18:987–1007. doi: 10.1093/plankt/18.6.987
- Lucas CH, Dawson MN (2014) What are jellyfishes and thaliaceans and why do they bloom? In: Pitt KA, Lucas CH (eds) *Jellyfish Blooms*. Springer Netherlands, Dordrecht, pp 9–44



- Lucas CH, Lawes S (1998) Sexual reproduction of the scyphomedusa *Aurelia aurita* in relation to temperature and variable food supply. *Mar Biol* 131:629–638. doi: 10.1007/s002270050355
- Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories: Role of polyps in forming and maintaining scyphomedusa populations. In: *Advances in Marine Biology*. Elsevier, pp 133–196
- Lucas CH, Jones DOB, Hollyhead CJ, Condon RH, Duarte CM, Graham WM, Robinson KL, Pitt KA, Schildhauer M, Regetz J (2014) Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. *Global Ecol Biogeogr* 23:701–714. doi: 10.1111/geb.12169
- Luttikhuisen PC, Campos J, Bleijswijk J van, Peijnenburg KTCA, van der Veer HW (2008) Phylogeography of the common shrimp, *Crangon crangon* (L.) across its distribution range. *Mol Phylogenet Evol* 46:1015–1030. doi: 10.1016/j.ympev.2007.11.011
- Lynam CP, Hay SJ, Brierley AS (2004) Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnol Oceanogr* 49:637–643. doi: 10.4319/lo.2004.49.3.0637
- Lynam CP, Gibbons J, Axelsen BE, Sparks CAJ, Heywood BG, Brierley AS (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Curr Biol* 16:2.
- Lynam CP, Lilley MKS, Bastian T, Doyle TK, Beggs SE, Hays GC (2011) Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Glob Change Biol* 17:767–782. doi: 10.1111/j.1365-2486.2010.02352.x
- Macaluso V (2019) Morphological and morphometrical analysis of two populations (Gulf of Trieste, Italy and Bages-Sigean Lagoon, France) of *Rhizostoma pulmo* (Scyphozoa, Rhizostomeae, Rhizostomatidae) with notes on phylogenesis of the genus *Rhizostoma*. *Universita degli studi di Trieste*
- Macdonald P, Du J (2018) Package ‘mixdist’. Version 0.5-5.
- Macias D, Garcia-Gorriz E, Stips A (2013) Understanding the causes of recent warming of Mediterranean waters. How much could be attributed to climate change? *PLOS ONE* 8:e81591. doi: 10.1371/journal.pone.0081591
- Macías D, Prieto L, García-Gorriz E (2021) A model-based management tool to predict the spread of *Physalia physalis* in the Mediterranean Sea. Minimizing risks for coastal activities. *Ocean & Coastal Management* 212:105810. doi: 10.1016/j.ocecoaman.2021.105810
- Malej A, Malej M (1992) Population dynamics of the jellyfish *Pelagia noctiluca* (Forsskal, 1775). In: Colombo Ferrara GI, Olsen & Olsen (eds) *Marine Eutrophication and Population dynamics*. Fredensborg, Denmark, pp 215–219
- Malej A, Kogovšek T, Ramšak A, Catenacci L (2012) Blooms and population dynamics of moon jellyfish in the northern Adriatic. *Cah Biol Mar* 53:337–342.
- Malej A, Kogovšek T, Uye SI (2014) Medusae - Pest or resource for humans. *Biol Mar Medit* 21:2–9.
- Malul D, Lotan T, Makovsky Y, Holzman R, Shavit U (2019) The Levantine jellyfish *Rhopilema nomadica* and *Rhizostoma pulmo* swim faster against the flow than with the flow. *Sci Rep* 9:20337. doi: 10.1038/s41598-019-56311-3
- Marambio M, Canepa A, Lòpez L, Gauci AA, Gueroun SKM, Zampardi S, Boero F, Yahia OK-D, Yahia MND, Fuentes V, Piraino S, Deidun A (2021) Unfolding jellyfish bloom dynamics along the Mediterranean basin by transnational citizen science initiatives. *Diversity* 13:274. doi: 10.3390/d13060274
- Marbà N, Jordà G, Agustí S, Girard C, Duarte CM (2015) Footprints of climate change on Mediterranean Sea biota. *Front Mar Sci*. doi: 10.3389/fmars.2015.00056

- Marchessaux G, Bejean M (2020) Growth and ingestion rates of the freshwater jellyfish *Craspedacusta sowerbii*. J Plankton Res 1–4. doi: 10.1093/plankt/fbaa047
- Mariani S, Ketmaier V, Mattheaïs E de (2002) Genetic structuring and gene flow in *Cerastoderma glaucum* (Bivalvia: Cardiidae): evidence from allozyme variation at different geographic scales. Mar Biol 140:687–697. doi: 10.1007/s00227-001-0753-x
- Mariottini GL, Pane L (2010) Mediterranean jellyfish venoms: A review on Scyphomedusae. Mar Drugs 8:1122–1152. doi: 10.3390/md8041122
- Marques R, Cantou M, Soriano S, Molinero JC, Bonnet D (2015a) Mapping distribution and habitats of *Aurelia* sp. polyps in Thau lagoon, north-western Mediterranean Sea (France). Mar Biol 162:1441–1449. doi: 10.1007/s00227-015-2680-2
- Marques R, Albouy-Boyer S, Delpy F, Carré C, Le Floch É, Roques C, Molinero J-C, Bonnet D (2015b) Pelagic population dynamics of *Aurelia* sp. in French Mediterranean lagoons. J Plankton Res 37:1019–1035. doi: 10.1093/plankt/fbv059
- Marques R, Bouvier C, Darnaude AM, Molinero J-C, Przybyla C, Soriano S, Tomasini J-A, Bonnet D (2016) Jellyfish as an alternative source of food for opportunistic fishes. J Exp Mar Biol Ecol 485:1–7. doi: 10.1016/j.jembe.2016.08.008
- Marques R, Darnaude AM, Schiariti A, Tremblay Y, Molinero JC, Soriano S, Hatey E, Colantoni S, Bonnet D (2019) Dynamics and asexual reproduction of the jellyfish *Aurelia coerulea* benthic life stage in the Thau lagoon (northwestern Mediterranean). Mar Biol 166:74. doi: 10.1007/s00227-019-3522-4
- Marques R, Rufino M, Darnaude AM, Carcaillet F, Meffre M, Bonnet D (2021a) Jellyfish degradation in a shallow coastal Mediterranean lagoon. Estuarine, Coastal and Shelf Science 261:107527. doi: 10.1016/j.ecss.2021.107527
- Marques R, Bonnet D, Carré C, Roques C, Darnaude AM (2021b) Trophic ecology of a blooming jellyfish (*Aurelia coerulea*) in a Mediterranean coastal lagoon. Limnol Oceanogr 66:141–157. doi: https://doi.org/10.1002/lno.11593
- Martinussen M, Båmstedt U (1995) Diet, estimated daily food ration and predator impact by the scyphozoan jellyfishes *Aurelia aurita* and *Cyanea capillata*. In: Skjoldal H, Hopkins C, Erikstad K, Leinaas H (eds) Ecology of fjords and coastal waters. Elsevier Science BV, Amsterdam, pp 127–145
- Matsakis S (1993) Growth of *Clytia* spp. hydromedusae (Cnidaria, Thecata): effects of temperature and food availability. J Exp Mar Biol Ecol 171:107–118. doi: 10.1016/0022-0981(93)90143-C
- Mauchline J (1998) The Biology of Calanoid Copepods. Academic Press, London
- Maury O, Poggiale J-C (2013) From individuals to populations to communities: A dynamic energy budget model of marine ecosystem size-spectrum including life history diversity. J Theor Biol 324:52–71. doi: 10.1016/j.jtbi.2013.01.018
- McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR (2015) Marine defaunation: Animal loss in the global ocean. Science 347:1255641–1255641. doi: 10.1126/science.1255641
- Melica V, Invernizzi S, Caristi G (2014) Logistic density-dependent growth of an *Aurelia aurita* polyps population. Ecol Model 291:1–5. doi: 10.1016/j.ecolmodel.2014.07.009
- Met Office (2019) Hadley Centre Sea Ice and Sea Surface Temperature data set (HadISST). In: Met Office Hadley Centre observations datasets. https://www.metoffice.gov.uk/hadobs/hadisst/index.html.

- Meteomeduse (2011) Natura Torna il MeteoMeduse. <https://www.focus.it/ambiente/natura/meteomeduse>.
- Milisenda G, Rossi S, Vizzini S, Fuentes VL, Purcell JE, Tilves U, Piraino S (2018) Seasonal variability of diet and trophic level of the gelatinous predator *Pelagia noctiluca* (Scyphozoa). *Sci Rep* 8:12140. doi: 10.1038/s41598-018-30474-x
- Miller M-EC, Graham WM (2012) Environmental evidence that seasonal hypoxia enhances survival and success of jellyfish polyps in the northern Gulf of Mexico. *J Exp Mar Biol Ecol* 432–433:113–120. doi: 10.1016/j.jembe.2012.07.015
- Mills CE (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? In: Purcell JE, Graham WM, Dumont HJ (eds) *Jellyfish blooms: Ecological and societal importance*. Springer Netherlands, Dordrecht, pp 55–68
- Miloslavich P, Bax NJ, Simmons SE, Klein E, Appeltans W, Aburto-Oropeza O, Andersen Garcia M, Batten SD, Benedetti-Cecchi L, Checkley Jr. DM, Chiba S, Duffy JE, Dunn DC, Fischer A, Gunn J, Kudela R, Marsac F, Muller-Karger FE, Obura D, Shin Y-J (2018) Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. *Glob Change Biol* 24:2416–2433. doi: 10.1111/gcb.14108
- Minamoto T, Fukuda M, Katsuhara KR, Fujiwara A, Hidaka S, Yamamoto S, Takahashi K, Masuda R (2017) Environmental DNA reflects spatial and temporal jellyfish distribution. *PLOS ONE* 12:e0173073. doi: 10.1371/journal.pone.0173073
- Minchin D, Gollasch S, Cohen AN, Hewitt CL, Olenin S (2009) Characterizing vectors of marine invasion. In: Rilov G, Crooks JA (eds) *Biological invasions in marine ecosystems. Ecological, management, and geographic perspectives*. Springer, pp 109–116
- Mir-Arguimbau J, Sabatés A, Tilves U (2019) Trophic ecology of *Trachurus mediterraneus* juveniles associated with the jellyfish *Rhizostoma pulmo* and *Cotylorhiza tuberculata*. *J Sea Res* 147:28–36. doi: 10.1016/j.seares.2019.02.004
- Mitchell EG, Wallace MI, Smith VA, Wiesenthal AA, Brierley AS (2021) Bayesian Network Analysis reveals resilience of the jellyfish *Aurelia aurita* to an Irish Sea regime shift. *Sci Rep* 11:3707. doi: 10.1038/s41598-021-82825-w
- Mizrahi GA, Shemesh E, Mizrahi A, Tchernov D (2021) Comparative genetics of scyphozoan species reveals the geological history and contemporary processes of the Mediterranean Sea. *Ecol Evol* ece3.7834. doi: 10.1002/ece3.7834
- Molinero JC, Casini M, Buecher E (2008) The influence of the Atlantic and regional climate variability on the long-term changes in gelatinous carnivore populations in the northwestern Mediterranean. *Limnol Oceanogr* 53:1456–1467. doi: 10.4319/lo.2008.53.4.1456
- Molinero JC, Vukanić V, Lučić D, Ibanez F, Nival P, Licandro P, Calbet A, Christou ED, Daly-Yahia N, Fernandez de Puellas ML, Mazzocchi MG, Siokou-Frangou I (2009) Mediterranean marine copepods: basin-scale trends of the calanoid *Centropages typicus*. *Hydrobiologia* 617:41–53. doi: 10.1007/s10750-008-9524-8
- Moon J-H, Pang I-C, Yang J-Y, Yoon WD (2010) Behavior of the giant jellyfish *Nemopilema nomurai* in the East China Sea and East/Japan Sea during the summer of 2005: A numerical model approach using a particle-tracking experiment. *J Marine Syst* 80:101–114. doi: 10.1016/j.jmarsys.2009.10.015
- Moore MV, De Stasio BT, Huizenga KN, Silow EA (2019) Trophic coupling of the microbial and the classical food web in Lake Baikal, Siberia. *Freshw Biol* 64:138–151. doi: 10.1111/fwb.13201
- Morandini AC (2022) Impacts of jellyfish: Gelatinous problems or opportunities? *ACMAR* 55:123–140. doi: 10.32360/acmar.v55iEspecial.78409

- Morandini AC, Schiariti A, Stampar SN, Maronna MM, Straehler-Pohl I, Marques AC (2016) Succession of generations is still the general paradigm for scyphozoan life cycles. *BMS* 92:343–351. doi: 10.5343/bms.2016.1018
- Moschella P (2008) The new CIESM Tropicalization Programme – effects of climate warming on Mediterranean key taxa. *CIESM Workshop Monographs* 35:4.
- Moullec F, Barrier N, Drira S, Guilhaumon F, Hattab T, Peck MA, Shin Y-J (2022) Using species distribution models only may underestimate climate change impacts on future marine biodiversity. *Ecol Model* 464:109826. doi: 10.1016/j.ecolmodel.2021.109826
- Mozetič P, Solidoro C, Cossarini G, Socal G, Precali R, Francé J, Bianchi F, De Vittor C, Smolaka N, Fonda Umani S (2010) Recent trends towards oligotrophication of the northern Adriatic: Evidence from chlorophyll a time series. *Estuaries Coasts* 33:362–375. doi: 10.1007/s12237-009-9191-7
- Mutlu E (2001) Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. *Mar Biol* 138:329–339.
- Mutlu E (2009) Recent distribution and size structure of gelatinous organisms in the southern Black Sea and their interactions with fish catches. *Mar Biol* 156:935–957. doi: 10.1007/s00227-009-1139-8
- Nagata R, Moreira M, Pimentel C, Morandini A (2015) Food web characterization based on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  reveals isotopic niche partitioning between fish and jellyfish in a relatively pristine ecosystem. *Mar Ecol Prog Ser* 519:13–27. doi: 10.3354/meps11071
- Nagata R, Morandini A, Colin S, Migotto A, Costello J (2016) Transitions in morphologies, fluid regimes, and feeding mechanisms during development of the medusa *Lychnorhiza lucerna*. *Mar Ecol Prog Ser* 557:145–159. doi: 10.3354/meps11855
- Nagata RM (2015) Bases morfo-funcionais da alimentacao e papel trófico de *Lychnorhiza lucerna* (Scyphozoa, Rhizostomeae).
- Nagata RM, Morandini AC (2018) Diet, prey selection, and individual feeding rates of the jellyfish *Lychnorhiza lucerna* (Scyphozoa, Rhizostomeae). *Mar Biol* 165:187. doi: 10.1007/s00227-018-3445-5
- NASA (2019) OceanColor WEB. In: EARTHDATA. <https://oceancolor.gsfc.nasa.gov/>.
- Nassogne A (1972) Etudes preliminaires sur le role du zooplancton dans la constitution et al transfert de la matiere organique au sein de la chaine alimentaire marine en mer Ligure. 244.
- Nastav B, Malej M, Malej Jr. A, Malej A (2013) Is it possible to determine the economic impact of jellyfish outbreaks on fisheries? A case study – Slovenia. *Medit Mar Sci* 14:214. doi: 10.12681/mms.382
- Nogueira M, Haddad MA (2006) Relações de tamanho e peso das grandes medusas (Cnidaria) do litoral do Paraná, Sul do Brasil. *Rev Bras Zool* 23:1231–1234.
- Nordstrom B, James M, Martin K, Worm B (2019) Tracking jellyfish and leatherback sea turtle seasonality through citizen science observers. *Mar Ecol Prog Ser* 620:15–32. doi: 10.3354/meps12978
- Oba A, Hidaka M, Iwanaga S (2004) Nematocyst composition of the cubomedusan *Chiropsalmus quadrigatus* changes with growth. *Hydrobiologia* 530/531:173–177.
- Ogle DH (2013) fishR Vignette – Von Bertalanffy Growth Models. Northland College, Ashland, USA.
- Ogle DH, Isermann DA (2017) Estimating age at a specified length from the von Bertalanffy growth function. *N Am J Fish Manag* 37:1176–1180. doi: <https://doi.org/10.1080/02755947.2017.1342725>

- Ogle DH, Wheeler P, Dinno A (2021) FSA: Fisheries Stock Analysis. R package version 0.8.32.
- Oguz T, Salihoglu B, Fach B (2008) A coupled plankton–anchovy population dynamics model assessing nonlinear controls of anchovy and gelatinous biomass in the Black Sea. *Mar Ecol Prog Ser* 369:229–256. doi: 10.3354/meps07540
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) *vegan*: Community Ecology Package.
- Olson MH (1996) Ontogenetic niche shifts in Largemouth Bass: Variability and consequences for first-year growth. *Ecology* 77:179–190. doi: 10.2307/2265667
- Omori M, Nakano E (2001) Jellyfish fisheries in southeast Asia. *Hydrobiologia* 451:19–26. doi: 10.1007/978-94-010-0722-1\_3
- Omori M, Ishii H, Fujinaga A (1995) Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES J Mar Sci* 52:597–603. doi: 10.1016/1054-3139(95)80074-3
- Padilla-Serrato JG, López-Martínez J, Acevedo-Cervantes A, Alcántara-Razo E, Rábago-Quiroz CH (2013) Feeding of the scyphomedusa *Stomolophus meleagris* in the coastal lagoon Las Guásimas, northwest Mexico. *Hydrobiológica* 23:9.
- Palmieri MG, Barausse A, Luisetti T, Turner K (2014) Jellyfish blooms in the Northern Adriatic Sea: Fishermen’s perceptions and economic impacts on fisheries. *Fish Res* 155:51–58. doi: 10.1016/j.fishres.2014.02.021
- Palomares MLD, Pauly D (2009) The growth of jellyfishes. *Hydrobiologia* 616:11–21. doi: 10.1007/s10750-008-9582-y
- Paramo J, Quiñones RA, Ramirez A, Wiff R (2003) Relationship between abundance of small pelagic fishes and environmental factors in the Colombian Caribbean Sea: an analysis based on hydroacoustic information. *Aquat Living Resour* 16:239–245. doi: 10.1016/S0990-7440(03)00043-3
- Parsons TR, Lalli CM (2002) Jellyfish population explosions: Revisiting a hypothesis of possible causes. *La mer* 40:111–121.
- Paspalef B (1938) Über die Entwicklung von *Rhizostoma pulmo* Agass. *Trud chernomorsk biol Sta Varna* 7:1–25.
- Pauly D, Graham WM, Libralato S, Morissette L, Palomares MLD (eds) (2009) Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia* 616:67–85. doi: 10.1007/s10750-008-9583-x
- Peach MB, Pitt KA (2005) Morphology of the nematocysts of the medusae of two scyphozoans, *Catostylus mosaicus* and *Phyllorhiza punctata* (Rhizostomeae): implications for capture of prey: Nematocysts and prey of rhizostome jellyfish. *Invertebr Biol* 124:98–108. doi: 10.1111/j.1744-7410.2005.00012.x
- Peijnenburg KTCA, Fauvelot C, Breeuwer JAJ, Menken SBJ (2006) Spatial and temporal genetic structure of the planktonic *Sagitta setosa* (Chaetognatha) in European seas as revealed by mitochondrial and nuclear DNA markers. *Mol Ecol* 15:3319–3338. doi: 10.1111/j.1365-294X.2006.03002.x
- Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for global biodiversity in the 21st century. *Science* 330:1496–1501. doi: 10.1126/science.1196624

- Pérez-Losada M, Nolte MJ, Crandall KA, Shaw PW (2007) Testing hypotheses of population structuring in the Northeast Atlantic Ocean and Mediterranean Sea using the common cuttlefish *Sepia officinalis*. *Mol Ecol* 16:2667–2679. doi: 10.1111/j.1365-294X.2007.03333.x
- Pérez-Ruzafa A, Gilabert J, Gutiérrez JM, Fernández AI, Marcos C, Sabah S (2002) Evidence of a planktonic food web response to changes in nutrient input dynamics in the Mar Menor coastal lagoon, Spain. *Hydrobiologia* 359–369. doi: 10.1007/978-94-017-2464-7\_26
- Pikesley SK, Godley BJ, Ranger S, Richardson PB, Witt MJ (2014) Cnidaria in UK coastal waters: description of spatio-temporal patterns and inter-annual variability. *J Mar Biol Ass* 94:1401–1408. doi: 10.1017/S0025315414000137
- Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science* 341:1239–1242. doi: 10.1126/science.1239352
- Pitt KA, Kingsford MJ (2003a) Temporal and spatial variation in recruitment and growth of medusae of the jellyfish, *Catostylus mosaicus* (Scyphozoa: Rhizostomeae). *Mar Freshwater Res* 54:117. doi: 10.1071/MF02110
- Pitt KA, Kingsford MJ (2003b) Temporal variation in the virgin biomass of the edible jellyfish, *Catostylus mosaicus* (Scyphozoa, Rhizostomeae). *Fish Res* 11.
- Pitt KA, Lucas CH (eds) (2013) Jellyfish blooms. Springer, Dordrecht
- Pitt KA, Connolly RM, Purcell JE (2009) Stable isotope and fatty acid tracers in energy and nutrient studies of jellyfish: a review. *Hydrobiologia* 616:119–132. doi: 10.1007/s10750-008-9581-z
- Pitt KA, Budarf AC, Browne JG, Condon RH (2013) Bloom and Bust: Why do blooms of jellyfish collapse? In: Pitt KA, Lucas CH (eds) Jellyfish Blooms. Springer, Dordrecht,
- Pitt KA, Lucas CH, Condon RH, Duarte CM, Stewart-Koster B (2018) Claims that anthropogenic stressors facilitate jellyfish blooms have been amplified beyond the available evidence: A systematic review. *Front Mar Sci* 5:451. doi: 10.3389/fmars.2018.00451
- PNRNM (2018) Réhabilitation et valorisation de l'étang de Bages-Sigean. In: Les Zones Humides. <http://www.zones-humides.org/agir/retours-experiences/rehabilitation-et-valorisation-de-l039etang-de-bages-sigean>. Accessed 25 Oct 2021
- PNRNM (2021) Observatoire des étangs. In: Parc naturel régional de la Narbonnaise en Méditerranée. <https://www.parc-naturel-narbonnaise.fr/actions-parc/environnement/biodiversite/observatoire-des-etangs>. Accessed 24 Feb 2021
- Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel CV, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013) Global imprint of climate change on marine life. *Nature Clim Change* 3:919–925. doi: 10.1038/nclimate1958
- Poloczanska ES, Burrows MT, Brown CJ, García Molinos J, Halpern BS, Hoegh-Guldberg O, Kappel CV, Moore PJ, Richardson AJ, Schoeman DS, Sydeman WJ (2016) Responses of marine organisms to climate change across oceans. *Front Mar Sci*. doi: 10.3389/fmars.2016.00062
- Prieto L (2018) Diagnosis, Prognosis, and Management of Jellyfish Swarms. In: Chassignet EP, Pascual A, Tintoré J, Verron J (eds) New Frontiers in Operational Oceanography. GODAE OceanView,
- Prieto L, Astorga D, Navarro G, Ruiz J (2010) Environmental control of phase transition and polyp survival of a massive-outbreaker jellyfish. *PLoS ONE* 5:e13793. doi: 10.1371/journal.pone.0013793

- Purcell J (1992) Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. *Mar Ecol Prog Ser* 87:65–76. doi: 10.3354/meps087065
- Purcell J, Atienza D, Fuentes V, Olariaga A, Tilves U, Colahan C (2012a) Temperature effects reproduction rates of scyphozoan species from the northwest Mediterranean Sea. *Hydrobiologia* 88–204. doi: 10.1007/978-94-007-5316-7\_13
- Purcell JE (1984) The functions of nematocysts in prey capture by epipelagic siphonophores (Coelenterata, Hydrozoa). *Biol Bull* 166:310–327. doi: 10.2307/1541219
- Purcell JE (1997) Pelagic cnidarians and ctenophores as predators: Selective predation, feeding rates, and effects on prey populations. *Ann Inst océanogr* 73:125–137.
- Purcell JE (2003) Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Mar Ecol Prog Ser* 16.
- Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *J Mar Biolog Assoc* 85:461–476. doi: 10.1017/S0025315405011409
- Purcell JE (2009) Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia* 616:23–50. doi: 10.1007/s10750-008-9585-8
- Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu Rev Mar Sci* 4:209–235. doi: 10.1146/annurev-marine-120709-142751
- Purcell JE (2018) Of jellyfish, fish, and humans. *ICES Journal of Marine Science* 75:1235–1244. doi: 10.1093/icesjms/fsx250
- Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. In: Purcell JE, Graham WM, Dumont HJ (eds) *Jellyfish Blooms: Ecological and Societal Importance*. Springer Netherlands, Dordrecht, pp 27–44
- Purcell JE, Mills CE (1988) The correlation between nematocyst types and diets in pelagic Hydrozoa. In: Hessinger DA, Lenhoff HM (eds) *The Biology of Nematocysts*. Academic Press, pp 464–483
- Purcell JE, Malej A, Benović A (1999) Potential links of jellyfish to eutrophication and fisheries. In: Malone TC, Malej A, Harding LW, Smolaka N, Turner RE (eds) *Coastal and Estuarine Studies*. American Geophysical Union, Washington, D. C., pp 241–263
- Purcell JE, Breitburg DL, Decker MB, Graham WM, Youngbluth MJ, Raskoff KA (2001) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: A review. In: Rabalais NN, Turner RE (eds) *Coastal and Estuarine Studies*. American Geophysical Union, Washington, D. C., pp 77–100
- Purcell JE, Uye S, Lo W (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar Ecol Prog Ser* 350:153–174. doi: 10.3354/meps07093
- Purcell JE, Fuentes V, Atienza D, Tilves U, Astorga D, Kawahara M, Hays GC (2010) Use of respiration rates of scyphozoan jellyfish to estimate their effects on the food web. *Hydrobiologia* 645:135–152. doi: 10.1007/s10750-010-0240-9
- Purcell JE, Atienza D, Fuentes V, Olariaga A, Tilves U, Colahan C, Gili J-M (2012b) Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. *Hydrobiologia* 690:169–180. doi: 10.1007/s10750-012-1047-7
- QGIS (2020) QGIS Geographic Information System.

- Quiñones J, Monroy A, Acha EM, Mianzan H (2013) Jellyfish bycatch diminishes profit in an anchovy fishery off Peru. *Fish Res* 139:47–50. doi: 10.1016/j.fishres.2012.04.014
- Quiñones J, Mianzan H, Purca S, Robinson KL, Adams GD, Marcelo Acha E (2015) Climate-driven population size fluctuations of jellyfish (*Chrysaora plocamia*) off Peru. *Mar Biol* 162:2339–2350. doi: 10.1007/s00227-015-2751-4
- R Core Team (2020) R: A language and environment for statistical computing.
- Rahi JE, Weeber MP, Serafy GE (2020) Modelling the effect of behavior on the distribution of the jellyfish Mauve stinger (*Pelagia noctiluca*) in the Balearic Sea using an individual-based model. *Ecol Modell* 433:109230. doi: 10.1016/j.ecolmodel.2020.109230
- Ramirez-Romero E, Molinero JC, Paulsen M, Javidpour J, Clemmesen C, Sommer U (2018) Quantifying top-down control and ecological traits of the scyphozoan *Aurelia aurita* through a dynamic plankton model. *J Plankton Res*. doi: 10.1093/plankt/fby041
- Ramondenc S, Ferrieux M, Collet S, Benedetti F, Guidi L, Lombard F (2019) From egg to maturity: a closed system for complete life cycle studies of the holopelagic jellyfish *Pelagia noctiluca*. *J Plankton Res* 41:207–217. doi: 10.1093/plankt/fbz013
- Ramondenc S, Eveillard D, Guidi L, Lombard F, Delahaye B (2020) Probabilistic modeling to estimate jellyfish ecophysiological properties and size distributions. *Sci Rep* 10:6074. doi: 10.1038/s41598-020-62357-5
- Ramšak A, Stopar K, Malej A (2012) Comparative phylogeography of meroplanktonic species, *Aurelia* spp. and *Rhizostoma pulmo* (Cnidaria: Scyphozoa) in European Seas. *Hydrobiologia* 690:69–80. doi: 10.1007/s10750-012-1053-9
- Randone M, Di Carlo G, Constantini M (2017) Reviving the economy of the Mediterranean Sea: Actions for a sustainable future. WWF Mediterranean Marine Initiative, Rome, Italy
- Raoult V, Gaston TF (2018) Rapid biomass and size-frequency estimates of edible jellyfish populations using drones. *Fish Res* 207:160–164. doi: 10.1016/j.fishres.2018.06.010
- Redfield A (1934) On the proportions of organic derivatives in sea water and their relation to the composition of plankton. James Johnstone Memorial Volume, University Press of Liverpool 176–192.
- Regula C, Colin S, Costello J, Kordula H (2009) Prey selection mechanism of ambush-foraging hydromedusae. *Mar Ecol Prog Ser* 374:135–144. doi: 10.3354/meps07756
- Riccio G, Martinez KA, Martín J, Reyes F, D’Ambra I, Lauritano C (2022) Jellyfish as an alternative source of bioactive antiproliferative compounds. *Marine Drugs* 20:350. doi: 10.3390/md20060350
- Richardson AJ (2008) In hot water: zooplankton and climate change. *ICES Journal of Marine Science* 65:279–295. doi: 10.1093/icesjms/fsn028
- Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol Evol* 24:312–322. doi: 10.1016/j.tree.2009.01.010
- Robinson K, Graham W (2014) Warming of subtropical coastal waters accelerates *Mnemiopsis leidyi* growth and alters timing of spring ctenophore blooms. *Mar Ecol Prog Ser* 502:105–115. doi: 10.3354/meps10739
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60. doi: 10.1038/nature01333



- Rosa S, Pansera M, Granata A, Guglielmo L (2013) Interannual variability, growth, reproduction and feeding of *Pelagia noctiluca* (Cnidaria: Scyphozoa) in the Straits of Messina (Central Mediterranean Sea): Linkages with temperature and diet. *J Marine Syst* 111–112:97–107. doi: 10.1016/j.jmarsys.2012.10.001
- Rossi JP (2011) rich: an R package to analyse species richness. *Diversity* 3:112–120.
- Roux J-P, van der Lingen CD, Gibbons MJ, Moroff NE, Shannon LJ, Smith AD, Cury PM (2013) Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fishes: Lessons from the Benguela. *BMS* 89:249–284. doi: 10.5343/bms.2011.1145
- Ruiz J, Prieto L, Astorga D (2012) A model for temperature control of jellyfish (*Cotylorhiza tuberculata*) outbreaks: A causal analysis in a Mediterranean coastal lagoon. *Ecol Modell* 233:59–69. doi: 10.1016/j.ecolmodel.2012.03.019
- Sage RF (2020) Global change biology: A primer. *Glob Change Biol* 26:3–30. doi: 10.1111/gcb.14893
- Salat J, Pascual J (2002) The oceanographic and meteorological station at L'Estartit (NW Mediterranean). Tracking long-term hydrological change in the Mediterranean Sea. *CIESM Workshop Series* 16:29–32.
- Salgado-Hernanz PM, Racault M-F, Font-Muñoz JS, Basterretxea G (2019) Trends in phytoplankton phenology in the Mediterranean Sea based on ocean-colour remote sensing. *Remote Sens Environ* 221:50–64. doi: 10.1016/j.rse.2018.10.036
- Salihoglu B, Fach BA, Oguz T (2011) Control mechanisms on the ctenophore *Mnemiopsis* population dynamics: A modeling study. *J Marine Syst* 87:55–65. doi: 10.1016/j.jmarsys.2011.03.001
- Salon S, Cossarini G, Bolzon G, Feudale L, Lazzari P, Teruzzi A, Solidoro C, Crise A (2019) Novel metrics based on Biogeochemical Argo data to improve the model uncertainty evaluation of the CMEMS Mediterranean marine ecosystem forecasts. *Ocean Science* 15:997–1022. doi: 10.5194/os-15-997-2019
- Sánchez-Hernández J, Nunn AD, Adams CE, Amundsen P-A (2019) Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models: Ontogenetic dietary shifts. *Biol Rev* 94:539–554. doi: 10.1111/brv.12468
- Sandonnini J, Del Pilar Ruso Y, Cortés Melendreras E, Barberá C, Hendriks IE, Kersting DK, Giménez Casalduero F (2021) The emergent fouling population after severe eutrophication in the Mar Menor coastal lagoon. *Reg Stud Mar* 44:101720. doi: 10.1016/j.rsma.2021.101720
- Sanford E (1999) Regulation of keystone predation by small changes in ocean temperature. *Science* 283:2095–2097. doi: 10.1126/science.283.5410.2095
- Sanz-Martín M, Pitt KA, Condon RH, Lucas CH, Santana CN de, Duarte CM (2016) Flawed citation practices facilitate the unsubstantiated perception of a global trend toward increased jellyfish blooms. *Glob Ecol Biogeogr* 25:1039–1049. doi: 10.1111/geb.12474
- Schaub J, Hunt B, Pakhomov E, Holmes K, Lu Y, Quayle L (2018) Using unmanned aerial vehicles (UAVs) to measure jellyfish aggregations. *Mar Ecol Prog Ser* 591:29–36. doi: 10.3354/meps12414
- Schiariti A, Kawahara M, Uye S, Mianzan HW (2008) Life cycle of the jellyfish *Lychnorhiza lucerna* (Scyphozoa: Rhizostomeae). *Mar Biol* 156:1–12. doi: 10.1007/s00227-008-1050-8
- Schnurr REJ, Walker TR (2019) Marine Transportation and Energy Use. In: Reference Module in Earth Systems and Environmental Sciences. Elsevier,

- Schultz CB, Brown LM, Pelton E, Crone EE (2017) Citizen science monitoring demonstrates dramatic declines of monarch butterflies in western North America. *Biol Conserv* 214:343–346. doi: 10.1016/j.biocon.2017.08.019
- Shaltout M, Omstedt A (2014) Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. *Oceanologia* 56:411–443. doi: 10.5697/oc.56-3.411
- Sharma S, Jackson DA, Minns CK, Shuter BJ (2007) Will northern fish populations be in hot water because of climate change? *Glob Change Biol* 13:2052–2064.
- Shiganova T, Nival P, Carlotti F, Alekseenko E (2017) Demographic modelling approach for assessment of environmental conditions which control the population of the invasive Ctenophore *Mnemiopsis leidyi* in the Mediterranean Seas. In: EGU General Assembly. Wien, Austria,
- Shiganova TA, Alekseenko E, Lidia M, Paul N (2018) Modelling assessment of interactions in the Black Sea of the invasive ctenophores *Mnemiopsis leidyi* and *Beroe ovata*. *Ecol Model* 376:1–14. doi: 10.1016/j.ecolmodel.2018.02.008
- Shoji J, Kudoh T, Takatsuji H, Kawaguchi O, Kasai A (2010) Distribution of moon jellyfish *Aurelia aurita* in relation to summer hypoxia in Hiroshima Bay, Seto Inland Sea. *Estuar Coast Shelf Sci* 86:485–490. doi: 10.1016/j.ecss.2009.03.001
- Siapatis A, Giannoulaki M, Valavanis VD, Palialexis A, Schismenou E, Machias A, Somarakis S (2008) Modelling potential habitat of the invasive ctenophore *Mnemiopsis leidyi* in Aegean Sea. In: Valavanis VD (ed) *Essential Fish Habitat Mapping in the Mediterranean*. Springer Netherlands, Dordrecht, pp 281–295
- Sieracki C, Sieracki M, Yentsch C (1998) An imaging-in-flow system for automated analysis of marine microplankton. *Mar Ecol Prog Ser* 168:285–296. doi: 10.3354/meps168285
- Sötje I, Dishon T, Hoffmann F, Holst S (2017) New methods of morphometric analyses on scyphozoan jellyfish statoliths including the first direct evidence for statolith growth using calcein as a fluorescent marker. *Microsc Microanal* 23:553–568. doi: 10.1017/S1431927617000344
- Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine Ecoregions of the World: A bioregionalization of coastal and shelf areas. *BioScience* 57:573–583. doi: 10.1641/B570707
- Sparre P, Venema SC (1998) *Introduction to tropical fish stock assessment - Part 1: Manual*. FAO, Rome, Italy
- Spot the Jellyfish (2012) Spot the Jellyfish. <https://oceania.research.um.edu.mt/jellyfish/>.
- Stabili L, Rizzo L, Fanizzi F, Angilè F, Del Coco L, Girelli C, Lomartire S, Piraino S, Basso L (2018) The jellyfish *Rhizostoma pulmo* (Cnidaria): biochemical composition of ovaries and antibacterial lysozyme-like activity of the oocyte lysate. *Mar Drugs* 17:17. doi: 10.3390/md17010017
- Stegert C, Kreuz M, Carlotti F, Moll A (2007) Parameterisation of a zooplankton population model for *Pseudocalanus elongatus* using stage durations from laboratory experiments. *Ecol Modell* 206:213–230.
- Strauss RE (1979) Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Trans Am Fish Soc* 108:344–352.
- Sugiura Y (1964) On the life-history of Rhizostome medusae. *Embryologia* 8:223–233. doi: 10.1111/j.1440-169X.1964.tb00200.x
- Sugiura Y (1966) On the life-history of Rhizostome medusae IV. *Cephea cephea*. *Embryologia* 9:105–122. doi: 10.1111/j.1440-169X.1966.tb00219.x

- Sun S, Zhang F, Li C, Wang S, Wang M, Tao Z, Wang Y, Zhang G, Sun X (2015) Breeding places, population dynamics, and distribution of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in the Yellow Sea and the East China Sea. *Hydrobiologia* 754:59–74. doi: 10.1007/s10750-015-2266-5
- Sunday JM, Bates AE, Dulvy NK (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proc R Soc B* 278:1823–1830. doi: 10.1098/rspb.2010.1295
- Syazwan WM, Then AY-H, Chong VC, Rizman-Idid M (2021) Trophic ecology of a tropical scyphozoan community in coastal waters: Insights from stomach content and stable isotope analyses. *Cont Shelf Res* 225:104481. doi: 10.1016/j.csr.2021.104481
- Thiel ME (1966) Untersuchungen über die Herkunft, das Auftreten, das Wachstum und die Fortpflanzung von *Rhizostoma octopus* L. Ag. im Elbmündungsgebiet. *Abh Verh Naturw Ver Hamburg NF* 10:59–88.
- Tinta T, Kogovšek T, Malej A, Turk V (2012) Jellyfish modulate bacterial dynamic and community structure. *PLoS ONE* 7:e39274. doi: 10.1371/journal.pone.0039274
- TNC (2019) Geospatial Conservation Atlas. <https://geospatial.tnc.org/>.
- Toggweiler J, Russell J (2008) Ocean circulation in a warming climate. *Nature* 451:286–288. doi: <https://doi.org/10.1038/nature06590>
- Torniainen J, Lehtiniemi M (2008) Potential predation pressure of littoral mysids on herring (*Clupea harengus membras* L.) eggs and yolk-sac larvae. *J Exp Mar Biol Ecol* 367:247–252. doi: 10.1016/j.jembe.2008.10.007
- Trégouboff G, Rose M (1978) Manuel de planctonologie méditerranéenne, CNRS. France
- Treible LM, Condon RH (2019) Temperature-driven asexual reproduction and strobilation in three scyphozoan jellyfish polyps. *J Exp Mar Biol Ecol* 520:151204. doi: 10.1016/j.jembe.2019.151204
- Tulloch AIT, Possingham HP, Joseph LN, Szabo J, Martin TG (2013) Realising the full potential of citizen science monitoring programs. *Biol Conserv* 165:128–138. doi: 10.1016/j.biocon.2013.05.025
- Turk V, Lučić D, Flander-Putrl V, Malej A (2008) Feeding of *Aurelia* sp. (Scyphozoa) and links to the microbial food web. *Mar Ecol* 29:495–505. doi: 10.1111/j.1439-0485.2008.00250.x
- Turley C, Bianchi M, Christaki U, Conan P, Harris J, Psarra S, Ruddy G, Stutt E, Tselepidis A, Van Wambeke F (2000) Relationship between primary producers and bacteria in an oligotrophic sea-the Mediterranean and biogeochemical implications. *Mar Ecol Prog Ser* 193:11–18. doi: 10.3354/meps193011
- United Nations (2017) World Population Prospects: The 2017 Revision.
- Uye S (1982) Length-weight relationships of important zooplankton from the Inland Sea of Japan. *OSJaJ* 38:149–158. doi: 10.1007/BF02110286
- Uye S (2008) Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian Marginal Seas. *Plankton Benthos Res* 3:125–131. doi: 10.3800/pbr.3.125
- Uye S (2011) Human forcing of the copepod–fish–jellyfish triangular trophic relationship. *Hydrobiologia* 666:71–83. doi: 10.1007/s10750-010-0208-9
- Uye SI, Brodeur RD (2017) Report of Working Group 26 on jellyfish blooms around the North Pacific rim: Causes and consequences. PICES, Sidney, British Columbia Canada.
- Vales DG, Saporiti F, Cardona L, De Oliveira LR, Dos Santos RA, Secchi ER, Aguilar A, Crespo EA (2014) Intensive fishing has not forced dietary change in the South American fur seal *Arctophoca* (= *Arctocephalus*) *australis* off Río de la Plata and adjoining areas. *Aquat Conserv* 24:745–759. doi: 10.1002/aqc.2397

- van der Molen J, van Beek J, Augustine S, Vansteenbrugge L, van Walraven L, Langenberg V, van der Veer HW, Hostens K, Pitois S, Robbens J (2015) Modelling survival and connectivity of *Mnemiopsis leidyi* in the south-western North Sea and Scheldt estuaries. *Ocean Sci* 11:405–424. doi: 10.5194/os-11-405-2015
- Van Walraven L, Langenberg VT, Dapper R, Witte JIJ, Zuur AF, van der Veer HW (2015) Long-term patterns in 50 years of scyphomedusae catches in the western Dutch Wadden Sea in relation to climate change and eutrophication. *J Plankton Res* 37:151–167. doi: 10.1093/plankt/fbu088
- Vargas-Yáñez M, Jesús García M, Salat J, García-Martínez MC, Pascual J, Moya F (2008) Warming trends and decadal variability in the Western Mediterranean shelf. *Glob Planet Change* 63:177–184. doi: 10.1016/j.gloplacha.2007.09.001
- Vélez-Rubio GM, Cardona L, López-Mendilaharsu M, Martínez Souza G, Carranza A, González-Paredes D, Tomás J (2016) Ontogenetic dietary changes of green turtles (*Chelonia mydas*) in the temperate southwestern Atlantic. *Mar Biol* 163:57. doi: 10.1007/s00227-016-2827-9
- Violic I, Kogovšek T, Pestorić B, Mačić V, Milić Beran I, Lučić D (2019) Recent changes (2013–2017) in scyphomedusan fauna in the Boka Kotorska Bay, Montenegro (Southeast Adriatic). *Acta Adriat* 60:25–39. doi: 10.32582/aa.60.1.2
- Violic I, Lučić D, Bojanić N, Pestorić B, Zovko BG, Onofri I, Hure M (2022) Long-term monitoring of carnivorous gelatinous macrozooplankton in the area of Dubrovnik-Neretva county (Croatia). *Naše more* 69:22–29. doi: 10.17818/NM/2022/1.4
- Vodopivec M, J Peliz Á, Malej A (2017) Offshore marine constructions as propagators of moon jellyfish dispersal. *Environ Res Lett* 12:084003. doi: 10.1088/1748-9326/aa75d9
- Wagner Z, Costello JH, Colin SP (2020) Fluid and predator-prey onteractions of scyphomedusae fed Calanoid copepods. *Fluids* 5:60. doi: 10.3390/fluids5020060
- Wang P, Zhang F, Liu M, Sun S, Xian H (2020) Isotopic evidence for size-based dietary shifts in the jellyfish *Cyanea nozakii* in the northern East China Sea. *J Plankton Res* 1–13. doi: 10.1093/plankt/fbaa042
- West EJ, Pitt KA, Welsh DT, Koop K, Rissik D (2009) Top-down and bottom-up influences of jellyfish on primary productivity and planktonic assemblages. *Limnol Oceanogr* 54:2058–2071. doi: <https://doi.org/10.4319/lo.2009.54.6.2058>
- Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis, 2nd edn. Springer International Publishing
- Widmer CL (2005) Effects of temperature on growth of north-east Pacific moon jellyfish ephyrae, *Aurelia labiata* (Cnidaria: Scyphozoa). *J Mar Biolog Assoc* 85:569–573. doi: 10.1017/S0025315405011495
- Willcox S, Moltschaniwskyj NA, Crawford CM (2008) Population dynamics of natural colonies of *Aurelia* sp. scyphistomae in Tasmania, Australia. *Mar Biol* 154:661–670. doi: 10.1007/s00227-008-0959-2
- Wolkovich EM, Cook BI, Davies TJ (2014) Progress towards an interdisciplinary science of plant phenology: building predictions across space, time and species diversity. *New Phytol* 201:1156–1162. doi: 10.1111/nph.12599
- Wukovits J, Bukenberger P, Enge AJ, Gerg M, Wanek W, Watzka M, Heinz P (2018) Food supply and size class depending variations in phytodetritus intake in the benthic foraminifer *Ammonia tepida*. *Biology Open* bio.030056. doi: 10.1242/bio.030056
- WWF (2014) Informe Planeta Vivo 2014. WWF, España

- Xie C, Fan M, Kang Y (2021) Population dynamics of the giant jellyfish *Nemopilema nomurai* with age structure. *Ecol Model* 441:109412. doi: 10.1016/j.ecolmodel.2020.109412
- Yan HF, Kyne PM, Jabado RW, Leeney RH, Davidson LNK, Derrick DH, Finucci B, Freckleton RP, Fordham SV, Dulvy NK (2021) Overfishing and habitat loss drive range contraction of iconic marine fishes to near extinction. *Sci Adv* 7:eabb6026. doi: 10.1126/sciadv.abb6026
- Yebra L, Bonnet D, Harris R, Lindeque P, Peijnenburg K (2011) Barriers in the pelagic: population structuring of *Calanus helgolandicus* and *C. euxinus* in European waters. *Mar Ecol Prog Ser* 428:135–149. doi: 10.3354/meps09056
- Young GA, Hagadorn JW (2010) The fossil record of cnidarian medusae. *Palaeoworld* 19:212–221. doi: 10.1016/j.palwor.2010.09.014
- Youssef J, Keller S, Spence C (2019) Making sustainable foods (such as jellyfish) delicious. *Int J Gastron Food Sci* 16:100141. doi: 10.1016/j.ijgfs.2019.100141
- Zahn VM (1981) Wie alt koennen Scyphomedusen werden? *Zoologische Beiträge* 27:491–495.
- Zaitsev IP, Mamaev VO (1997) Marine biological diversity in the Black Sea: a study of change and decline. United Nations Publications, New York
- Zenetos A, Koutsogiannopoulos D, Ovalis P, Poursanidis D (2013) The role played by citizen scientists in monitoring marine alien species in Greece. *Cah Biol Mar* 54:419–426.
- Zhang F, Sun S, Jin X, Li C (2012) Associations of large jellyfish distributions with temperature and salinity in the Yellow Sea and East China Sea. *Hydrobiologia* 690:81–96. doi: 10.1007/s10750-012-1057-5