Lara Colaço Martins

Modelling the occurrence of *Physalia physalis* in the North Atlantic Ocean at different spatial and temporal scales

Universidade do Algarve

Faculdade de Ciências e Tecnologia

2021-2022

Lara Colaço Martins

Modelling the occurrence of *Physalia physalis* in the North Atlantic Ocean at different spatial and temporal scales

Mestrado em Biologia Marinha

Supervisor
Jorge Assis
Co-supervisor
José Nuno Gomes-Pereira

Universidade do Algarve

Faculdade de Ciências e Tecnologia

2021-2022

Declaração de autoria de trabalho

Modelling the occurrence of *Physalia physalis* in the North Atlantic Ocean at different spatial and temporal scales

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

Abstract

Frequent jellyfish blooms cause human health issues and closures of coastal areas, impacting different economic sectors like tourism, fisheries, aquaculture farms and industry. Understanding the drivers of jellyfish bloom and predicting their occurrence is therefore essential to develop effective management plans. The Portuguese Man-of-War (*Physalia physalis)* is a dangerous cosmopolitan siphonophore and its ecology remains largely understudied. The objective of this study is to understand the main environmental drivers (e.g., temperature, productivity, wind and ocean patterns) that explain the occurrence of *P. physalis* at a macroecological scale (the North Atlantic Ocean) and at a regional scale (Faial Island from the Azores archipelago), and to predict its distribution and temporal trends. We implemented machine learning modelling that fed on high-resolution environmental data and occurrence data describing its distribution in the North Atlantic Ocean and long-term temporal variability in the Faial Island (Azores). Models retrieved high accuracy scores and showed that the distribution of *P. physalis* is mainly explained by primary productivity, temperature and currents direction at the macroecological scale and by primary productivity and wind patterns at the regional scale. The models also showed a higher probability of occurrence on both Atlantic coasts and offshore North-northwest Atlantic. Models fed on temporal datasets demonstrate decadal fluctuations rather than significant increases over time, contradicting the previously established hypothesis that jellyfish blooms are increasing. By using species distribution modelling, we provide a better understanding on how environmental variability shapes the occurrence of *P. physalis* at different spatial and temporal scales (macroecological and regional), which can be considered in management plans and policies. In the future, projected global warming and decreased primary productivity in the North Atlantic may cause significant poleward shifting of this species, adversely affecting human health, socioeconomics and ecosystems in regions not currently used to deal with such impacts.

Resumo

Os frequentes *blooms* de medusas causam problemas de saúde humana e encerramentos de zonas costeiras, que têm impactos em diferentes sectores económicos como o turismo, pescas, explorações aquícolas e indústria. Compreender quais os factores ambientais que levam aos *blooms* de medusas e prever a sua ocorrência é, portanto, essencial para desenvolver planos de gestão eficazes. A caravela portuguesa (*Physalia physalis*) é um perigoso sifonóforo cosmopolita com um pneumatóforo flutuante e longos tentáculos com células urticantes cuja ecologia permanece pouco estudada. O objetivo deste estudo é compreender os principais fatores ambientais (por exemplo, temperatura, produtividade, vento e padrões oceânicos) que explicam a ocorrência da *P. physalis* à escala macroecológica (o Oceano Atlântico Norte) e à escala regional (Ilha do Faial do arquipélago dos Açores), e prever a sua distribuição e tendências temporais. Implementámos modelos de *machine learning* que se alimentam de dados ambientais de alta resolução e dados de ocorrência descrevendo a sua distribuição no Oceano Atlântico Norte e a variabilidade temporal a longo prazo na Ilha do Faial (Açores). Os modelos de alta precisão e mostraram que a distribuição de *P. physalis* é principalmente explicada pela produtividade primária, temperatura e direção das correntes à escala macroecológica e pela produtividade primária e padrões de vento à escala regional. Os modelos também mostraram uma maior probabilidade de ocorrência da espécie na costa e região Norte-noroeste do Atlântico Norte. Os modelos alimentados com conjuntos de dados temporais demonstram flutuações decadais em vez de aumentos significativos ao longo do tempo, contradizendo a hipótese previamente estabelecida de que os *blooms* de medusas estão a aumentar. Ao modelar a distribuição da espécie, fornecemos uma melhor compreensão de como a variabilidade ambiental molda a ocorrência de *P. physalis* em diferentes escalas espaciais e temporais (macroecológicas e regionais), o que pode ser considerado em planos e políticas de gestão. No futuro, o aquecimento global projetado e a diminuição da produtividade primária no Atlântico Norte podem causar deslocamentos significativos desta espécie em direção ao pólo, afetando negativamente a saúde humana, a socioeconómica e os ecossistemas em regiões que atualmente não estão habituadas a lidar com tais impactos.

Resumo Estendido

As medusas são conhecidas pelo seu carácter urticante assim como por *blooms* rápidos e extensos que podem ter numerosas consequências negativas para os ecossistemas marinhos, incluindo impactos nas teias tróficas e em processos bioquímicos. Os *blooms* também impactam atividades socioeconómicas como o turismo, a pesca, a aquacultura e o sector industrial.

Na ecologia, a compreensão dos padrões e processos que regulam a distribuição das espécies é a chave para o desenvolvimento de princípios de gestão ambiental. Para desenvolver modelos de previsão necessários à gestão, e adequados ao contexto das alterações climáticas, é necessário estabelecer uma ligação entre as diferentes escalas. As escalas restringem diferentes padrões ecológicos, pois numa escala mais fina são encontrados diferentes padrões do que a uma escala macroecológica. Assim, estes processos podem ser mal interpretados por razões de perspetiva. No presente estudo, serão investigados quais os fatores que melhor explicam a ocorrência de *Physalia physalis*, através de modelação ecológica desenvolvida a escalas espaciais e temporais contrastantes – macroecológicas e regionais (o Oceano Atlântico Norte e a Ilha do Faial do arquipélago dos Açores), e prever a sua distribuição e tendências temporais. *Physalia physalis* ou caravela portuguesa é um sifonóforo pleustónico. Apesar de a *P. physalis* ser uma espécie conspícua e cosmopolita, o conhecimento sobre a sua ecologia e comportamento continua bastante limitado. Existe uma lacuna de conhecimento acerca dos fatores que atuam a diferentes escalas nesta espécie e é importante saber o que mais influencia as ocorrências e sob que condições estas aparecem. Devido à sua natureza perigosa, é muito importante saber mais sobre a espécie e prever este tipo de acontecimentos no futuro.

Os principais objetivos deste trabalho são (1) compreender os principais fatores ambientais responsáveis pela ocorrência de *P. physalis* à escala macroecológica (Oceano Atlântico) e regional (Ilha do Faial no arquipélago dos Açores) e (2) prever a ocorrência de *P. physalis* às escalas espaciais e temporais. Este trabalho serve para melhorar o conhecimento ecológico de *P. physalis* e fornecer linhas de base para ações de conservação e gestão, especialmente face a futuras alterações climáticas, uma vez que o aquecimento dos oceanos pode beneficiar a ocorrência da espécie.

Neste estudo, modelos de *machine learning* foram alimentados com dados ambientais de alta resolução e dados de ocorrência. Para uma abordagem à escala macroecológica, os

dados de ocorrência no Atlântico Norte foram obtidos a partir de repositórios de biodiversidade online e literatura disponível e os dados ambientais foram obtidos a partir do repositório Bio-ORACLE. Para uma abordagem à escala regional, foram considerados conjuntos de dados a longo prazo de observações de *P. physalis* na Ilha do Faial fornecidos pela associação sem fins lucrativos Atlantic Naturalist (AtlanticNaturalist.org). Para esta abordagem foram recolhidos dados ambientais do Copernicus Marine and Environment Monitoring Service (CMEMS). De forma a percebermos quais os preditores ambientais mais adequados para treinar o modelo, comparámos os dados dos padrões oceânicos com o dos padrões dos ventos, e os dados da produtividade primária com os de fitoplâncton. Selecionámos os preditores a serem usados no treino do modelo e avaliámos o seu desempenho. O modelo à escala macroecológica permitiu a previsão da ocorrência da espécie, através da produção de mapas, de acordo com as condições ambientais no Atlântico Norte. À escala regional, foi prevista uma série temporal de ocorrência de *P. physalis*, utilizando a probabilidade média de ocorrência.

Os modelos de distribuição da espécie, com elevada precisão, mostraram que diferentes fatores atuavam a diferentes escalas. À escala macroecológica, a distribuição da espécie é principalmente regulada pela produtividade primária e pela temperatura e, com menos significância, pela direção das correntes. À escala regional, a distribuição é regulada pelos padrões de vento, pela produtividade primária e, com menos significância, a localização da amostragem. Isto corrobora estudos anteriores que demonstraram que as correntes e ventos são os fatores que melhor explicam a distribuição desta espécie. Pela primeira vez, o presente estudo realça o papel da produtividade primária. Para a escala regional o modelo previu a direção da origem dos ventos como sendo de Sudoeste, Sul-Sudoeste, Oeste e Norte. Estas são as regiões proximais com maior probabilidade de ocorrência da espécie a nível macroecológico (região Norte-Noroeste do Oceano Atlântico). Esta maior probabilidade de ocorrência pode ser devida à localização geográfica das correntes oceânicas: a corrente do Golfo dá origem à corrente dos Açores, que, pode transportar a caravela portuguesa até ao arquipélago através de um transporte de latitudes inferiores. Foi, também, possível compreender quais as áreas mais adequadas para a espécie, tanto em ambas as costas atlânticas, como em mar aberto, na região Norte-Noroeste do Atlântico, onde a água é quente e produtiva. Foi possível reconstruir uma série temporal à escala regional que mostrou uma elevada variabilidade temporal, com maior

probabilidade de ocorrência nos períodos de 1996-1999, 2002-2004 e anos recentes. Foram também encontrados padrões de sazonalidade de maior ocorrência da espécie entre março e outubro. Os resultados mostraram a importância da temperatura e da produtividade primária à escala global e regional para a ocorrência da espécie.

O aumento da temperatura da água do mar tem várias consequências no ciclo de vida das espécies, acelera o crescimento e desenvolvimento das medusas, promove a estratificação da coluna de água. Leva a mudanças na teia alimentar e à expansão e deslocação da distribuição de medusas em direção aos pólos. Isto aumenta a possibilidade de que haja uma maior incidência de impactos. Prevê-se que a produtividade primária diminua no futuro como consequência do aquecimento global antropogénico, quer a nível do Atlântico Norte, quer a nível global. Dito isto, é de esperar que no futuro a temperatura aumente e a produtividade primária diminua no Atlântico Norte. A espécie é mais suscetível de ocorrer quanto maior for o aumento tanto da temperatura como da produtividade. É possível inferir que no futuro a espécie poderá ter maior ocorrência em latitudes mais elevadas, porque acompanhará a diminuição da produtividade e deslocar-se-á para o Norte. Estas mudanças terão efeitos negativos num futuro próximo. Esta informação, até agora desconhecida, é crucial para a ecologia, mas também como linha de base para orientar as ações de gestão. Particularmente face às futuras alterações climáticas, uma vez que o aquecimento dos oceanos parece beneficiar a ocorrência desta espécie. Assim, será necessário compreender melhor como a variabilidade ambiental regula a ocorrência da *P. physalis* e considerar políticas de gestão a curto e longo prazo, devido aos grandes impactos socioeconómicos e sanitários que esta espécie tem.

Keywords: *Physalia physalis*, species distribution modelling, climate change, jellyfish blooms, drivers

Acknowledgments

To all volunteers from AtlanticNaturalist.org that have been monitoring *Physalia physalis*, in the Azores, as well as several staff of Naturalist - Science and Tourism, under project MONIJELLY. To Gisela and José Nuno, for the data, the photos, the opportunity. Without you none of this would have been possible. Thank you for giving me the opportunity to know the world of jellyfish, especially the Portuguese Man-of-War.

To Professor Rita, for the moral support and the wake-up calls at the perfect time. Thank you for helping me to keep the initial planning, since I had such a "tight" deadline.

To Professor Jorge, for giving me, this challenge. I did exactly what I wanted to do, learn more about ecological modelling and not only that, the world of jellies and everything around it. I learned a lot, so thank you very much.

Thank you to the *Bentastic* team, who will be greatly missed. You always gave me the strength and motivation I needed, you never let me give up. You gave me the time I needed to write. You guys were great, thank you all.

To my friends for all their support and dedication, for giving me constructive criticism and strength.

To my family who got to know that the Portuguese Man-of-War is not a “real” jellyfish, who so often heard me talk about "maps" and "code". They also understood that I was annoyed when the code "didn't run" without knowing exactly what it was doing on my computer. Thank you for the support, for the ready-made snacks, for the "how's that thesis coming along?" and for the "you can always finish it tomorrow". You were all very important in this great journey, each one in his or her own way. For this, I have only you to thank.

To João, you were undoubtedly my great support, psychological, emotional and also computer support. For listening to me complaining and “speaking in biology” and even so you knew what I needed. Thank you for always being with me and encouraging me, for believing in me when I myself did not.

List of abbreviations

BRT – Boosted regression trees

CMEMS - Copernicus Marine and Environment Monitoring Service

ENSO - El Niño Southern Oscillation

GBIF - Global Biodiversity Information Facility

iDigBio - Integrated Digitized Biocollections

JeDI - Jellyfish Database Initiative

NAC – North Atlantic Current

NAO – North Atlantic Oscillation

NPP – Net primary productivity

OBIS - Ocean Biodiversity Information System

TSS - True skill statistics

List of tables

List of figures

Table of contents

Chapter 1

General Introduction

Jellyfish impacts and their consequences for humans

Jellyfish, here referred to all gelatinous zooplankton taxa, including the medusae and ctenophores, are known for rapid and extensive blooms (Purcell, 2005) that can have numerous negative consequences for marine ecosystems, impacting food webs and biochemical processes. These blooms also cause socio-economic disruptions in tourism, fisheries, aquaculture and the industry sector. Jellyfish can be dangerous to humans due to the venom released by their nematocysts, capsule-like organelle that opens when touched (Fautin, 2009; Geetha et al., 2019) (Figure 1.1), which can produce several kinds of symptoms (Figure 1.2) including gastrointestinal, muscular, cardiac, neurological, allergic and can even be fatal (Cegolon et al., 2013). They interact negatively with fisheries through predation and competition: leading to desynchronization in the feeding periods of the juveniles' stocks and a decrease in the survival of fish communities (Lynam et al., 2004; Tilves et al., 2016). Large species of jellyfish clogged and burst the set-nets of fishers which affected fishing efficiency, could damage the gear (Conley & Sutherland, 2015) and deteriorate the catches (Bosch-Belmar et al., 2021). In the aquaculture farms, jellyfish can cause damage to caged fish (Licandro et al., 2010), producing skin and gill injuries, or even death due to vectors of pathogens (Bosch-Belmar et al., 2016, 2021). There is interspecific competition for nutrition, resulting in high production mortality rates (Mghili et al., 2021), pen's clogging, interrupted water circulation (Bosch-Belmar et al., 2021) and high cleaning costs (Graham et al., 2014). The industry sector could also be affected by jellyfish blockage of water pipe systems, decreasing its productivity, or even interrupting power and freshwater production (Graham et al., 2014; Purcell, 2005) (Figure 1.3).

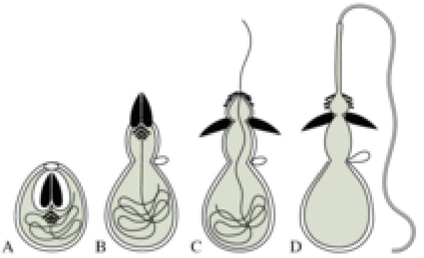


Figure 1.1 - Discharge mechanism of a nematocyst, different stages. Source: Wikipedia.

Figure 1.2 - Jellyfish sting. Source: Jornal de Notícias accessed on 29/07/2022.

Figure 1.3 - Jellyfish impacts in society: A)Beach full of stranded Portuguese Man-of-War, Azores (source: Jovens reporters para o ambiente at https://jra.abae.pt/ accessed on 29/07/2022; photo: João Furtado); B)Nemopilema nomurai clogging fish net, coast of Japan (from: Condon et al. 2012; photo: Schin-ichi Uye); C)Jellyfish barrier to prevent them from being present on aquaculture farms (source: www.ribolanetting.com accessed on 29/07/2022); D) Jellyfish blockage of water pipe system (source: The Guardian, accessed on 29/07/2022; photo: Jack Guez).

Lack of available data and a matter of perception

A present-day concern regarding climate change is the degradation of the oceans' health and its consequences in the increasing abundance of jellyfish. This is a relevant problem with no consensual answer. The lack of long-term temporal records makes it difficult to analyse jellyfish abundance over time (Canepa et al., 2020; Condon et al., 2012; Mills, 2001; Purcell, 2005). Condon et al., (2012) even stats that it is a question based on "perception". Currently, the effort of recording gelatinous zooplankton has grown exponentially, with the scientific community involved, but also the general public. Some studies show jellyfish species increasing in abundance in different parts of the world, but also few species declining due to ecological or human-related causes (Edelist et al., 2021; Mills, 2001). These changes in abundance could be a consequence of environmental variability driven by climate change (bottom-up trophic chain control) (Condon et al., 2012, 2013) rather than a consequence of high levels of fishing pressure (top-down trophic chain control) (Gibbons & Richardson, 2008). However, it remains difficult to identify the specific drivers of jellyfish increases in abundance due to the large complexity of ecosystems (Purcell, 2005).

Climate change and its consequences in jellyfish blooms

There is consensus that environmental changes in the ocean are a cumulative effect of anthropogenic effects (Brotz et al., 2012; Mills, 2001) and their presence will have consequences for the environment and society (Condon et al., 2012). It is known that jellyfish blooms can be promoted by several situations: climate change, overfishing, eutrophication, translocations and habitat modification (Figure 1.4 and 1.5). Climate change and all its consequences, e.g., rising temperatures, ocean acidification, and changing circulation patterns are the environmental and ecosystem precursors to the increase in jellyfish abundance. The rising of sea water temperatures has consequences in the species' life cycle, their expansion to higher latitudes and it promotes water column stratification. Warmer temperatures will alter the synchronicity of fish larvae with its planktic prey, accelerate medusae growth and development, and change the timing and duration of life stages (Purcell et al., 2007). Strobilation - a form of asexual reproduction - may no longer be seasonal and begins to take place over a longer period of time. Water column stratification favours jellyfish over fish, because they can better survive and thrive in low oxygen concentration areas. Stratification will also lead to nutrient-poor surface waters and reduced levels of primary and secondary production (Gibbons & Richardson, 2008). This will act as a change in the food web. The primary

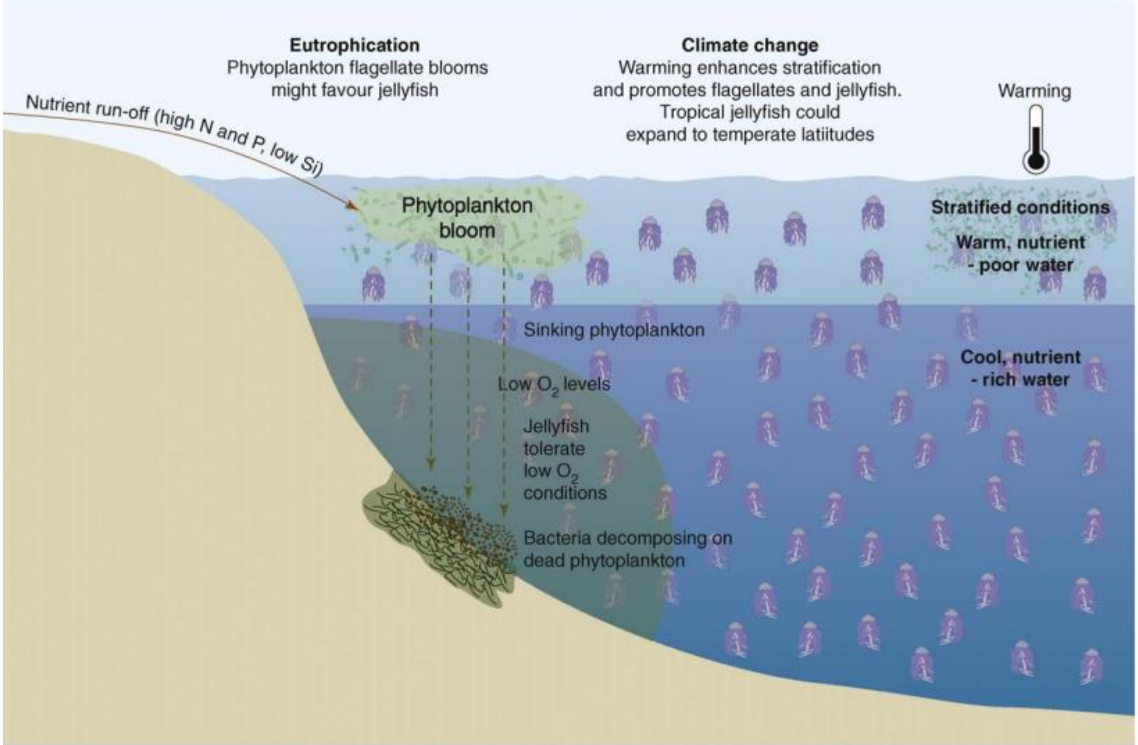


Figure 1.4 - Impacts of climate change, eutrophication and its consequences in jellyfish blooms. From Richardson et al. (2009).

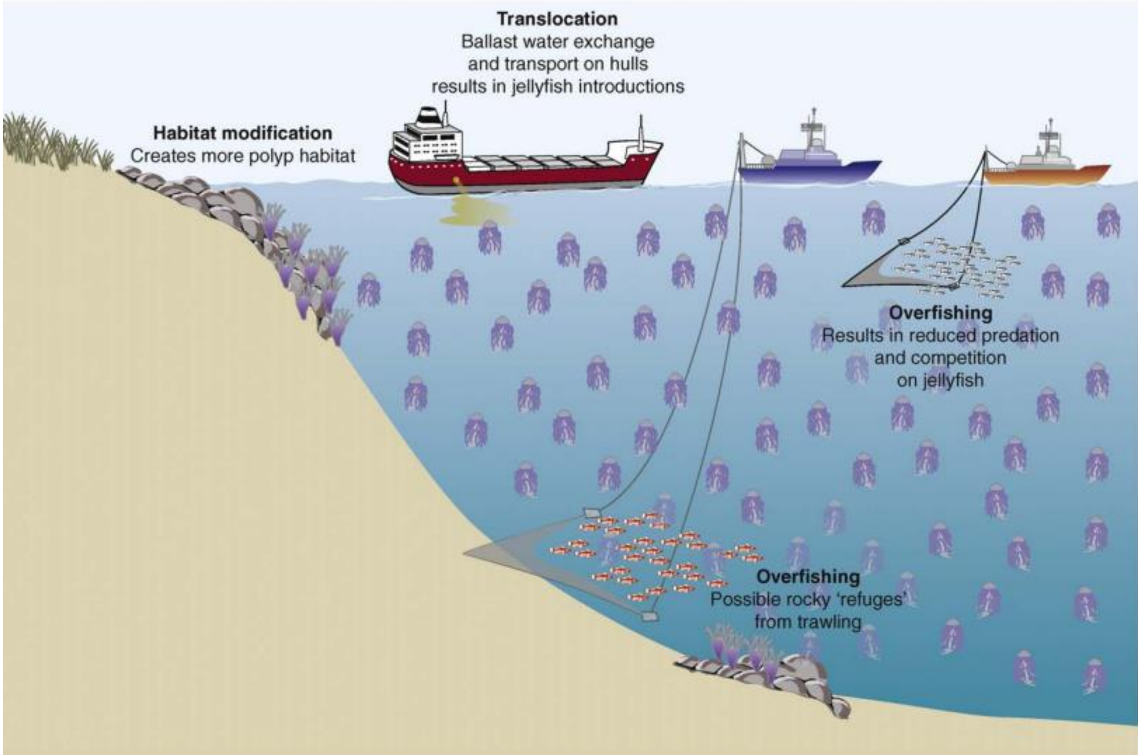


Figure 1.5 - Impacts of overfishing, translocation and habitat modification. From Richardson et al. (2009).

producers will be replaced by flagellates in these conditions. They can migrate vertically to more nutrient rich waters and outcompete diatoms. Flagellates are the dominant primary producers that lead to the production of jellyfish and ctenophores. These trophic chains are considered "low-energy", as opposed to the ones initiated by diatoms that supports fish production (Parsons & Lalli, 2002; Purcell, 2005). Another consequence of rising temperatures is the potential expansion of jellyfish to higher latitudes (Purcell, 2005; Richardson et al., 2009). Ocean acidification due to the increase of dissolved carbon dioxide can also benefit jellyfish indirectly (Attrill et al., 2007), by declining the conditions on calcifying plankton. This leads to more ecological space for jellyfish. However, the acidification can also affect them negatively: some jellyfish have calcium carbonate statoliths used for orientation which could be affected due to the reducing pH (Richardson et al., 2009). Although there is no scientific consensus on this subject. Altered circulation patterns could be a consequence of climate change that leads to fluctuations in jellyfish abundance (Lynam et al., 2004). NAO Index (North Atlantic Oscillation) represents local changes in winds, circulations patterns (e.g. North Atlantic Current - NAC) and temperatures. It has an influence on the abundance and distribution of various species, from phytoplankton to macrofauna (Gibbons & Richardson, 2008). However, there is still no consensus about the relationship of these variations to the overall increase in jellyfish. Some studies found a negative correlation between jellyfish abundance and NAO index (Lynam et al., 2004), others found a positive one (Attrill et al., 2007) or even no significant link (Gibbons & Richardson, 2008). On the other hand, El Niño Southern Oscillation (ENSO) dynamics, which causes significant changes in the distribution of the surface water temperature of the Pacific Ocean, was the cause for *P. physalis* stranding in Chile (Canepa et al., 2020).

Human activities and its consequences in jellyfish blooms

Overfishing can also promote the increase of the jellyfish populations. The diet of jellyfish is generalist, including eggs and larvae, as well as juveniles and adults of different fish species, planktonic organisms, crustaceans and other jellyfish. The decrease of competitive predators through overfishing opens an ecological space for jellyfish as resources become available (Lynam et al., 2004; Mills, 2001; Purcell, 2005). For example, the collapsed Northern Benguela upwelling sardine stocks have allowed jellyfish populations to increase significantly (Lynam et al., 2006). In addition, feeding energy previously directed to fish, when diverted to jellyfish, can lead to irreversible shifts in the trophic dynamics. Jellyfish have few obligate predators (Richardson et al., 2009) and higher trophic level organisms do not consume them, leading to a trophic dead-end and limited top-down control of jellyfish (Lynam et al., 2006). The trophic transfer of energy and organic matter, such as carbon, up the food chain is shifted to the microbial community, provoking changes in biogeochemical processes and food web structure (Condon et al., 2011). There are other explanations for the increase in jellyfish, such as eutrophication, alien translocations and increasing amounts of hard substrate, which should only be taken into consideration when analysing coastal data (Gibbons & Richardson, 2008). Excess nutrients from fertilizer runoff, pollution sources, and sewage in waters can lead to changes in the trophic web and to hypoxic events (Purcell et al., 1999). The lack of silica in this environment will cause only flagellates to proliferate as opposed to diatoms, which favour jellyfish instead of fish. The same happens with hypoxia, scyphomedusae and ctenophores are tolerants to that, they can survive and thrive in extreme environments (Purcell et al., 1999; Richardson et al., 2009). Translocations or ballast water's exchange opens up environments for jellyfish that would otherwise be difficult to reach (Graham & Bayha, 2008). This results in jellyfish introductions, and it leads to negative effects on the food web (Richardson et al., 2009). The expansion of coastal areas can also cause the proliferation of jellyfish because it creates a more suitable and additional habitat for the initial stages of jellyfish life's - polyps. They can settle and proliferate over a larger area (Dong et al., 2018; Gibbons & Richardson, 2008; Parsons & Lalli, 2002).

Different drivers acting at different scales

Understanding the patterns and processes driving natural systems, such as the variability of jellyfish occurrence, is very important to develop effective management principles. In this scope, it is necessary to establish baselines of knowledge at different spatial and temporal scales (Levin, 1992; Wiens, 1989). Ecological processes or patterns may be scale dependent (Hernández, 2020; Hobbs, 2003; Thrush et al., 2005), or in other words, variables may drive or not processes or patterns when acting at different scales (Hobbs, 2003). Thus, it is the sampling methodology that will influence how the ecology of the species is portrayed, as it depends on the heterogeneity of the natural habitat (Hernández, 2020; Wiens, 1989). However, reports of increasing jellyfish populations in specific regions, on a decadal scale, requires careful and in-depth research on the drivers of change, from regional-scale (wind direction) to global-scale, e.g., climate fluctuations (Condon et al., 2013; Purcell, 2005). In addition to scale being important in management and policy application, it can give different perspectives on the variation in abundance of populations. This can be misinterpreted for perspective reasons. At short time scales, blooms can be reported, but if they are analysed at a large time scale, they may occur due to natural fluctuations. There is a lack of long time scale data to understand whether or not gelatinous zooplankton are actually increasing in the oceans (Condon et al., 2012).

There is a gap in knowledge regarding drivers acting at different scales in this jellyfish. Some can be considered local scales drivers such as currents, tides, and wind. Wind is considered by most authors to be a local-scale driver because it plays the largest contribution in its drift as well as its strength and direction (Ferrer & Pastor, 2017; Headlam et al., 2020; Iosilevskii & Weihs, 2009; Prieto et al., 2015). The jellyfish sails with its pneumatophore aligned with the wind direction. Others are considered global drivers, such as temperature, which influences the species' growth, life cycle and reproduction (Purcell, 2005). The increase in abundance of these species causes major impacts at various levels, and knowing what most influences their occurrence at different scales, may allow us to develop appropriate management strategies (Condon et al., 2013; Ferrer et al., 2015). Only then it is possible to predict its occurrence and create measures to prevent it. With this information, we can alert coastal services about strandings and prevent the health problems mentioned earlier. To prevent economic losses in the tourism sector the cleanliness of the beaches in question should be reinforced. Due to their dangerous nature, it is very important to know more about the species and predict these types of events in the future.

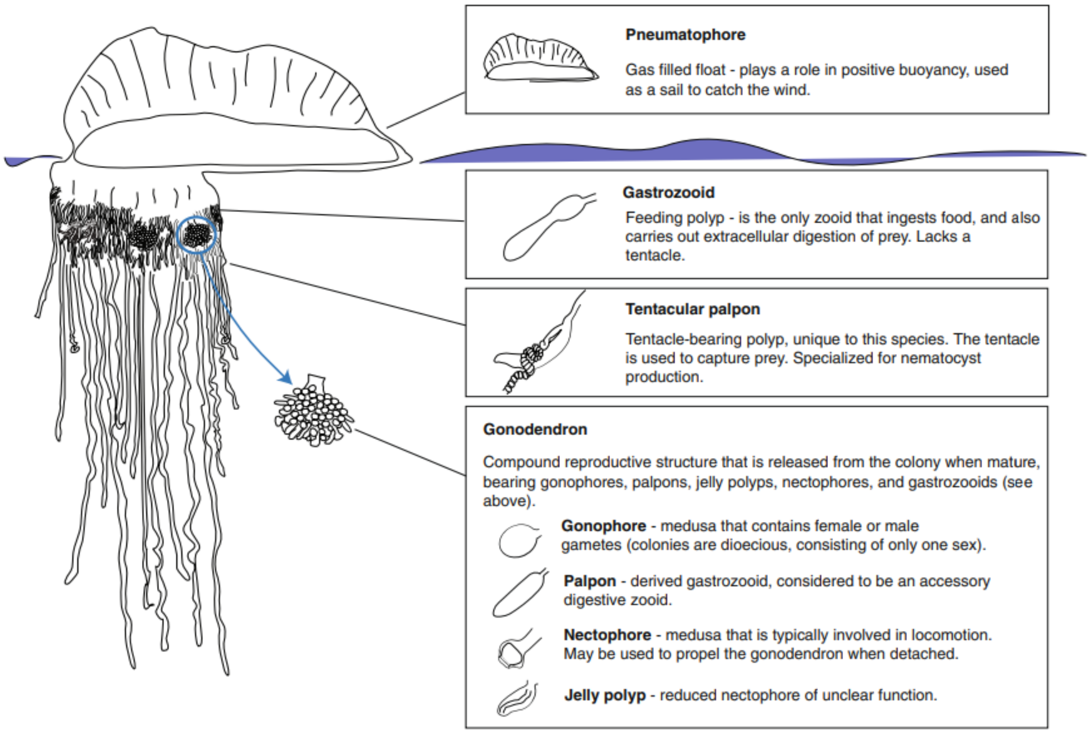
Figure 1.6 - Portuguese Man-of-War stranded on the beach. The pneumatophore and part of the tentacles are visible. Source: www.naturalist.pt accessed on 29/07/2022.

Species introduction

One of the species that have been reported as dangerous is *Physalia physalis* or the Portuguese Man-of-War, as it is informally known (Figure 1.6). It is a pleuston, hydrozoan that belongs to the order Siphonophorae and suborder Cystonectae (Bardi & Marques, 2007). It is widely distributed in tropical, subtropical and temperate regions of the Atlantic Ocean (as far as the British Isles), where it strands along shorelines (Castriota et al., 2017). Only one species is recognized - *Physalia physalis* (Figure 1.7) - although some individuals display differences in size, colour and even distribution. Munro et al., (2019) suggest that there are diverse development stages, instead of different species as originally thought. The morphological characteristics used to differentiate *P. utriculus* from *P. physalis*, used to be a single tentacle and a smaller size. Thus, Indo-Pacific populations should be considered a different species. Pontin & Cruickshank, (2012) suggest the need to do a taxonomic revision. According to their study, *Physalia* genetic diversity does not correspond to their findings, or this species could have a very high level of intraspecific diversity. There is a possibility that genus *Physalia* could contain hidden cryptic diversity, although in the ocean there are few chances for allopatric divergence (Pontin & Cruickshank, 2012).

Figure 1.7 - Side view of P. physalis *in Azores. Pneumatophore out of the water and tentacles in the water. Naturalist's boat in the background - Photo: Nuno Vasco Rodrigues*

P. physalis is a colony of different zooids (Figure 1.8), where each zooid has its own function (Munro et al., 2019). The pneumatophore floats on the water surface, and the tentacles have an opposite direction of motion (Woodcock, 1944). The pneumatophore is used as a "sail" allowing *P. physalis* to travel long distances (Iosilevskii & Weihs, 2009). Pneumatophore size can vary from 3 to 23 centimetres (Macías et al., 2021; Mghili et al., 2021; Wilson, 1947) and is filled with carbon monoxide (Clark & Lane, 1961). There are left and right-handed colonies - dimorphism - and the alignment of the pneumatophore is determined at early development (Munro et al., 2019). Ferrer & González, (2021) suggest that the majority of the individuals are right-handed in the Northern hemisphere. The long tentacles drag the colony and catch the prey in the lower part. Their average length, in mature colonies, varies from 15 centimetres to 30 meters (Munro et al., 2019). The underwater body is composed by different zooids with different functions: gastrozooid (feeding polyp), gonodendron (reproductive structure) and tentacular palpon. The latter is where the nematocysts - capsule-like organelle that opens when touched and releases toxins - (Daly et al., 2007) are formed, and the venom is kept.



Pneumatophore

Gas filled float - plays a role in positive buoyancy, used as a sail to catch the wind.

Gastrozooid

Feeding polyp - is the only zooid that ingests food, and also carries out extracellular digestion of prey. Lacks a tentacle.

Tentacular palpon

Tentacle-bearing polyp, unique to this species. The tentacle is used to capture prey. Specialized for nematocyst production.

Gonodendron

Compound reproductive structure that is released from the colony when mature, bearing gonophores, palpons, jelly polyps, nectophores, and gastrozooids (see above).

Gonophore - medusa that contains female or male gametes (colonies are dioecious, consisting of only one sex).

Palpon - derived gastrozooid, considered to be an accessory digestive zooid.

Nectophore - medusa that is typically involved in locomotion. May be used to propel the gonodendron when detached.

Jelly polyp - reduced nectophore of unclear function.

Figure 1.8 - Schematic showing the anatomy *of a* Physalia physalis *colony, with descriptions of each zooid and its functions. From Munro et al. 2019.*

Physalia physalis is a fish-eater: fish larvae, bigger fish, including herring, flying fish, and silverside (Herring, 1971), leptocephalus larvae (Purcell, 1984). And it is a prey for marine animals like *Eretmochelys imbricata imbricata, Caretta caretta, Dermochelys coriacea* (Torres-Conde et al., 2021) (Figure 1.9), nudibranchs (Thompson & Bennett, 1969), some subspecies of *Janthina* and *Glaucus marinus* (Bingham & Albertson, 1974) and likely to be prey of the heaviest fish in the world, the giant sunfish (*Mola alexandrini*) known for its diet in gelatinous organisms (Gomes-Pereira et al., 2022). Little is known about the life cycle of *Physalia physalis*, growth, reproduction rates, lifespan, its behaviour and even ecology (Munro et al., 2019), although *P. physalis* is a conspicuous and cosmopolitan species (Headlam et al., 2020). One of the reasons for that is the fact that this siphonophore is not captured in fishery surveys, that is one of the common traditional sampling methodologies used. The limited information available shows *Physalia physalis* reproduction happening between summer and autumn and the lifespan is approximately one year, where it can grow around 3 cm per month (Kennedy, 1972 in Ferrer & González, 2021). Our data shows a general increase in size during the year (Figure 2.13 and 2.14) like other jellyfish do (Houghton et al., 2007).

Figure 1.9 - Marine turtle eating a Portuguese Man-of-War in Azores. Source: Naturalist

General Objectives

The main objectives of this work are to (1) understand the environmental drivers that explain the occurrence of *P. physalis* at a macroecological scale (the North Atlantic Ocean) and at a regional scale (Faial Island from the Azores archipelago) and (2) predict its distribution and temporal trends. The species environmental drivers were assessed by linking climate with occurrence datasets through regression models, in line with previous studies (e.g., Ferrer et al., 2015; Ferrer & González, 2021; Headlam et al., 2020; Macías et al., 2021; Prieto et al., 2015). Individual distribution models considering several ecological predictors were used at contrasting spatial and temporal scales: (1) a macroecological scale - Atlantic Ocean - and (2) a regional scale - Faial Island, Azores archipelago. The model was fed on high-resolution environmental data and occurrence data describing its distribution in the North Atlantic Ocean (macroecological scale approach) and long-term temporal variability in the Faial Island, Azores (regional scale approach). The predictors considered in both scales were primary productivity, wind speed and direction, ocean currents direction and speed, minimum and maximum temperature. These were chosen based on what is currently known about the species: the occurrence of *Physalia physalis* is influenced by productivity (Lucas et al., 2014), wind patterns as well, as its pneumatophore is dragged by the wind, like a sail (Iosilevskii & Weihs, 2009). The ocean currents patterns influence *Physalia physalis* since it is a planktonic organism (Graham & Hamner, 2001) and increasing temperature causes an increase in growth and reproduction rates of jellyfish (Aouititen et al., 2019). This work aims to improve the ecological knowledge of *P. physalis* and to provide baselines for conservation and management actions, especially in the face of future climate change since the warming of the oceans may benefit the occurrence of the species (Canepa et al., 2020).

References

Aouititen, M., Bekkali, R., Nachit, D., Luan, X., & Mrhraoui, M. (2019). Predicting jellyfish strandings in the Moroccan North-West mediterranean coastline. *European Scientific Journal*, *15*(2), 72–84. https://doi.org/10.19044/esj.2019.v15n2p72

Araya, J., Aliaga, J., & Araya, M. (2016). On the distribution of Physalia physalis (Hydrozoa: Physaliidae) in Chile. *Marine Biodiversity*, *46*(3), 731–735. https://doi.org/10.1007/s12526-015-0417-6

Assis, J., Berecibar, E., Claro, B., Alberto, F., Reed, D., Raimondi, P., & Serrão, E. (2017). Major shifts at the range edge of marine forests: the combined effects of climate changes and limited dispersal. *Scientific Reports*, *7*(1), 1–10. https://doi.org/10.1038/srep44348

Attrill, M., Wright, J., & Edwards, M. (2007). Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography*, *52*(1), 480–485. https://doi.org/10.4319/lo.2007.52.1.0480

Barbet-Massin, M., Jiguet, F., Albert, C., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, *3*(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Bardi, J., & Marques, A. (2007). Taxonomic redescription of the Portuguese man-of-war, Physalia physalis (Cnidaria, Hydrozoa, Siphonophorae, Cystonectae) from Brazil. *Iheringia, Série Zoologia*, *97*, 425–433. https://doi.org/10.1590/S0073-47212007000400011

Bashmachnikov, I., Lafon, V., & Martins, A. (2004). Sea surface temperature distribution in the Azores region. Part II: space-time variability and underlying mechanisms. *Arquipélago*, *21A*, 19–32.

Bergier, P., Thévenot, M., & Qninba, A. (2013). Notes naturalistes au Sahara Atlantique marocain-5. *Go-South Bulletin*, *10*, 113–197.

Bingham, F., & Albertson, H. (1974). Observations on beach strandings of the Physalia (Portuguese-man-of-war) community. *Veliger*, *17*, 220–224.

Bo, M., Mabruk, S., Balistreri, P., Bariche, M., Batjakas, I., Betti, F., Bilan, M., Canese, S., Cattaneo-Vietti, R., Corsini-Foka, M., Crocetta, F., Deidun, A., Dulčić, J., Grinyo, J., Kampouris, T., Ketsilis-Rinis, V., Kousteni, V., Koutsidi, M., Lubinevsky, H., … Gerovasileiou, V. (2020). New records of rare species in the Mediterranean Sea (October 2020). *Mediterranean Marine Science*, *21*(3), 608–630. https://doi.org/10.12681/mms.23674

Bopp, L., Resplandy, L., Orr, J., Doney, S., Dunne, J., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Seferian, R., Tjiputra, J., & Vichi, M. (2013). Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences*, *10*(10), 6225–6245. https://doi.org/10.5194/bg-10-6225-2013

Bosch-Belmar, M., M'Rabet, C., Dhaouadi, R., Chalghaf, M., Yahia, M., Fuentes, V., Piraino, S., & Yahia, K. (2016). Jellyfish stings trigger gill disorders and increased mortality in farmed Sparus aurata (Linnaeus, 1758) in the Mediterranean Sea. *PLoS One*, *11*(4), 11. https://doi.org/10.1371/journal.pone.0154239

Bosch-Belmar, M., Milisenda, G., Basso, L., Doyle, T., Leone, A., & Piraino, S. (2021). Jellyfish impacts on marine aquaculture and fisheries. *Reviews in Fisheries Science & Aquaculture*, *29*(2), 242–259. https://doi.org/10.1080/23308249.2020.1806201

Bourg, N., Schaeffer, A., Cetina-Heredia, P., Lawes, J., & Lee, D. (2022). Driving the blue fleet: Temporal variability and drivers behind bluebottle (Physalia physalis) beachings off Sydney, Australia. *PloS One*, *17*(3), 17. https://doi.org/10.1371/journal.pone.0265593

Brotz, L., Cheung, W., Kleisner, K., Pakhomov, E., & Pauly, D. (2012). Increasing jellyfish populations: trends in large marine ecosystems. In J. Purcell, H. Mianzan, & J. Frost (Eds.), *Jellyfish Blooms IV* (pp. 3–20). Springer. https://doi.org/10.1007/978-94-007-5316-7_2

Caldeira, R., & Reis, J. (2017). The Azores confluence zone. *Frontiers in Marine Science*, *4*, 37. https://doi.org/10.3389/fmars.2017.00037

Canepa, A., Purcell, J., Córdova, P., Fernández, M., & Palma, S. (2020). Massive strandings of pleustonic Portuguese Man-of-War (Physalia physalis) related to ENSO events along the southeastern Pacific Ocean. *Latin American Journal of Aquatic Research*, *48*(5), 806–817. https://doi.org/10.3856/vol48-issue5-fulltext-2530

Castriota, L., Falautano, M., Battaglia, P., Maraventano, G., Prazzi, E., Ammendolia, G., & Andaloro, F. (2017). First record of Physalia physalis in the Pelagie Islands (Strait of Sicily) and additional records in the Strait of Messina. *Cahiers de Biologie Marine*, *58*, 1–4. https://doi.org/10.21411/CBM.A.E207E474

Cavalcante, M., Rodrigues, Z., Hauser-Davis, R., Siciliano, S., Junior, H., & Nunes, J. (2020). Health-risk assessment of Portuguese man-of-war (Physalia physalis) envenomations on urban beaches in São Luís city, in the state of Maranhão, Brazil. *Revista Da Sociedade Brasileira De Medicina Tropical*, *53*, 7. https://doi.org/10.1590/0037-8682-0216-2020

Cazorla-Perfetti, D., & Posso, C. (2015). Presencia del Cnidario Hidrozoario Porpita porpita (anthoathecata: porpitidae) en los balnearios de Buchuaco, península de Paraguaná, estado Falcón, Venezuela y su importancia médica. *SABER. Revista Multidisciplinaria Del Consejo de Investigación de La Universidad de Oriente*, *27*(3), 508–510.

Cegolon, L., Heymann, W., Lange, J., & Mastrangelo, G. (2013). Jellyfish stings and their management: a review. *Marine Drugs*, *11*(2), 523–550. https://doi.org/10.3390/md11020523

Clark, F., & Lane, C. (1961). Composition of float gases of Physalia physalis.

Proceedings of the Society for Experimental Biology and Medicine, *107*(3), 673–674. https://doi.org/10.3181/00379727-107-26724

Condon, R., Duarte, C., Pitt, K., Robinson, K., Lucas, C., Sutherland, K., Mianzan, H., Bogeberg, M., Purcell, J., Decker, M., Uye, S., Madin, L., Brodeur, R., Haddock, S., Malej, A., Parry, G., Eriksen, E., Quiñones, J., Acha, M., … Graham, W. (2013). Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences*, *110*(3), 1000–1005. https://doi.org/10.1073/pnas.1210920110

Condon, R., Graham, W., Duarte, C., Pitt, K., Lucas, C., Haddock, S., Sutherland, K., Robinson, K., Dawson, M., Decker, M., Mills, C., Purcell, J., Malej, A., Mianzan, H., Uye, S., Gelcich, S., & Madin, L. (2012). Questioning the rise of gelatinous zooplankton in the world's oceans. *BioScience*, *62*(2), 160–169. https://doi.org/10.1525/bio.2012.62.2.9

Condon, R., Steinberg, D., Giorgio, P., Bouvier, T., Bronk, D., Graham, W., & Ducklow, H. (2011). Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proceedings of the National Academy of Sciences*, *108*(25), 10225–10230. https://doi.org/10.1073/pnas.1015782108

Costa, A., Marques, F., Hildenbrand, A., Sibrant, A., & Catita, C. (2014). Large-scale catastrophic flank collapses in a steep volcanic ridge: the Pico–Faial Ridge, Azores Triple Junction. *Journal of Volcanology and Geothermal Research*, *272,* 111–125. https://doi.org/10.1016/j.jvolgeores.2014.01.002

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

Dong, Z., Wang, L., Sun, T., Liu, Q., & Sun, Y. (2018). Artificial reefs for sea cucumber aquaculture confirmed as settlement substrates of the moon jellyfish Aurelia coerulea. *Hydrobiologia*, *818*(1), 223–234. https://doi.org/10.1007/s10750-018-3615-y

Edelist, D., Angel, D., Canning-Clode, J., Gueroun, S., Aberle, N., Javidpour, J., & Andrade, C. (2021). Jellyfishing in Europe: Current Status, Knowledge Gaps, and Future Directions towards a Sustainable Practice. *Sustainability*, *13*(22), 12445. https://doi.org/10.3390/su132212445

Ekwu, S., & Sikoki, F. (2005). Species composition and distribution of zooplankton in the Lower Cross River Estuary. *African Journal of Applied Zoology and Environmental Biology*, *7*, 5–10. https://doi.org/10.4314/ajazeb.v7i1.41137

Elith, J., & Leathwick, J. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Faerber, M., & Baird, R. (2010). Does a lack of observed beaked whale strandings in military exercise areas mean no impacts have occurred? A comparison of stranding and detection probabilities in the Canary and main Hawaiian Islands. *Marine Mammal Science*, *26*(3), 602–613. https://doi.org/10.1111/j.1748-7692.2010.00370.x

Fathalli, A., Zaafrane, S., Maatouk, K., Hafi, O., Hamza, A., & Missaoui, H. (2020). First record of the Siphonophore physalia physalis (Linnaeus, 1758) in the gulf of Tunis (Tunisia). *Bulletin de l'Institut National Des Sciences et Technologies de La Mer de Salammbô, 47*, 203–207.

Fautin, D. (2009). Structural diversity, systematics, and evolution of cnidae. *Toxicon*, *54*(8), 1054–1064. https://doi.org/10.1016/j.toxicon.2009.02.024

Ferrer, L., & González, M. (2021). Relationship between dimorphism and drift in the Portuguese man-of-war. *Continental Shelf Research*, *212*, 104269. https://doi.org/10.1016/j.csr.2020.104269

Ferrer, L., & Pastor, A. (2017). The Portuguese man-of-war: Gone with the wind. *Regional Studies in Marine Science*, *14*, 53–62. https://doi.org/10.1016/j.rsma.2017.05.004

Ferrer, L., Zaldua-Mendizabal, N., Campo, A., Franco, J., Mader, J., Cotano, U., Fraile, I., Rubio, A., Uriarte, A., & Caballero, A. (2015). Operational protocol for the sighting and tracking of Portuguese man-of-war in the southeastern Bay of Biscay: Observations and modeling. *Continental Shelf Research*, *95*, 39–53. https://doi.org/10.1016/j.csr.2014.12.011

Flores-Galicia, L., & Cruz-Francisco, V. (2018). Primeros registros de medusas (cubozoa, scyphozoa), sifonóforos (hydrozoa) y ctenóforos (tentaculata) del sistema arrecifal Lobos-tuxpan, México. *CICIMAR Oceánides*, *33*(1), 25–38. https://doi.org/10.37543/oceanides.v33i1.222

Geetha, S., Kumar, J., Mohapatra, A., & Sornaraj, R. (2019). Occurrence of Portuguese man-of war along Digha coast, West Bengal: a threat to tourists and fisherfolk. *Indian Journal of Geo-Marine Sciences*, *48*(1), 96–98.

Gibbons, M., & Richardson, A. (2008). Patterns of jellyfish abundance in the North Atlantic. In K. Pitt & J. Purcell (Eds.), *Jellyfish Blooms: Causes, Consequences, and Recent Advances* (pp. 51–65). Springer. https://doi.org/10.1007/978-1-4020-9749-2_4

Graham, W., & Bayha, K. (2008). Biological invasions by marine jellyfish. In W. Nentwig (Ed.), *Biological invasions* (pp. 239–255). Springer. https://doi.org/10.1007/978-3-540-36920-2_14

Graham, W., Gelcich, S., Robinson, K., Duarte, C., Brotz, L., Purcell, J., Madin, L., Mianzan, H., Sutherland, K., Uye, S., Pitt, K., Lucas, C., Bøgeberg, M., Brodeur, R., & Condon, R. (2014). Linking human well-being and jellyfish: ecosystem services, impacts, and societal responses. *Frontiers in Ecology and the Environment*, *12*(9), 515–523. https://doi.org/10.1890/130298

Graham, W., & Hamner, W. (2001). A physical context for gelatinous zooplankton aggregations: a review. In J. Purcell, W. Graham, & H. Dumont (Eds.), *Jellyfish blooms: ecological and societal importance* (pp. 199–212). Springer. https://doi.org/10.1007/978-94-010-0722-1_16

Gomes-Pereira, J., Pham, C., Catarino, D., Miodonski, J., Santos, M., Dionísio, G., Nyegaard, M., Sawai, E., Carreira, G., Afonso, P. (2022. In press). The heaviest bony fish in the world: a 2744 kg giant sunfish Mola alexandrini (Ranzani, 1839) from the North Atlantic. *Journal of Fish Biology.*

Headlam, J., Lyons, K., Kenny, J., Lenihan, E., Quigley, D., Helps, W., Dugon, M., & Doyle, T. (2020). Insights on the origin and drift trajectories of Portuguese man of war (Physalia physalis) over the Celtic Sea shelf area. *Estuarine, Coastal and Shelf Science*, *246*, 107033. https://doi.org/10.1016/j.ecss.2020.107033

Hernández, F. (2020). Ecological discord and the importance of scale in scientific inquiry. *The Journal of Wildlife Management*, *84*(8), 1427–1434. https://doi.org/10.1002/jwmg.21942

Herring, P. (1971). Biliprotein coloration of Physalia physalis. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*, *39*(4), 739–746. https://doi.org/10.1016/0305-0491(71)90099-X

Hobbs, N. (2003). Challenges and opportunities in integrating ecological knowledge across scales. *Forest Ecology and Management*, *181*(1–2), 223–238. https://doi.org/10.1016/S0378-1127(03)00135-X

Houghton, J. D. R., Doyle, T. K., Davenport, J., Lilley, M. K. S., Wilson, R. P., & Hays, G. C. (2007). Stranding events provide indirect insights into the seasonality and persistence of jellyfish medusae (Cnidaria: Scyphozoa). *Hydrobiologia*, *589*(1), 1–13.

Iosilevskii, G., & Weihs, D. (2009). Hydrodynamics of sailing of the Portuguese man-of-war Physalia physalis. *Journal of the Royal Society Interface*, *6*(36), 613–626. https://doi.org/10.1098/rsif.2008.0457

Jenkins, R. (1983). Observations on the commensal relationship of Nomeus gronovii with Physalia physalis. *Copeia*, *1983*(1), 250–252.

Johnson, D., Perry, H., & Burke, W. (2001). Developing jellyfish strategy hypotheses using circulation models. In J. Purcell, W. Graham, & H. Dumont (Eds.), *Jellyfish Blooms: Ecological and Societal Importance* (pp. 213–221). Springer. https://doi.org/10.1007/978-94-010-0722-1_17

Junior, V., Virga, R., Bechara, A., Silveira, F., & Morandini, A. (2013). An outbreak of Portuguese man-of-war (Physalia physalis-Linnaeus, 1758) envenoming in Southeastern Brazil. *Revista Da Sociedade Brasileira de Medicina Tropical*, *46*(5), 641–644. https://doi.org/10.1590/0037-8682-1518-2013

Kennedy, F. (1972). Distribution and abundance of Physalia in Florida waters. *Florida Department of Natural Resources Marine Research Laboratory. Professional Papers Series*, *18*, 1–38.

Kwiatkowski, L., Naar, J., Bopp, L., Aumont, O., Defrance, D., & Couespel, D. (2019). Decline in Atlantic primary production accelerated by Greenland ice sheet melt. *Geophysical Research Letters*, *46*(20), 11347–11357. https://doi.org/10.1029/2019GL085267

Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., Buitenhuis, E., Doney, S. C., Dunne, J., Hashioka, T., Hauck, J., Hirata, T., John, J., Quéré, C., Lima, I., Nakano, H., Seferian, R., Totterdell, I., Vichi, M., & Völker, C. (2015). Drivers and uncertainties of future global marine primary production in marine ecosystem models. *Biogeosciences*, *12*(23), 6955–6984. https://doi.org/10.5194/bg-12-6955-2015

Levin, S. (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, *73*(6), 1943–1967. https://doi.org/10.2307/1941447

Licandro, P., Conway, D., Yahia, M., Puelles, M., Gasparini, S., Hecq, J., Tranter, P., & Kirby, R. (2010). A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters*, *6*(5), 688–691. https://doi.org/10.1098/rsbl.2010.0150

Lopes, A., Baptista, M., Rosa, I., Dionísio, G., Gomes-Pereira, J., Paula, J., Figueiredo, C., Bandarra, N., Calado, R., & Rosa, R. (2016). "Gone with the wind": Fatty acid biomarkers and chemotaxonomy of stranded pleustonic hydrozoans (Velella velella and Physalia physalis). *Biochemical Systematics and Ecology*, *66*, 297–306. https://doi.org/10.1016/j.bse.2016.03.016

Löscher, C., Fischer, M., Neulinger, S., Fiedler, B., Philippi, M., Schütte, F., Singh, A., Hauss, H., Karstensen, J., Körtzinger, A., Künzel, S., & Schmitz, R. (2015). Hidden biosphere in an oxygen-deficient Atlantic open-ocean eddy: future implications of ocean deoxygenation on primary production in the eastern tropical North Atlantic. *Biogeosciences*, *12*(24), 7467–7482. https://doi.org/10.1016/j.bse.2016.03.016

Luana, M. (2017). *Distribuição de caravelas (Physalia physalis) e envenenamentos humanos nas praias urbanas de São Luís, Maranhão-Brasil* [Universidade Federal do Maranhão]. https://tedebc.ufma.br/jspui/bitstream/tede/1355/2/MayanaLuana.pdf

Lucas, C., Jones, D., Hollyhead, C., Condon, R., Duarte, C., Graham, W., Robinson, K., Pitt, K., Schildhauer, M., & Regetz, J. (2014). Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. *Global Ecology and Biogeography*, *23*(7), 701–714. https://doi.org/10.1111/geb.12169

Lynam, C., Gibbons, M., Axelsen, B., Sparks, C., Coetzee, J., Heywood, B., & Brierley, A. (2006). Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology*, *16*(19), R492–R493. https://doi.org/10.1016/j.cub.2006.09.012

Lynam, C., Hay, S., & Brierley, A. (2004). Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography*, *49*(3), 637–643. https://doi.org/10.4319/lo.2004.49.3.0637

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. https://doi.org/10.1016/j.ocecoaman.2021.105810

Mghili, B., Analla, M., & Aksissou, M. (2021). Medusae (Scyphozoa and hydrozoa) from the Moroccan Mediterranean coast: abundance and spatiotemporal dynamics and their economic impact. *Aquatic Ecology*, *56*, 213–226. https://doi.org/10.1007/s10452-021-09910-0

Mills, C. (2001). Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, *451*(1), 55–68. https://doi.org/10.1023/A:1011888006302

Munro, C., Vue, Z., Behringer, R., & Dunn, C. (2019). Morphology and development of the Portuguese man of war, Physalia physalis. *Scientific Reports*, *9*, 1–12. https://doi.org/10.1038/s41598-019-51842-1

Nakamura, Y., & Oka, A. (2019). CMIP5 model analysis of future changes in ocean net primary production focusing on differences among individual oceans and models. *Journal of Oceanography, 75*(5), 441–462.

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

Pikesley, S., Godley, B., Ranger, S., Richardson, P., & Witt, M. (2014). Cnidaria in UK coastal waters: description of spatio-temporal patterns and inter-annual variability. *Journal of the Marine Biological Association of the United Kingdom, 94*(7), 1401–1408. https://doi.org/10.1017/S0025315414000137

Pontin, D., & Cruickshank, R. (2012). Molecular phylogenetics of the genus Physalia (Cnidaria: Siphonophora) in New Zealand coastal waters reveals cryptic diversity. *Hydrobiologia, 686*, 91–105. https://doi.org/10.1007/s10750-011-0994-8

Prieto, L., Macías, D., Peliz, A., & Ruiz, J. (2015). Portuguese Man-of-War (Physalia physalis) in the Mediterranean: A permanent invasion or a casual appearance? *Scientific Reports, 5*, 11545. https://doi.org/10.1038/srep11545

Purcell, J. (1984). Predation on fish larvae by Physalia physalis, the Portuguese man of war. *Marine Ecology Progress Series, 19*, 189–191.

Purcell, J. (2005). Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom, 85*(3), 461–476. https://doi.org/10.1017/S0025315405011409

Purcell, J., Malej, A., & Benović, A. (1999). Potential Links of Jellyfish to Eutrophication and Fisheries. *Coastal and Estuarine Studies, 55*, 241–263.

Purcell, J., Uye, S., & Lo, W. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series, 350*, 153–174. https://doi.org/10.3354/meps07093

Richardson, A., Bakun, A., Hays, G., & Gibbons, M. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution, 24*(6), 312–322. https://doi.org/10.1016/j.tree.2009.01.010

Richardson, A., & Gibbons, M. (2008). Are jellyfish increasing in response to ocean acidification? *Limnology and Oceanography, 53*(5), 2040–2045. https://doi.org/10.4319/lo.2008.53.5.2040

Schuchert, P. (2020). World hydrozoa database. *Cryptospongia Enigmatica*.

Scott-Frías, J., & Jorquera, E. (2020). La Fragata Portuguesa o Aguamala (Physalia physalis): Importancia en la salud pública. *Bionatura, 5*(4), 1418–1422. https://doi.org/10.21931/RB/2020.05.04.24

Steinacher, M., Joos, F., Frölicher, T., Bopp, L., Cadule, P., Cocco, V., Doney, S., Gehlen, M., Lindsay, K., Moore, J., Schneider, B., & Segschneider, J. (2010). Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences, 7*(3), 979–1005. https://doi.org/10.5194/bg-7-979-2010, 2010.

Thompson, T., & Bennett, I. (1969). Physalia nematocysts: utilized by mollusks for defense. *Science, 166*(3912), 1532–1533. https://doi.org/10.1126/science.166.3912.1532

Thrush, S., Hewitt, J., Herman, P., & Ysebaert, T. (2005). Multi-scale analysis of species–environment relationships. *Marine Ecology Progress Series*, *302*, 13–26. https://doi.org/10.3354/meps302013

Tiralongo, F., Badalamenti, R., Arizza, V., Prieto, L., & Brutto, S. (2022). The Portuguese Man-of-war, One of The Most Dangerous Marine Species, Has Always Entered The Mediterranean Sea: Strandings, Sightings And Museum Collections. *Frontiers in Marine Science*, *9*(856979), 14. https://doi.org/10.3389/fmars.2022.856979

Torres-Conde, E., Martínez-Daranas, B., & Prieto, L. (2021). The Havana littoral, an area of distribution for Physalia physalis in the Atlantic Ocean. *Regional Studies in Marine Science*, *44*, 101752. https://doi.org/10.1016/j.rsma.2021.101752

Wiens, J. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*(4), 385–397. https://doi.org/10.2307/2389612

Wilson, D. (1947). The Portuguese Man-of-War, Physalia physalis L., in British and adjacent seas. *Journal of the Marine Biological Association of the United Kingdom*, *27*(1), 139–172. https://doi.org/10.1017/S0025315400014156

Woodcock, A. (1944). A theory of surface water motion deduced from the wind-induced motion of the Physalia. *Journal of Marine Research*, *5*(3), 196–205.

Chapter 2

Modelling the occurrence of *Physalia physalis* in the North Atlantic Ocean at different spatial and temporal scales

Lara Martins[1], José Gomes-Pereira[2], Gisela Dionísio[3,4], Jorge Assis[1]

[1]Centre for Marine Sciences, CCMAR-CIMAR, University of Algarve, Faro, Portugal

[2]Atlantic Naturalist Association, Largo Manuel de Arriaga, 9900-029 Horta, Portugal.

[3]Departamento de Biologia & CESAM, Universidade de Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

[4]MARE - Marine and Environmental Sciences Centre, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

Corresponding author.

E-mail address: laram.t5d@gmail.com (L. Martins).

Keywords: *Physalia physalis*, species distribution modelling, climate change, jellyfish blooms, marine ecology

Abstract

Frequent jellyfish blooms cause human health issues and closures of coastal areas, impacting different economic sectors like tourism, fisheries, aquaculture farms and industry. Understanding the drivers of jellyfish bloom and predicting their occurrence is therefore essential to develop effective management plans. The Portuguese Man-of-War (*Physalia physalis)* is a dangerous cosmopolitan siphonophore and its ecology remains largely understudied. The objective of this study is to understand the main environmental drivers (e.g., temperature, productivity, wind and ocean patterns) that explain the occurrence of *P. physalis* at a macroecological scale (the North Atlantic Ocean) and at a regional scale (Faial Island from the Azores archipelago), and to predict its distribution and temporal trends. We implemented machine learning modelling that fed on high-resolution environmental data and occurrence data describing its distribution in the North Atlantic Ocean and long-term temporal variability in the Faial Island (Azores). Models retrieved high accuracy scores and showed that the distribution of *P. physalis* is mainly explained by primary productivity, temperature and currents direction at the macroecological scale and by primary productivity and wind patterns at the regional scale. The models also showed a higher probability of occurrence on both Atlantic coasts and offshore North-northwest Atlantic. Models fed on temporal datasets demonstrate decadal fluctuations rather than significant increases over time, contradicting the previously established hypothesis that jellyfish blooms are increasing. By using species distribution modelling, we provide a better understanding on how environmental variability shapes the occurrence of *P. physalis* at different spatial and temporal scales (macroecological and regional), which can be considered in management plans and policies. In the future, projected global warming and decreased primary productivity in the North Atlantic may cause significant poleward shifting of this species, adversely affecting human health, socioeconomics and ecosystems in regions not currently used to deal with such impacts.

Introduction

Jellyfish, here referred to all gelatinous zooplankton taxa, including the medusae and ctenophores, are known for rapid and extensive blooms (Purcell, 2005) that can have numerous negative consequences for marine ecosystems, impacting food webs and biochemical processes. These blooms, consisting of rapid population growths, can also cause socioeconomic disruptions in tourism, fisheries, aquaculture and the industry sector. Jellyfish can be dangerous to humans due to the venom released by their nematocysts, capsule-like organelle that opens when touched (Fautin, 2009; Geetha et al., 2019), which can produce several kinds of symptoms and even be fatal in some situations (Cegolon et al., 2013). Jellyfish blooms interact negatively with fisheries through predation and competition: leading to desynchronization in the feeding periods of the juveniles' stocks and a decrease in the survival of fish communities (Lynam et al., 2004; Tilves et al., 2016), as well as clogging and damaging the gear (Conley & Sutherland, 2015) and deteriorating the catches (Bosch-Belmar et al., 2021). In the aquaculture farms, jellyfish can lead to damage to caged fish (Licandro et al., 2010) due to vectors of pathogens (Bosch-Belmar et al., 2016). There is interspecific competition for nutrition, resulting in high production mortality rates (Mghili et al., 2021), along with clogging and interrupting water circulation (Bosch-Belmar et al., 2021). The industry sector could also be affected by jellyfish blockage of water pipe systems, decreasing productivity, or even interrupting power and freshwater production (Graham et al., 2014; Purcell, 2005).

Climate change-related environmental precursors of increased jellyfish abundance are diverse: rising temperatures, ocean acidification and changing circulation patterns. The rising of sea water temperatures has consequences in the species' life cycle, their expansion to higher latitudes (Purcell, 2005; Richardson et al., 2009) and it promotes water column stratification. Warmer temperatures will alter the synchronicity of fish larvae with its planktic prey, accelerate medusae growth and development, and change the timing and duration of life stages (Purcell et al., 2007). Water column stratification leads to nutrient-poor surface waters and changes in the food web (Gibbons & Richardson, 2008). Stratification favours the jellyfish over fish because they can better survive and thrive in dead zones. Primary producers will be replaced by flagellates in these conditions. These are "low-energy" trophic chains, as opposed to the ones initiated by diatoms that support fish production (Parsons & Lalli, 2002; Purcell, 2005). Ocean acidification due to the increase of dissolved carbon dioxide can also benefit jellyfish indirectly (Attrill et al., 2007), by declining the conditions on calcifying plankton. This leads to more ecological space for jellyfish. Altered circulation patterns could be a consequence of climate change that leads to fluctuations in jellyfish abundance (Lynam et al., 2004)**.** NAO Index (North Atlantic Oscillation) represents local changes in winds, circulation patterns (North Atlantic Current - NAC) and temperatures. It has an influence on the abundance and distribution of various species, from phytoplankton to macrofauna (Gibbons & Richardson, 2008). However, there is still no consensus about the relationship of these variations to the overall increase in jellyfish. Some studies found a negative correlation between jellyfish abundance and NAO index (Lynam et al., 2004), others found a positive one (Attrill et al., 2007) or even no significant link (Gibbons & Richardson, 2008). Other processes such as overfishing (decrease of competitive predators) also play a role in the distribution of jellyfish. The diet of jellyfish is generalist, including eggs and larvae, as well as juveniles and adults of different fish species. The decrease of competitive predators through overfishing and intense predation opens an ecological space for jellyfish to increase as resources become available (Lynam et al., 2004; Mills, 2001; Purcell, 2005). For example, the collapsed Northern Benguela upwelling sardine stocks have allowed jellyfish populations to increase significantly (Lynam et al., 2006). The feeding energy (generated by the trophic web) previously directed to fish, is then diverted to jellyfish, which causes the food chain to be shifted to the microbial community. This shift causes changes in biogeochemical processes and food web structure (Condon et al., 2011).

Understanding the patterns and processes driving natural systems, such as the variability of jellyfish occurrence, is very important to develop effective management principles. In this scope, it is necessary to establish baselines of knowledge at different spatial and temporal scales (Levin, 1992; Wiens, 1989). Ecological processes or patterns may be scale dependent (Hernández, 2020; Hobbs, 2003; Thrush et al., 2005), or in other words, the variables may drive or not the processes or patterns by acting at different scales (Hobbs, 2003). Thus, it is the sampling methodology that will influence how the ecology of the species is portrayed, as it depends on the heterogeneity of the natural habitat (Hernández, 2020; Wiens, 1989). In addition to scale being important in management and policy application, it can give different perspectives on the variation in abundance of populations. This can be misinterpreted for perspective reasons. At short time scales, blooms can be reported, but if they are analysed at a large time scale, they may occur due to natural fluctuation. The fact that jellyfish populations have been increasing in specific regions on a decadal scale requires careful and in-depth research on the drivers of change, from regional-scale (wind direction) to global-scale, e.g., climate fluctuations (Condon et al., 2013; Purcell, 2005). There is a lack of long time scale data to understand whether or not gelatinous zooplankton are actually increasing in the oceans (Condon et al., 2012). There is a gap in knowledge regarding drivers acting at different scales in these species. Some can be considered local scales drivers such as currents, tides, and wind. Wind is considered by most authors to be a local-scale driver because it plays the largest contribution in its drift as well as its strength and direction (Ferrer & Pastor, 2017; Headlam et al., 2020; Iosilevskii & Weihs, 2009; Prieto et al., 2015), such as the case of *Physalia physalis* that sails with its pneumatophore aligned with the wind direction. Others are considered global drivers, such as temperature, which influences the growth, life cycle and reproduction of the species (Purcell, 2005). Knowing what drives influence occurrences the most and under what conditions they appear, allows us to develop management strategies (Condon et al., 2013; Ferrer et al., 2015). Because the increased abundance of these animals causes major impacts at various scales, it is necessary to know the drivers of the species at different scales. Only then it is possible to predict its occurrence and create measures to deal with it. With this information, we can alert coastal services about strandings and prevent health problems mentioned earlier. To prevent economic losses in the tourism sector the cleanliness of the beaches in question should be reinforced. Due to their dangerous nature, it is very important to know more about the species and predict these types of events in the future.

Physalia physalis, the Portuguese Man-of-War is a pleuston, hydrozoan that belongs to the order Siphonophorae (Bardi & Marques, 2007). Despite being a conspicuous and cosmopolitan species in the Atlantic (Munro et al., 2019), information about the ecology and behaviour of the dangerous *P. physalis* remains scarce (Ferrer et al., 2015; Ferrer & González, 2021; Munro et al., 2019), precluding adequate conservation and management strategies.

The main objectives of this work are to (1) understand the environmental drivers that explain the occurrence of *P. physalis* at a macroecological scale (the North Atlantic Ocean) and at a regional scale (Faial Island from the Azores archipelago) and (2) predict its distribution and temporal trends. In line with additional studies (e.g., Ferrer et al., 2015; Ferrer & González, 2021; Headlam et al., 2020; Macías et al., 2021; Prieto et al., 2015), machine learning models were produced to infer the species drivers by linking climate data and occurrence datasets. This work serves to improve the ecological knowledge of *P. physalis* and provide baselines for conservation and management actions, especially in the face of future climate change since the warming of the oceans may benefit the occurrence of the species (Canepa et al., 2020).

Methods

Focal species

The present study focus on *Physalia physalis*, a cosmopolitan pleustonic siphonophore widely distributed in tropical, subtropical and temperate regions of the Atlantic Ocean (as far as the British Isles), where it strands along shorelines (Castriota et al., 2017). *P. physalis* is a colony of different zooids, where each zooid has its function. Even with the current nomenclature problems that do not quite sort out the genus, the additional species of *Physalia* only occur in the Pacific Ocean - *P. utriculus* - (Pontin & Cruickshank, 2012), being *P. physalis* exclusive to the Atlantic (Pontin & Cruickshank, 2012, suggest a taxonomic revision of the genus).

Climatic predictors and biodiversity data collection

We used individual distribution models to explain and predict the occurrence of *P. physalis* at contrasting spatial and temporal scales: (1) a macroecological scale – Atlantic Ocean, approximately 72.5°N to 0°N, and (2) a regional scale – Faial Island, central group of the Azores archipelago, approximately 38.5°N to 38.6°N and 28.8ºW to 28.5ºW, from 2008 to 2021.

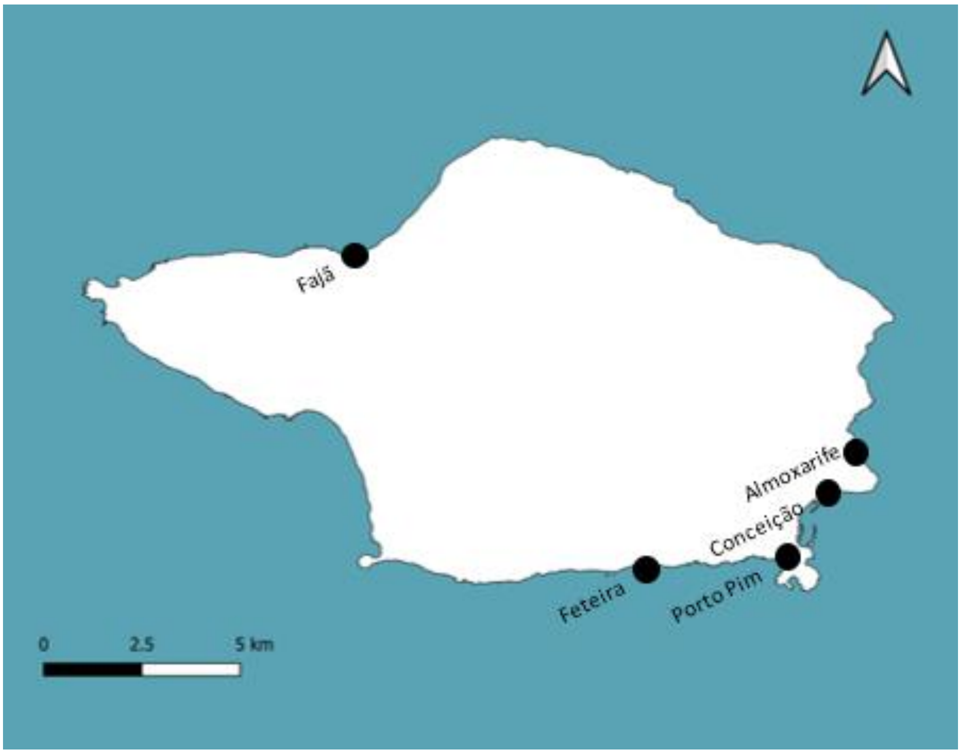
The predictors considered in both the macroecological and regional scales were primary productivity, as total primary production of phytoplankton (milligrams of carbon per cubic meter per day) and total phytoplankton (millimoles per cubic meter), wind and ocean patterns (speed and direction), minimum and maximum temperature. These predictors were chosen based on what is currently known about the drivers of the species occurrence (Elith & Leathwick, 2009): the occurrence of *Physalia physalis* is influenced by primary productivity, as a predictor derived from phytoplankton and is a direct indicator of nutrient availability (Lucas et al., 2014), with increasing values leading to jellyfish outbreaks (Aouititen et al., 2019). The speed and direction of the prevailing winds influence *Physalia physalis*, as its pneumatophore is dragged by the wind, like a sail (Iosilevskii & Weihs, 2009). The speed and direction of the ocean currents influences *Physalia physalis* since it is a planktonic organism and is therefore unable to move against the broad patterns of ocean currents (Graham & Hamner, 2001). Increasing temperature causes may cause an increase in growth and reproduction rates as in other gelatinous plankton species (Aouititen et al., 2019).

Macroecological data

The North Atlantic Ocean was the considered study region for a macroecological scale approach. Occurrence data was obtained from online biodiversity repositories, the available literature and museum collections. We accessed big data repositories such as the Global Biodiversity Information Facility (GBIF; source: World Hydrozoa Database in Schuchert, 2020), Ocean Biodiversity Information System (OBIS), iNaturalist, Jellyfish Database Initiative (JeDI), Jellywatch and Integrated Digitized Biocollections (iDigBio). We also considered the studies of Araya et al., 2016; Bergier et al., 2013; Bo et al., 2020; Castriota et al., 2017; Cavalcante et al., 2020; Cazorla-Perfetti & Posso, 2015; Ekwu & Sikoki, 2005; Fathalli et al., 2020; Ferrer et al., 2015; Flores-Galicia & Cruz-Francisco, 2018; Junior et al., 2013; Lopes et al., 2016; Luana, 2017; Lucas et al., 2014; Mghili et al., 2021; Munro et al., 2019; Scott-Frías & Jorquera, 2020; Tiralongo et al., 2022; Torres-Conde et al., 2021; Woodcock, 1944. Regarding museum collections, we considered the collection of the Yale Peabody Museum of Natural History, available at https://collections.peabody.yale.edu/search/ to date (06/04/2022) and the collection of the Smithsonian National Museum of Natural History, Department of Invertebrate Zoology Collections, available on https://collections.nmnh.si.edu/search/iz/ to date (06/04/2022). The compilation of *P. physalis* distribution from the available records - Figure 2.25 - see supplements. Environmental data for the macroecological scale approach was obtained from Bio-ORACLE. This is a platform making available geophysical, biotic, and climatic data as raster layers at a spatial resolution of 0.08º, approximately 9km at the Equator. Both spatial and temporal variables are consistent with the biological response being modelled. The dataset was prepared to be used in modelling by removing non available data (NAs), duplicates and overland occurrence records.

Regional data

For a regional scale approach, presence and absence data were provided by the Atlantic Naturalist Association under project MONIJELLY. This dataset consists of beach-based surveys of stranded *P. physalis*, registered routinely from 2008 to 2021 (at least every 15 days, yet with some yearly interruptions) (Table 2.3 and figure 2.12). Surveys were done on five beaches in Faial Island (Azores), namely Fajã, a rocky and sandy beach in the northwest, Almoxarife beach in the southeast of the island, Conceição beach and Porto Pim beach (sheltered sandy bay) and in Porto da Feteira, a rocky beach in the south (Figure 2.1).



.

Figure 2.1 - Sampling location on Faial Island on black dots. From left to right are the beaches of Fajã, Feteira, Porto Pim, Conceição and Almoxarife. Presence and absence of P. physalis *were recorded during 144 coastal surveys.*

Environmental data at the regional scale was collected from Copernicus Marine and Environment Monitoring Service (CMEMS). This provides up-to-date information on the physics and related biogeochemistry of the Global Ocean and European Seas on monthly basis, from 1993 to 2021 (Figure 2.17-2.24 of supplements). The temporal resolution of CMEMS data is consistent with the presences and absences data (2008-2021). The dataset of stranded *P. physalis* was prepared to use in the model by removing NAs, and by aggregating data per month (date, location and presence).

Modelling approach

We chose the machine-learning algorithm boosted regression trees (BRT) to perform species distribution modelling. This combines the advantages of both regression trees and boosting algorithms. It can handle interaction effects between different predictors (environmental data) and various response variables (species occurrence) and accommodates missing data. BRT fits complex nonlinear relationship, avoid overfitting and enables models transferability through proper hyperparametrization and forced monotonicity which increases the level of generality (Assis et al., 2017).

Correlation tests between predictors were conducted to determine which predictors could be included in the model, in macroecological and regional scales (Figure 2.15 - supplements). To this end, we first analyzed the effect between wind patterns (direction and intensity), against the effect of ocean currents patterns. And, also, the effect of total phytoplankton, against the primary production of phytoplankton. The performance of the various variables was assessed by comparing the following statistic values: total sum of squares, sensitivity, specificity and AUC for macroecological scale and threshold, AUC, omission rate, sensitivity, specificity, proportion of correctly predicted and kappa for regional scale.

To perform the BRT model algorithm, it is necessary to have information on presences and absences of the chosen species. In the case of the macroecological scale there was a lack of species absence data. Therefore, artificial absence data or pseudo absences were randomly generated. Pseudo absences need to be the same number as presences (Barbet-Massin et al., 2012). At the regional scale were used presences and absences. Observation and environmental information were combined. The machine learning algorithm overfitting and complexity was controlled by the best combinations of hyperparameter values using cross-validation and monotonicity constraints (Assis et al., 2017). An automated gridSearch approach (SDMtune package in R studio) was chosen, which searched all possible combinations of values: a range of learning rates (0. 1, 0.01, 0.001) and tree complexities (from one to four, in steps of one), for the macroecological scale approach and a range of learning rates (0.01, 0.005, 0.001, 0.0005, 0.0001), tree complexities (2-4), bag fraction (0.1 to 0.9, step 0.1), number of trees (50 to 500, step 50) and minimum observations per node (5 to 10, step 1) for the regional scale approach. Predictors were forced to produce different monotonic responses. For the macroecological approach: a negative monotonicity response was defined for maximum temperature (i.e., high values result in the absence of species), non-monotonicity for ocean currents and wind direction, and positive monotonicity response for productivity and minimum temperature (i.e., higher values will result in the presence of species). For the regional approach was defined non-monotonicity response for sampling location and wind direction and positive monotonicity response for productivity, temperature and wind speed.

Both scales' models were evaluated by determining its performance as the area under the curve (AUC) and the relative variable contribution. Model complexity was reduced by dropping one variable at a time in order to get a more parsimonious model. Predictors resulting in contributions below 5% were not considered. Response curves were evaluated for ecological realism, to understand if the model was consistent with the previous ecological knowledge (Elith & Leathwick, 2009).

The model at the macroecological scale (North Atlantic) allowed the prediction of the occurrence of the species, through the production of maps, according to the environmental conditions. At the regional scale, the model allowed us to predict a time series of *P. physalis* occurrence from 1993 to 2021. To detect the trend of the species occurrence was performed a decomposition of the predicted time series by using the average probability of occurrence predicted and its seasonality.

Results

Macroecological scale

Distribution records to model the distribution of *P. physalis* were compiled along the Atlantic Ocean from available literature records (see methods) in one dataset with 7643 coastal and offshore presences.

Table 2.1 – Accuracy of predictive models developed for *Physalia physalis* in the Atlantic Ocean. Model variables (Model_var) – water (direction and speed), wind (direction and speed), primary production of phytoplankton (PP), total phytoplankton (phyt) - threshold, true skill statistics (TSS), sensitivity (sens), specificity (specif), AUC of reduced model. The model with the best accuracy is highlighted in bold.

Model_var	threshold	TSS	sens	specif	AUC
Wind (speed and direction), PP	0.55	0.575844	0.823204	0.75264	0.871898
Wind (speed and direction), Phyt	0.54	0.617747	0.834937	0.782809	0.889503
Water (speed and direction), PP	**0.46**	**0.715795**	**0.865260**	**0.850534**	**0.890667**
Water (speed and direction), Phyt	0.59	0.686595	0.808174	0.878421	0.873603

By testing different combinations of predictions, we verified that the model including water direction and speed, as well as primary production, was the one with better accuracy (threshold =0.46 - assess the agreement between observed data and the model output -, true skill statistics=0.715795, sensitivity=0.865260, specificity=0.850534 and AUC of reduced model=0.890667; Table 2.1).

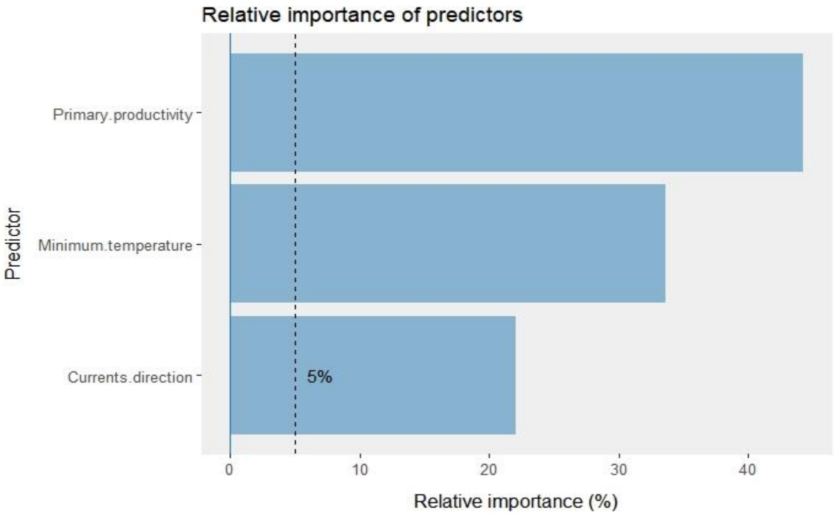


Figure 2.2 - Relative importance of each environmental predictor in the reduced model used to model the distribution of P. physalis *for the macroecological scale.*

The environmental predictors that contribute the most to explaining the distribution of *P. physalis* at a macroecological scale were primary productivity, minimum temperature and the direction of ocean currents. Maximum temperature and water speed were the predictors that less explained the distribution at the macroecological scale, and therefore were excluded from the reduced model (Figure 2.2).

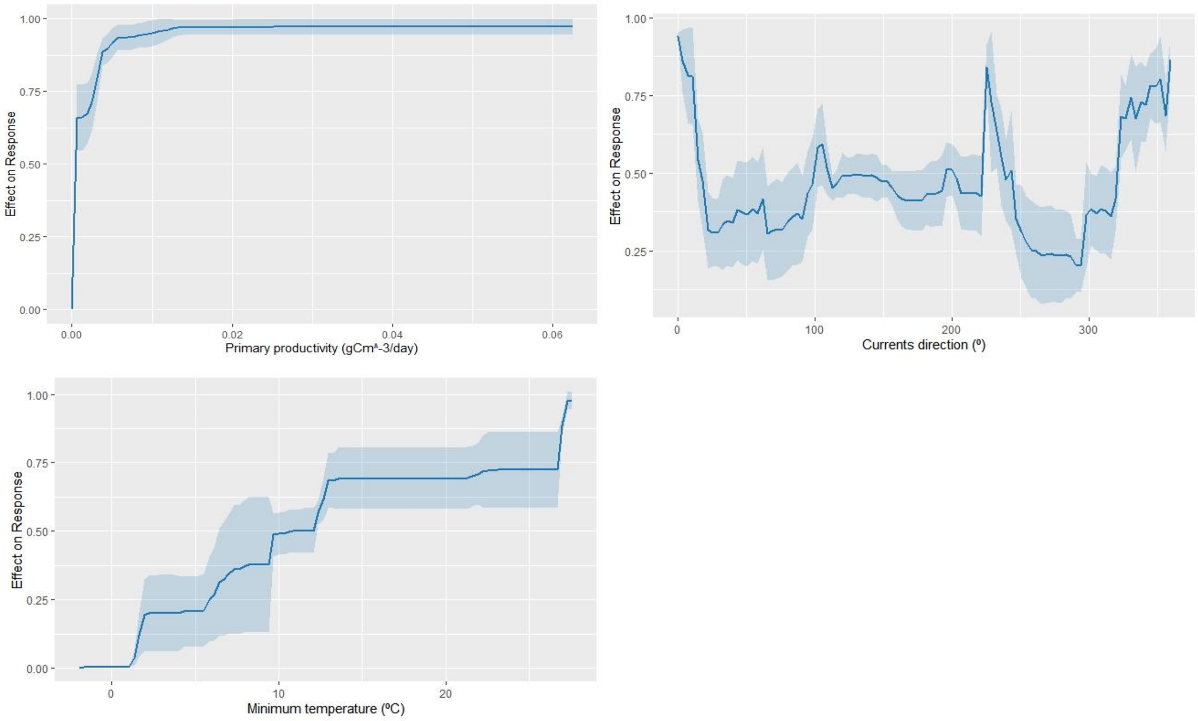


Figure 2.3 - Partial dependency plots showing the effect of primary productivity at the sea surface, direction of ocean currents and minimum temperature at the sea surface in the probability of occurrence of P. physalis.

At the macroecological scale, the partial dependence plots show the occurrence of *P. physalis* when productivity is higher than 0.44 mgC/m^3 /day (top left panel) and water temperature is higher than 12.07°C, with a significant increase in the probability of occurrence starting at 26.71ºC (bottom left panel). *P. physalis* will most likely occur in regions with well-defined patterns of the direction of ocean currents, specifically between 223.79º-232.90º - Southwest - and between 322.68º-14.31º - North-Northwest and North - (top right panel) – Figure 2.3.

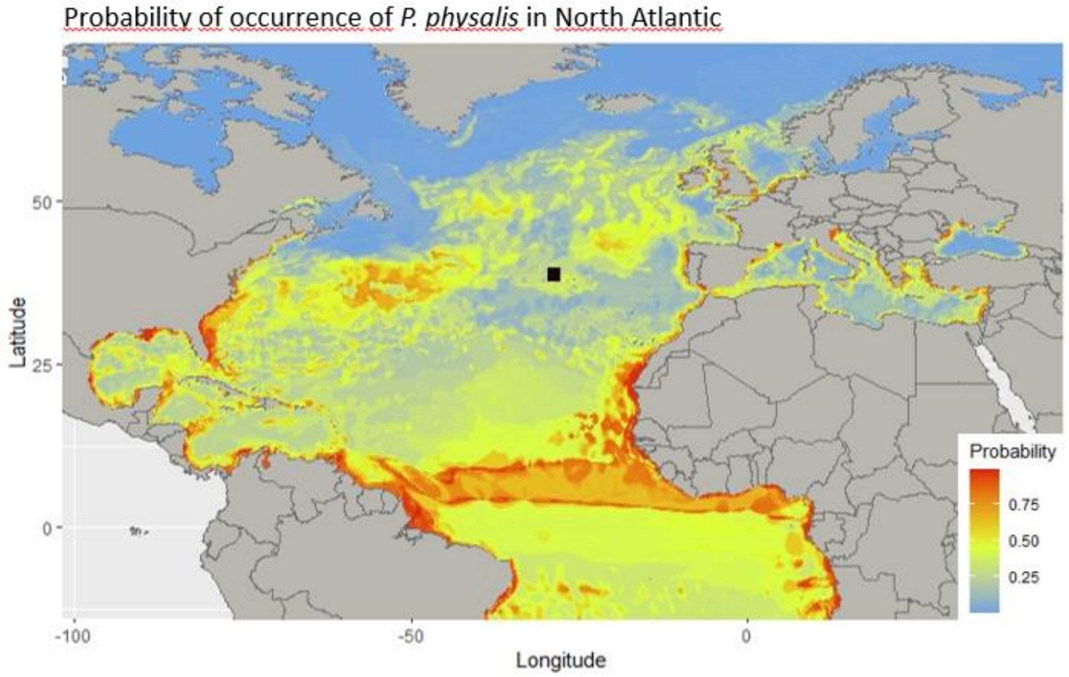


Figure 2.4 - Probability of P.physalis *occurrence in the Atlantic Ocean. The black square locates the Azores archipelago.*

The probability of occurrence of *P. physalis* in the Atlantic Ocean is highest in coastal areas, on both Atlantic coasts, where the habitat is highly suitable for the species. The coastal areas with the largest area and highest probability of occurrence are the Northeast of South America, the West African coast and the coast of the Florida peninsula. In fact, the Portuguese man-of-war is a common siphonophore in the Gulf Stream along the East coast of Florida (Jenkins, 1983). These areas of high probability of occurrence extend to the open sea, far exceeding the coastal area. Although less extensive, there is a high habitat suitability in the Gulf of Mexico, Caribbean Sea and Greater Antilles, as well as throughout the European west coast, the Mediterranean and British Isles. In the open ocean, on the other hand, the species has a generally lower probability of occurrence. There is a higher probability of occurrence in warmer areas (Tropic of Cancer) and a lower probability in colder areas, and it decreases significantly until it disappears near the pole (Arctic Circle). In the North-Northwest Atlantic Ocean, there is a large offshore area with a high probability of occurrence of the species. The same is true in the northeast, with a smaller area. In the central gyre of the North Atlantic, the habitat is less suitable for the presence of the species and therefore the probability of occurrence of the species is lower (Figure 2.4).

Regional scale

Distribution records to model the distribution of *P. physalis* were recorded during 142 coastal surveys along the coast of Faial Island, which retrieved 82 presences and 60 absences from 2008 to 2021, with interruptions.

Table 2.2 – Accuracy of predictive models developed for *Physalia physalis* in Faial Island. Model variables (Model_var) - ocean currents (currents), wind, primary production of phytoplankton (PP), total phytoplankton (phyt) - deviance explained (DE), threshold, AUC, omission rate (OR), sensitivity (sens), specificity (specif), proportion of correctly predicted (PCP). The model with the best accuracy is highlighted in bold.

Model_var	DE	Threshold	AUC	OR	sens	specif	PCP
currents_Phyt	0.8090377	0.4724725	0.979167	0.041667	0.9583333	1	0.96875
currents_PP	0.4177847	0.7797798	0.895833	0.083333	0.9166667	0.875	0.90625
wind_PP	**0.9283478**	**0.5835836**	**1**	**0**	**1**	**1**	**1**
wind_Phyt	0.7054833	0.7667668	0.9375	0.125	0.875	1	0.90625

By testing different combinations of predictions, we verified that the model fitting wind direction and intensity and primary production of phytoplankton was the one with better accuracy (deviance explained=0.9283478, threshold=0.5835836, AUC=1, omission rate=0, sensitivity=1, specificity=1, proportion of correctly predicted=1 and kappa=1; Table 2.2).

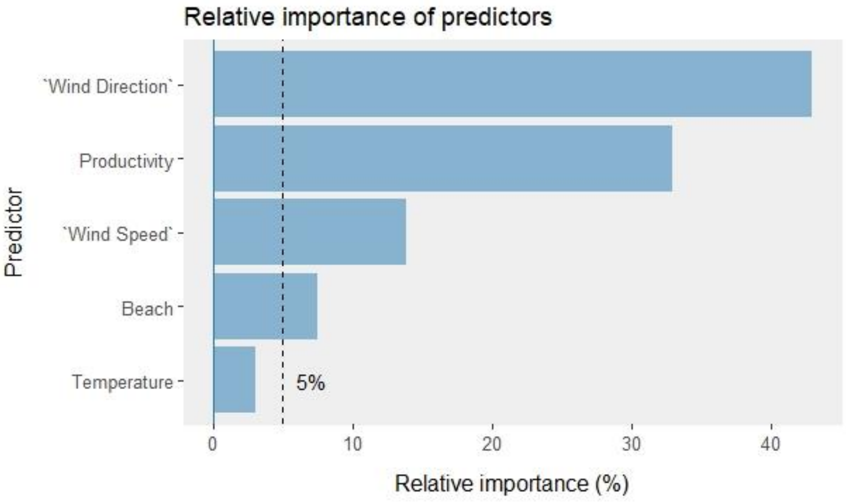


Figure 2.5 - Relative importance of each environmental predictor in the model used to model the distribution of P. physalis *for the regional scale.*

The environmental predictors that contribute the most to explaining the distribution of *P. physalis* at a regional scale were wind direction, followed by productivity and wind speed. The sampling site (beach) and regional temperature were the predictors that had a lower ability to predict the distribution at the regional scale and therefore were excluded from the reduced model (Figure 2.5).

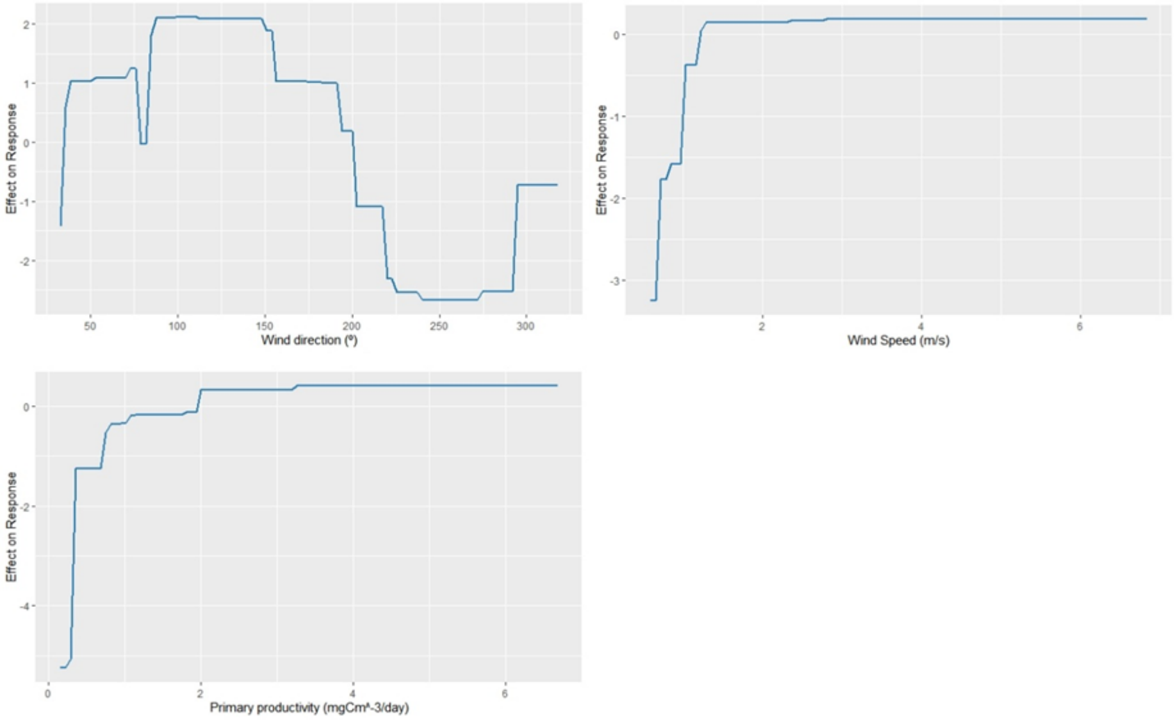


Figure 2.6 - Partial dependency plots: the effect of wind origin direction, wind speed, primary productivity in the probability of occurrence of P. physalis *– from top to bottom and from left to right.*

The partial dependency plots show that *P. physalis* has a higher probability of occurrence at the regional scale when the wind blows towards 38.61°-75.32° and 87.97°-191.77° (Northeast and East-northeast, East to South, respectively), i.e., when the wind is blowing from Southwest and West-Southwest, West to North (top left panel). The probability of occurrence is highest when productivity is higher than 0.36 mgC/m^3 /day (top right panel), with wind speed higher than 1.03 m/s (bottom right panel) (Figure 2.6).

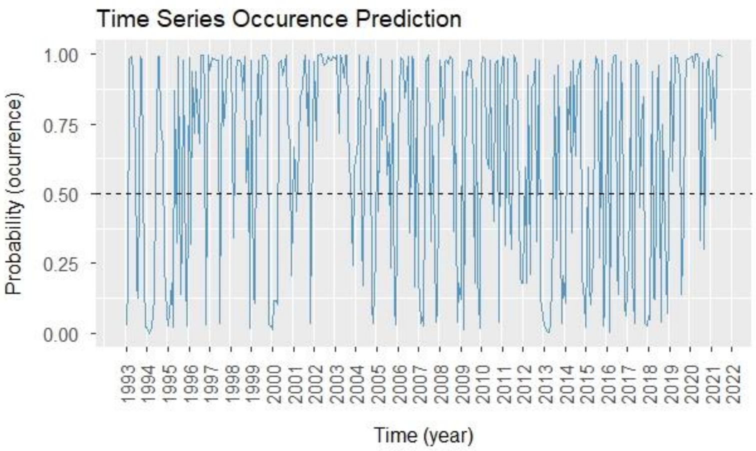


Figure 2.7 - Time series occurrence prediction from 1993 to 2021, per month.

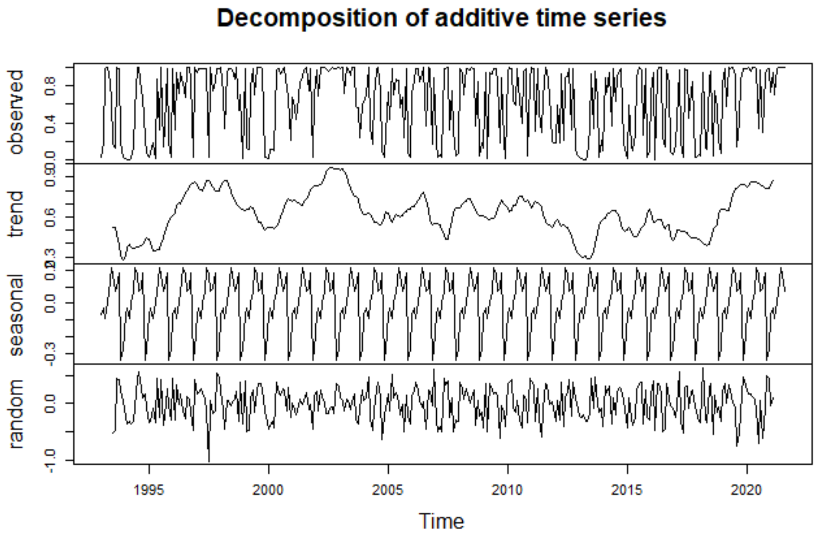


Figure 2.8 – Additive decomposition of prediction occurrence data (observed) from 1993 to 2021. Three components trend, seasonal and random are shown.

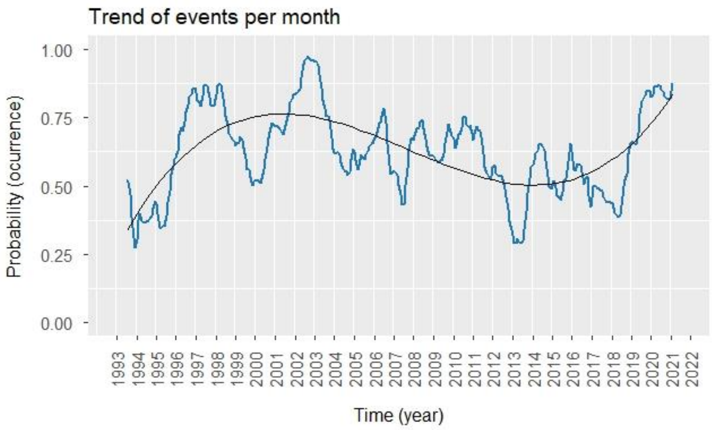


Figure 2.9 - Trend-cycle component of events per month. The trend cycle ignores the seasonality and small fluctuations.

The predicted probability of occurrence of the species has been different from year to year since 1993 (Figure 2.7). The decomposition of this prediction showed higher occurrence in the summer months, specifically June through September, and a lower occurrence in the winter months, November through March (Figure 2.16 - supplements). The probability of occurrence of *P. physalis*, removing the effect of seasonality and small fluctuations, has a sigmodal trend from 1993 to 2021. In the years 1994 to 1996 the model predicted a low probability of occurrence, followed by an increase, with a maximum in the years 1996 to 1999 and 2002 to 2004. In the following years the results show a decrease in probability, especially in the years 2007 and 2012, 2013. Recently, the results showed a sharp increase in the probability of occurrence starting in 2018, with a maximum in 2020 and 2021 (Figure 2.8 and 2.9).

Discussion

This study inferred the major environmental drivers shaping the distribution of an important species. Machine learning distribution models performing with high accuracy showed that different drivers acted at different scales. At the macroecological scale the distribution of the species is mostly driven by primary productivity, temperature and currents direction, while on the regional scale is driven by wind patterns and primary productivity. This corroborates the general message that currents, drifting winds and open ocean currents are the drivers that best shape the distribution, and for the first time, the study highlights the role of primary productivity. The results allowed us to propose which areas are most suitable for the species in the North Atlantic and also to reconstruct a timeseries at regional scale that showed high temporal variability, with higher probability of occurrence in the periods of 1996-1999, 2002-2004 and recent years. This information, unknown until now, is crucial for ecology, but also as a baseline to guide management actions. Particularly in the face of future climate change, since ocean warming seems to benefit the occurrence of the species.

Drivers and macroecological patterns

The macroecological model run with good performance, capturing 85% of the presences and allowed exploring the main drivers of the species. At the macroecological scale the distribution of *P. physalis* is mainly explained by primary productivity, temperature and ocean patterns. The model's results show the higher the temperature and productivity, the higher the probability of occurrence. Several studies relate the occurrence of jellyfish or even large groups of *P. physalis* to areas of high coastal productivity - upwelling areas and large rivers - (Cavalcante et al., 2020) and consequently to the high productivity of the trophic web of marine ecosystems (Gibbons & Richardson, 2008; Graham et al., 2014). Other studies also show the species occurrence at high temperatures (Torres-Conde et al., 2021). At a lower extent we also found a relationship between our species and ocean currents. This was unknown until now, due to scarce information on the species ecology, although it had previously been related to remarkable fluctuations in local jellyfish population densities (Gibbons & Richardson, 2008; Johnson et al., 2001). The model points to a greater increase in the probability of occurrence of the species when the direction of ocean currents is between Southwest, North-Northwest and North. These conditions favoured the occurrence of the species on both Atlantic coasts (Figure 2.4). Note that the western part of the North Atlantic has a noticeably higher probability of occurrence of the species than the eastern part. Overall, regions with the highest probability of occurrence are the warmest and most productive coastal zones and where marine offshore currents predominate (Figure 2.10). Take for example in the Northeast of South America, the coast of West Africa, and the coast of the Florida peninsula. The largest offshore area with the highest probability is in the North-Northwest Atlantic, at the same latitude as the Azores archipelago. The second largest area is located in the Northeast Atlantic (Figure 2.4).

Drivers and regional patterns

At the regional scale, models had an excellent performance, with the ability to capture 100% of the presences. Models showed a higher probability of regional occurrence with increasing productivity levels and wind patterns originated from Southwest, South-southwest, West and North. These are the proximal regions with the highest probability of occurrence at the macroecological level (North-Northwest of Atlantic Ocean). This may be due to the location of the currents and their directions relative to the Azores. The Gulf Stream gives rise to the Azores current (Bashmachnikov et al., 2004; Caldeira & Reis, 2017), which is going to transport *P. physalis* until Faial Island, from lower latitudes (Figure 2.10). In addition to wind direction, wind speed is also important. The results show a higher *P. physalis* probability of occurrence when the wind speed is higher than 1 m/s. This is in line with other studies, where the wind component is significant even at low speeds, such as 5 m/s (Headlam et al., 2020; Prieto et al., 2015). The importance of wind has been proven as well as in other studies (Bourg et al., 2022; Ferrer et al., 2015;

Ferrer & González, 2021; Headlam et al., 2020; Iosilevskii & Weihs, 2009; Macías et al., 2021). Just as at the macroecological scale, primary productivity was very important at the regional scale, higher productivity levels result in a higher probability of occurrence of the species.

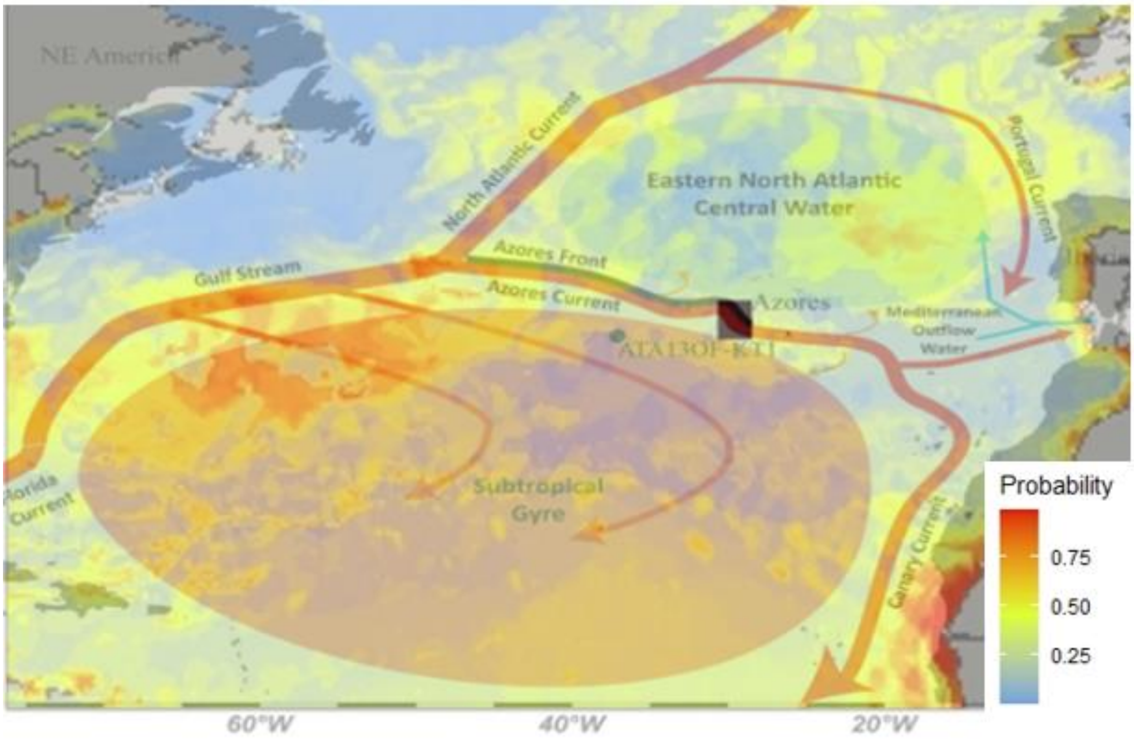


Figure 2.10 - Overlapping maps of the probability of species occurrence in the North Atlantic combined with surface circulation adapted from (Bonfardeci et al., 2018). The black square locates the Azores archipelago and red arrows the main ocean currents.

This regional-scale model when used in a timeseries decomposition analysis allowed us to infer seasonality patterns. We detected that the months of highest occurrence are from March to October (Figure 2.16 - supplements) which is in agreement with data from Azores (gelavista.ipma.pt) and from studies in the North Atlantic (Mghili et al., 2021; Pikesley et al., 2014). The fluctuations over time (1993 to 2021 - Figure 2.8/2.9) show a sigmodal trend, over almost three decades, and these large seasonal fluctuations are in line with the literature (Purcell, 2005). The model predicted a low probability of occurrence followed by an increase in the years between 1999-2004. This prediction is supported by other jellyfish population studies (Condon et al., 2013; Gibbons & Richardson, 2008). The probability of occurrence decreased during the years 2004-2013, until it reached lower probabilities in 2013. If we compare the sigmoid curve (Figure 2.9), the probability of occurrence of this year, although lower, it is higher than the probability of the years 1993-1996. From 2014 onwards there was a considerable increase in the probability of occurrence of the species. These fluctuations demonstrate not an occurrence increase of the *P.physalis* in the Azores, but rather oscillations on long-term, in line with climatic oscillations (Condon et al., 2012, 2013).

Expectations in the face of future climate change

This study allowed us to understand which drivers mediate the species. The fact that temperature and productivity are determinants on both global and regional scale poses challenges that we must acknowledge. The projected rising sea water temperatures may have consequences in species' life cycle, their expansion to higher latitudes and it is promoting water column stratification. Warmer temperatures will modify the synchronicity of fish larvae with its planktic prey, accelerate medusae growth and change their life cycle (Purcell et al., 2007); Water column stratification are favouring the jellyfish over fish, because they can survive and even reproduce in dead zones. Stratification will lead to nutrient-poor surface waters and reduced levels of primary and secondary productivity (Richardson & Gibbons, 2008). This will act as a change in the food web. Warming temperatures will contribute to an expansion and shift of the distribution of jellyfish poleward (Purcell et al., 2007; Richardson et al., 2009). The suitable habitats' expansion increases the possibility that there will be a higher incidence of stings and medical issues (Graham et al., 2014).

Net primary productivity (NPP) is the first link in open-ocean marine food webs (Bopp et al., 2013) and it is the energy source for higher trophic levels (Löscher et al., 2015). NPP depends on the amount of nutrients available at a given location (surface macro-nutrient concentrations), the stratification of the water layers, mixed-layer depth, and water circulation patterns (Steinacher et al., 2010). Different authors and different types of models agree on a predicted decline of NPP in the future as a consequence of anthropogenic global warming, either at the North Atlantic level or globally (Bopp et al., 2013; Kwiatkowski et al., 2019; Steinacher et al., 2010). Primary productivity will strongly decrease in most North Atlantic, with few exceptions - Figure 2.11 - (Laufkötter et al., 2015; Nakamura & Oka, 2019; Steinacher et al., 2010) while polar regions will have a mild increase (Steinacher et al., 2010). The regions most affected in North Atlantic will be between 20º S and 65º N (Steinacher et al., 2010), in which the Azores archipelago is included, as well as the Atlantic subtropical gyre (Kwiatkowski et al., 2019).

According to estimations, it can be expected that in the future temperature increases and primary productivity decreases in the North Atlantic. At a finer scale it is possible to say that the region of the Azores Archipelago, where today the species has a great possibility of occurrence, may become a region with lower levels of primary productivity and, consequently, with less occurrence of the species. The species is more likely to occur the greater the increase in both temperature and productivity. Thus, we predict that the species might have a higher occurrence at higher latitudes because it might follow the decrease in productivity and move poleward.

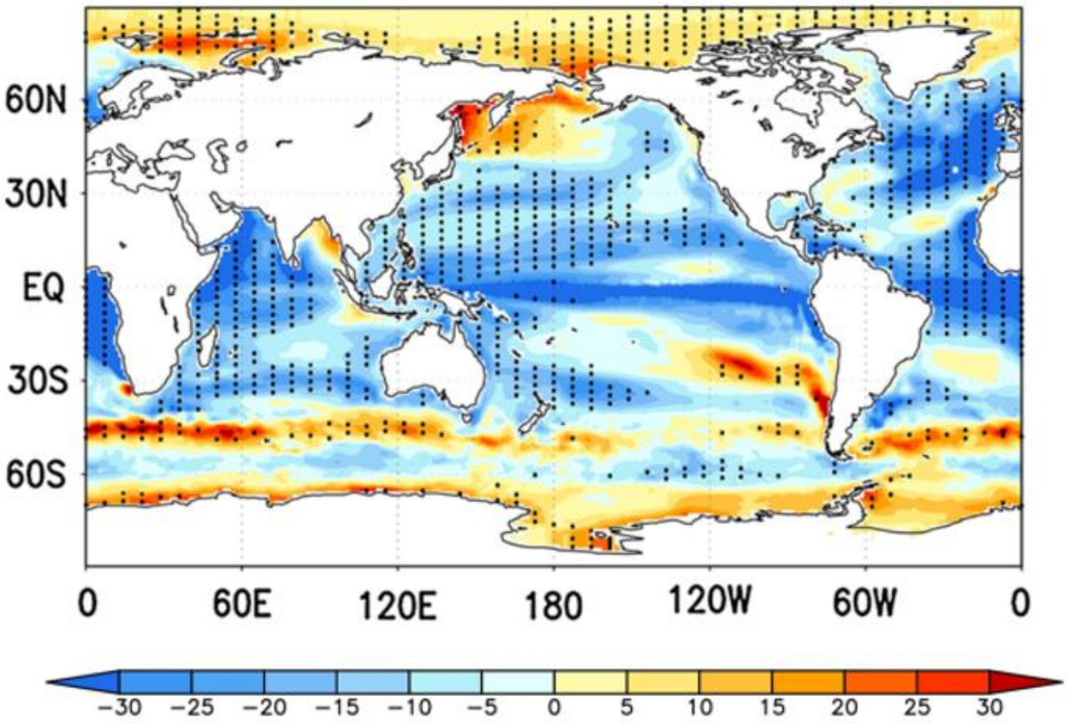


Figure 2.11 - Difference in NPP between the RCP 8.5 (2070–2099) mean and the historical mean (i.e., ΔNPP) from the CMIP results. Adapted from (Nakamura & Oka, 2019).

In terms of conservation, we can say that *P. physalis* is a species indicator of major disturbances like climate change, by being so cosmopolitan and resilient (Canepa et al., 2020). It will be easier for the species surviving and persisting in the new climate if climate predictions hold. Human intervention may be needed in its management, as well as many other species of jellyfish. Richardson et al., (2009) show several potential management responses, not all of which apply to the *P. physalis* species. In the short term, a management possibility could be to develop jellyfish products for consumption and medicine, to mechanically destroy it in the water column or to do so using bioagents. It is possible to prevent larvae settlement by reducing artificial structures, strengthen and improve protocols for cleaning of boat hulls and treatment of ballast water, and to prohibit translocation of the species. In the long term, eutrophication should be reduced, increase fisheries management, reduce overfishing, and minimize global warming through increased energy efficiency. It is also noted in the same study that it is necessary to combine more than one technique to achieve results (Richardson et al., 2009). Thus, it is necessary that research on these beings continues because knowledge is still limited.

Limitations of the models

Despite the models' good performance, they have limitations that must be discussed. Our macroecological model resulted in high accuracy, but it was highly dependent on records of occurrence. There are no long-term abundance data from jellyfish in Atlantic open ocean waters, neither of presence nor seasonality, which limits the model (Figure 2.25). This is a difficulty that will take time to overcome, due to the complexity of economic and human resources required to do offshore surveys. There is a lack of study in this area (Gibbons & Richardson, 2008). Even with a possible bias in the data for the reasons explained above, it is possible to say that the model matches up with the knowledge we have today.

The regional model is limited to data from Faial Island, even though the sampling points were five, in different directions of the island, North, South and East coast. Thus, generalizations should be careful, particularly relating to the main quadrant of *P. physalis* provenance, as this may be affected by island proximity or particular coastal morphology. It is not possible to generalize the model results to the other islands, as well as the other island groups (western and eastern) belonging to the same archipelago. A limiting factor for stranding detection and data sampling (Faerber & Baird, 2010) in the Azores Archipelago is the morphology of most of the islands, which, being volcanic, contain steep coast (Costa et al., 2014) and many places of difficult access.

Conclusion

To conclude, the most important drivers at the macroecological scale are primary productivity, temperature and currents direction and at the regional scale are wind patterns and primary productivity. Our results coincides with the study of Macías et al., (2021), where only the variables of hydrodynamics and wind conditions were used. Both models, regional and macroecological, performed well and fulfilled their purpose. The main drivers for the occurrence of *P. physalis* at both spatial scales were found and it was possible to predict the occurrence of *P. physalis* at a spatial scale in the North Atlantic and also at a large temporal scale on Faial Island. This study made it possible to map the probability of occurrence of the species for the North Atlantic, which can serve as a baseline for the management of the species. Contrary to what would be expected, in the Azores, *Physalia physalis* abundance does not appear to be increasing, but rather oscillations on a scale of decades. It can be said that temperature and productivity are determinants on both a global and regional scale for the occurrence of species. Climate change might cause changes at this level, and this will have effects in the near future. Thus, it will be necessary to consider short- and long-term management policies, due to the major socio-economic and health impacts that this species has.

Supplements

Ecological modelling data

P.physalis distribution along the Atlantic Ocean in one dataset with 7643 presences (longitude and latitude). Data used in macroecological approach available in: https://figshare.com/s/8b0bbf16adf41bf07eed

Table 2.3 – Data provided by Atlantic Naturalist Association with date, sampling location (PA:Praia do Almoxarife; PC: Praia da Conceição; PP: Praia de Porto Pim; PFet: Praia da Feteira; PFaj: Praia da Fajã), presence of *Physalia physalis* (1:yes; 0:no) and number of individuals.

Year	Month	Day	Location	Beach	Present	Number
2008	3	20	Coast	PA	1	246
2008	3	28	Coast	PA	0	0
2008	3	29	Coast	PA	0	0
2008	3	30	Coast	PA	0	0
2008	3	31	Coast	PA	0	0
2008	4	1	Coast	PC	0	0
2008	4	2	Coast	PC	1	>100
2008	4	3	Coast	PC	0	0
2008	4	4	Coast	PA	1	NA
2008	4	5	Coast	PA	1	37
2008	4	6	Coast	PA	0	0
2008	4	7	Coast	PC	0	0
2008	4	8	Coast	PC	0	0
2008	4	8	Coast	PA	0	0
2008	4	9	Coast	PA	0	0
2008	4	10	Coast	PC	1	0
2008	4	11	Coast	PP	1	23
2008	4	12	Coast	PP	1	NA
2008	4	13	Coast	PP	1	13
2008	4	13	Coast	PC	1	NA
2008	4	14	Coast	PC	1	NA
2008	4	15	Coast	PP	1	>100
2008	4	16	Coast	PP	1	64
2008	4	17	Coast	PP	1	55
2008	4	18	Coast	PP	1	128
2008	4	19	Coast	PP	1	NA
2008	4	20	Coast	PP	1	NA
2008	4	22	Coast	PP	1	NA
2008	4	23	Coast	PP	1	40-100
2008	4	24	Coast	PP	1	104
2008	4	26	Coast	PP	0	NA
2008	4	27	Coast	PP	0	NA
2008	4	28	Coast	PP	0	0
2008	4	29	Coast	PP	0	0
2008	4	30	Coast	PP	0	0
2008	5	1	Coast	PP	0	0
2008	5	2	Coast	PP	0	0
2008	5	3	Coast	PP	0	0
2008	5	6	Coast	PP	1	23
2008	5	7	Coast	PP	1	7
2008	5	9	Coast	PP	1	62
2008	5	11	Coast	PP	1	73
2008	5	12	Coast	PP	1	8
2008	5	13	Coast	PP	1	434

2008	5	14	Coast	PP	1	35
2008	5	20	Coast	PP	1	250-300
2008	5	24	Coast	PP	0	NA
2008	6	4	Coast	PP	1	8
2008	6	5	Coast	PP	1	0
2010	1	5	Coast	PP	1	0
2010	2	3	Coast	PP	1	NA
2010	2	4	Coast	PFet	1	NA
2010	2	5	Coast	PFet	1	NA
2010	2	6	Coast	PFet	1	NA
2010	2	7	Coast	PFet	1	NA
2010	2	8	Coast	PP	1	NA
2010	2	9	Coast	PP	1	NA
2010	2	10	Coast	PP	1	NA
2010	2	16	Coast	PP	NA	NA
2010	2	17	Coast	PP	0	NA
2010	2	18	Coast	PP	0	NA
2010	2	19	Coast	PP	1	NA
2010	2	20	Coast	NA	NA	NA
2010	2	28	Coast	PP	1	NA
2010	3	2	Coast	PP	0	0
2010	3	3	Coast	PP	1	NA
2010	3	7	Coast	PP	1	27
2010	3	27	Coast	PP	1	800-1500
2010	6	2	Coast	PP	1	NA
2016	6	3	Coast	PP	1	600
2016	6	4	Coast	PP	0	0
2016	6	5	Coast	PP	1	130
2016	6	7	Coast	PP	1	750
2016	6	8	Coast	PP	1	450
2016	6	10	Coast	PA	1	3
2016	6	11	Coast	PP	1	700
2016	6	13	Coast	PP	1	550
2016	7	25	Coast	PP	0	0
2016	8	9	Coast	PP	0	0
2016	8	26	Coast	PP	0	0
2016	11	20	Coast	PP	0	0
2016	11	22	Coast	PP	0	0
2016	11	23	Coast	PP	0	0
2016	11	24	Coast	PP	0	0
2016	11	25	Coast	PP	0	0
2017	2	20	Coast	PP	0	0
2017	3	2	Coast	PP	0	0
2017	3	3	Coast	PP	1	NA
2017	3	4	Coast	PP	1	NA
2017	3	5	Coast	PP	1	NA
2017	3	6	Coast	PP	1	351
2017	3	8	Coast	PP	1	43
2017	3	11	Coast	PP	0	0
2017	3	12	Coast	PP	0	0
2017	3	28	Coast	PP	1	86
2017	6	1	Coast	PP	0	0
2017	6	9	Coast	PP	1	72
2018	1	10	Coast	PP	0	0
2018	1	15	Coast	PP	0	0
2018	1	18	Coast	PP	0	0
2018	1	25	Coast	PP	0	0
2018	3	12	Coast	PP	0	NA
2018	3	16	Coast	PP	0	0
2018	3	23	Coast	PP	1	17

2018	3	28	Coast	PP	0	0
2018	3	30	Coast	PP	0	0
2018	4	2	Coast	PP	0	0
2020	3	4	Coast	PP	1	85
2020	3	10	Coast	PP	1	7
2020	3	13	Coast	PP	0	0
2020	3	31	Coast	PP	0	0
2020	4	6	Coast	PP	1	>1000
2020	4	30	Coast	PP	1	NA
2020	5	4	Coast	PP	1	>1000
2020	5	8	Coast	PP	1	>1000
2020	5	11	Coast	PP	1	13
2020	5	15	Coast	PP	1	80-90
2020	5	18	Coast	PP	1	177-230
2020	5	22	Coast	PP	1	67-200
2020	5	25	Coast	PP	1	181
2020	5	29	Coast	PP	1	10
2020	6	1	Coast	PP	0	0
2020	6	5	Coast	PFaj	1	>1000
2020	6	8	Coast	PP	0	0
2020	6	12	Coast	PP	0	0
2020	6	15	Coast	PP	0	0
2020	6	19	Coast	PP	1	42
2020	9	9	Coast	PP	0	0
2020	9	15	Coast	PP	0	0
2020	9	15	Coast	PP	0	0
2020	9	15	Coast	PP	0	0
2020	7	3	Coast	PP	0	0
2020	7	22	Coast	PP	0	0
2021	5	25	Coast	PP	1	3
2021	5	26	Coast	PP	1	8
2021	6	4	Coast	PP	1	2
2021	6	5	Coast	PP	1	11
2021	6	13	Coast	PP	0	0
2021	6	28	Coast	PP	1	1
2021	6	29	Coast	PP	1	13
2021	7	1	Coast	PP	1	2
2021	7	2	Coast	PP	1	3
2021	7	3	Coast	PP	0	0
2021	7	5	Coast	PP	1	8

Population Dynamics

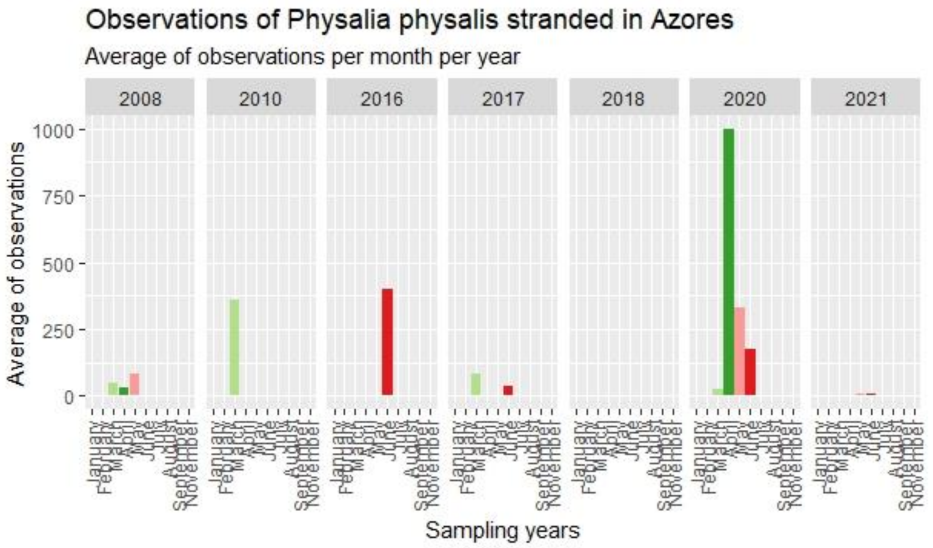


Figure 2.12 - Average observations of Physalia physalis *stranded in Faial Island, Azores per month per year.*

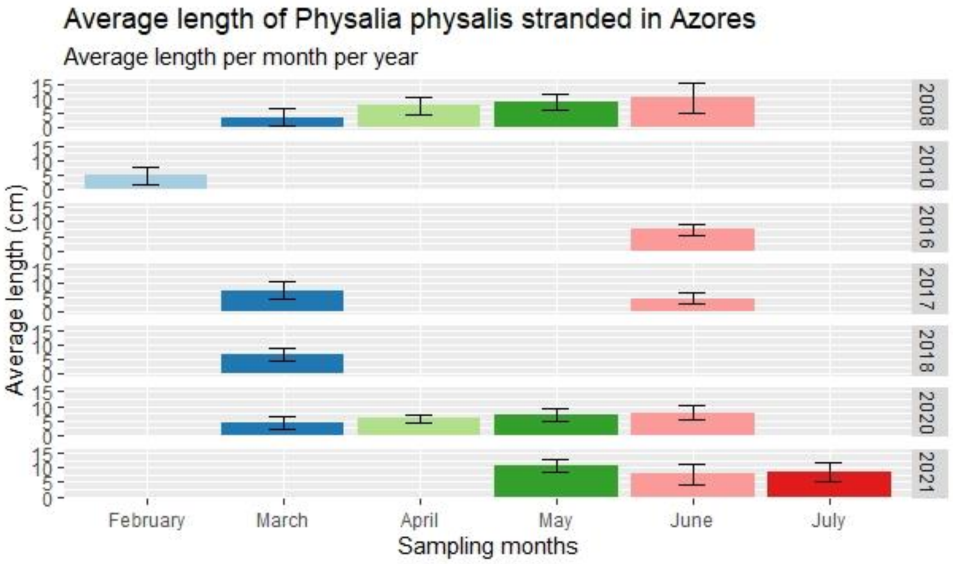


Figure 2.13 - Average length of Physalia physalis' *pneumatophore done in Faial Island, Azores per month per year.*

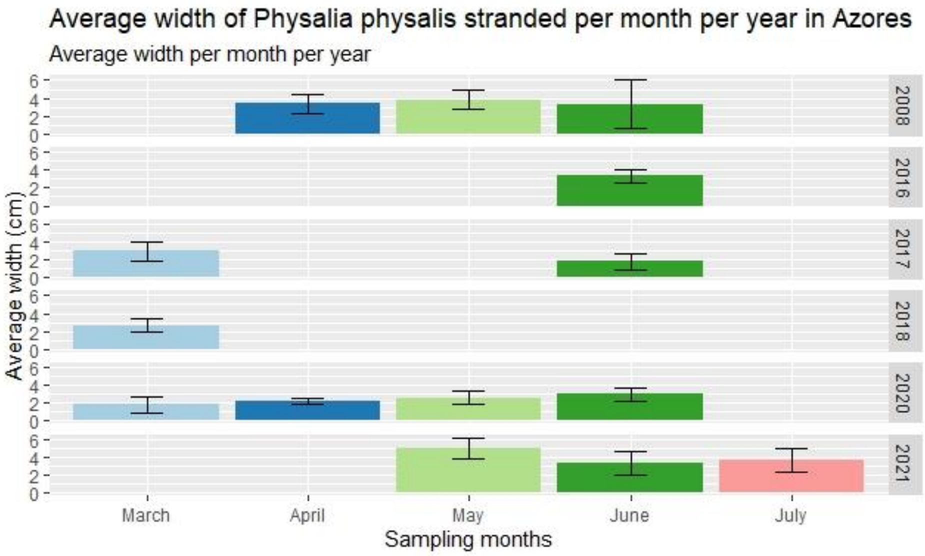


Figure 2.14 - Average width of Physalia physalis' *pneumatophore done in Faial Island, Azores per month per year.*

In the years 2010, 2016 and 2020, there were many observations of *P. physalis* on average on Faial Island, Azores (Figure 2.2). However, regarding pneumatophore size, more data is available for the years 2008, 2020 and 2021, (Figure 2.3). It is possible to see an increase, on average per month, in the length of the individuals during the years 2008 and 2020 and an increase, on average per month, in the width of the individuals during the year 2020, (Figure 2.4).

Ecological Modelling

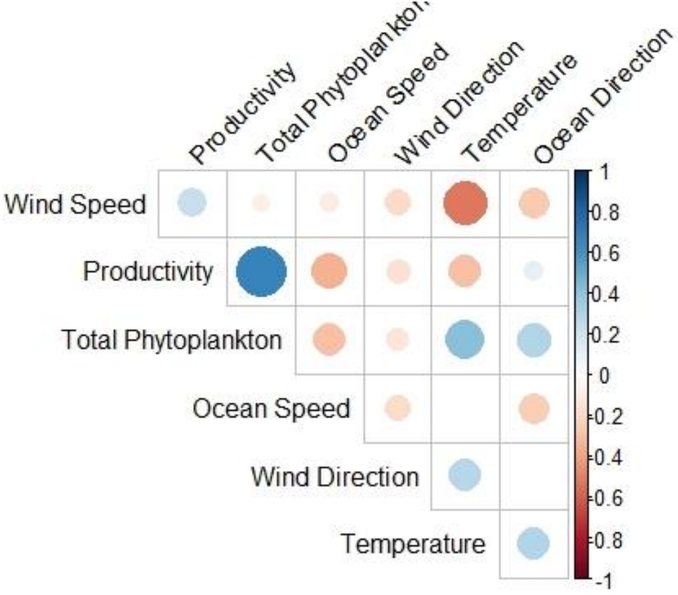


Figure 2.15 - Correlation between environmental variables used in the model.

Productivity is correlated with total phytoplankton, they are collinear. Temperature and wind speed are negatively correlated; when it is windy, the temperature tends to drop.

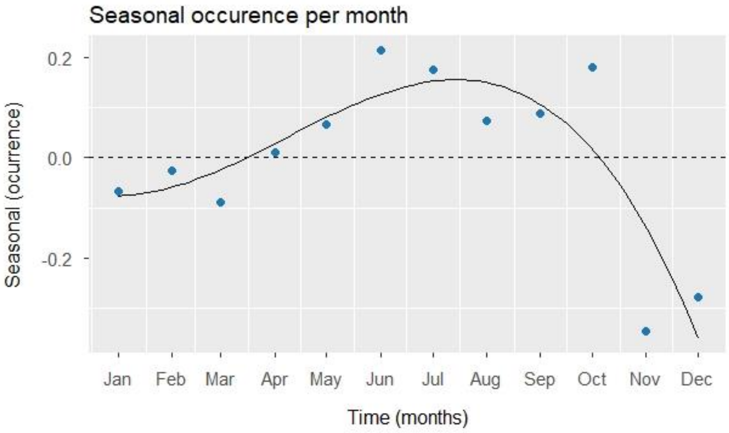


Figure 2.16 - Seasonal occurrence of Physalia physalis *per month in Faial Island.*

The effect of seasonality shows a higher occurrence in the summer months, specifically from June to September, and a lower occurrence in the winter months, from November to March.

Climatic Data

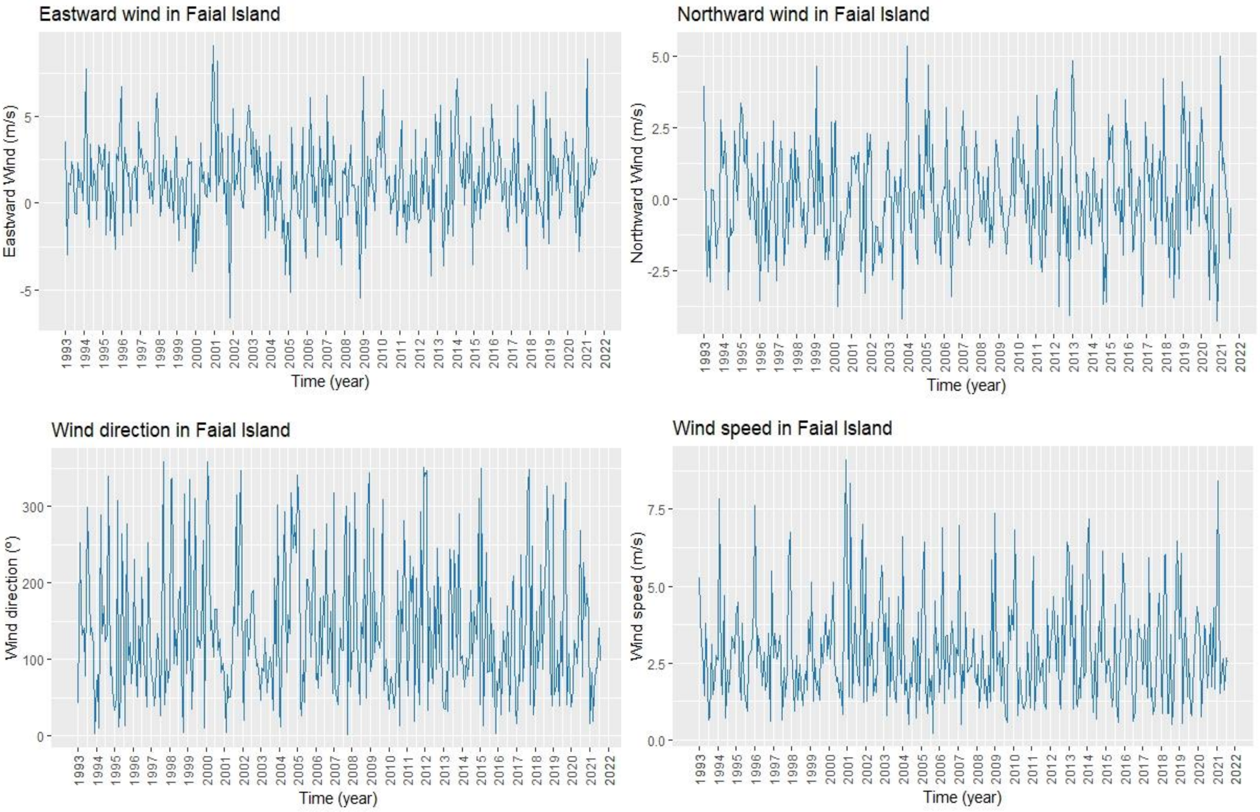


Figure 2.17 - Wind components in Faial Island, Azores from 1993 to July 2021: Eastward wind, Northward wind, wind direction and speed – from top to bottom and from left to right.

On the top left panel, it is possible to see which winds come from the East (positive values) and which come from the West (negative values). On the top right panel, you can see which winds come from the North (positive values) and which come from the South (negative values) and their average speed per month. The bottom left panel shows that in the years 2000-2001, 2002-2004, 2009-2010, 2015-2017 and from 2021 onwards there was a predominance of winds from directions of the first and second quadrant (0º-180º). In the bottom right panel, you can see the different wind speeds and an oscillation between them.

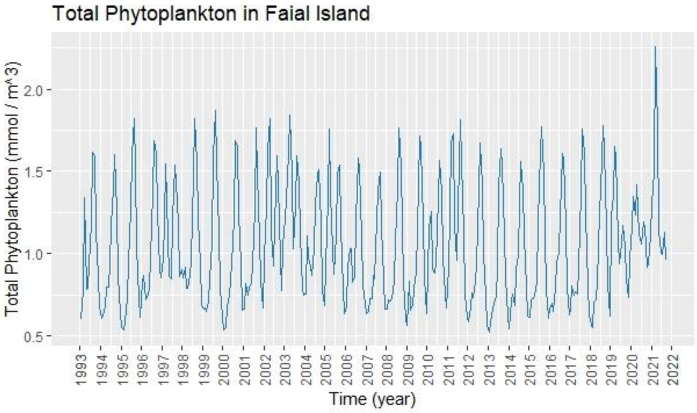


Figure 2.18 - Total phytoplankton in Faial Island, Azores in millimoles per cubic meter.

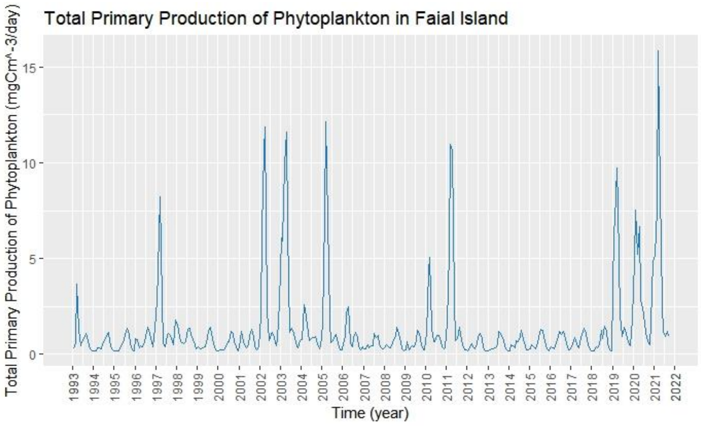


Figure 2.19 – Total primary production of phytoplankton in Faial Island, Azores in milligrams of carbon per cubic meter per day.

Total phytoplankton has remained more or less constant in recent years. In early 2019, there was a decrease, followed by a productivity peak in early 2021 (Figure 2.7). Total primary production of phytoplankton had some high peaks in 1997, 2002, 2003, 2005, 2011, 2019, 2020 and 2021 (Figure 2.8).

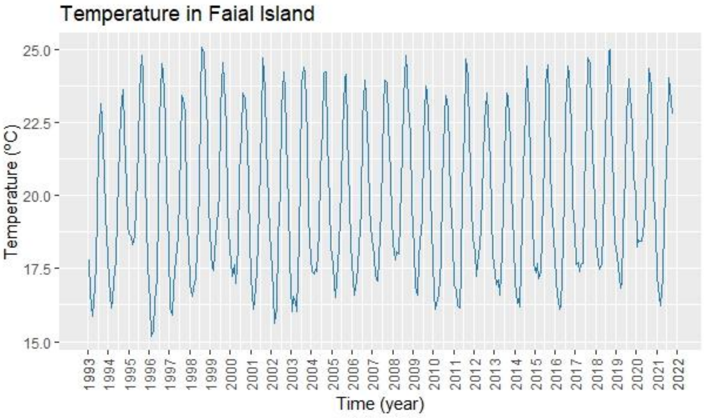


Figure 2.20 - Temperature in Faial Island in Celsius degrees.

The temperature in Faial Island oscillates between 15ºC and 25ºC, according to the seasons.

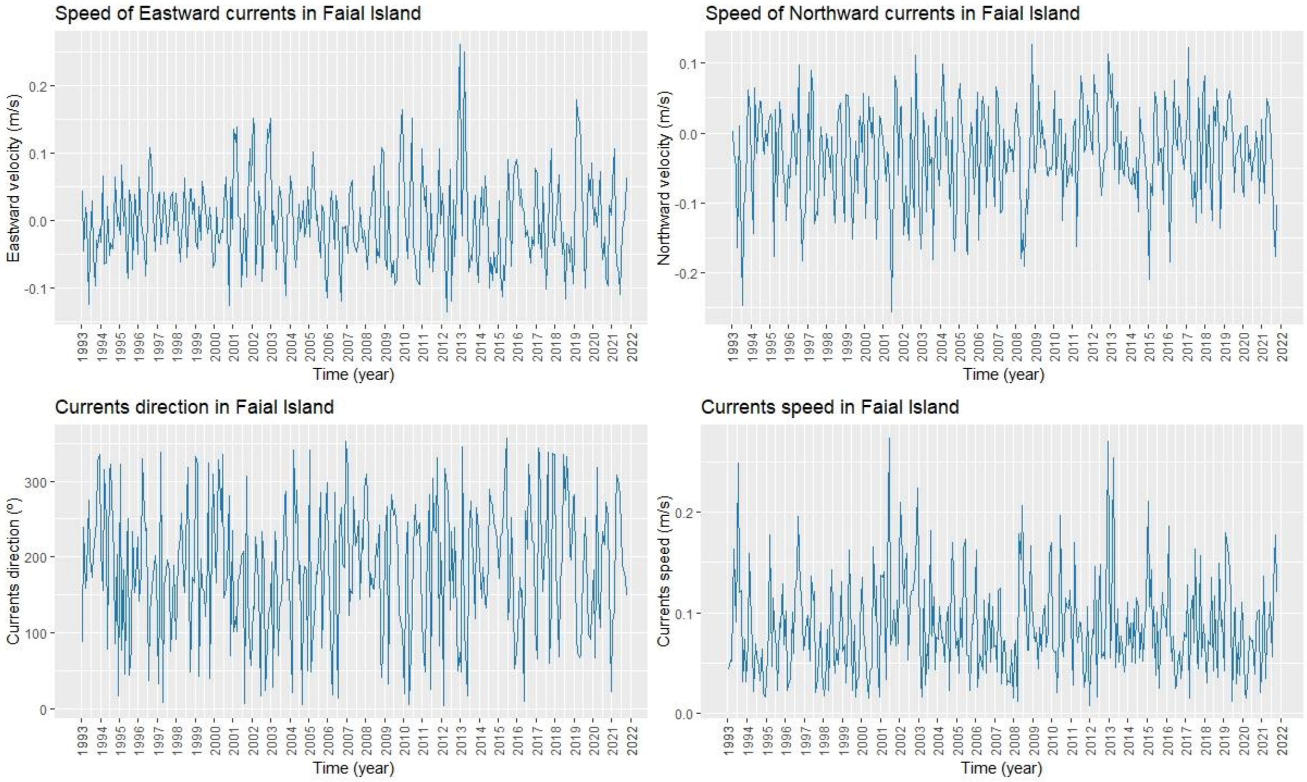


Figure 2.21 - Ocean currents components in Faial Island, Azores from 1993 to July 2021: Eastward, Northward, direction and speed of currents – from top to bottom and from left to right.

On the top left panel, it is possible to see which ocean currents originated from the East (positive values) and which come from the West (negative values). On the top right panel, you can see ocean currents originated the North (positive values) and from the South (negative values) and their average speed per month. The bottom left panel shows that in the years 1996, 2000-2001, 2006-2008, 2013-2016 and 2018-2019 there was a predominance of winds from directions of the third and fourth quadrant (180º-360º). In the bottom right panel, you can see the different ocean current speeds with higher values in 1994, 2001, 2002, 2003,2013 and 2015.

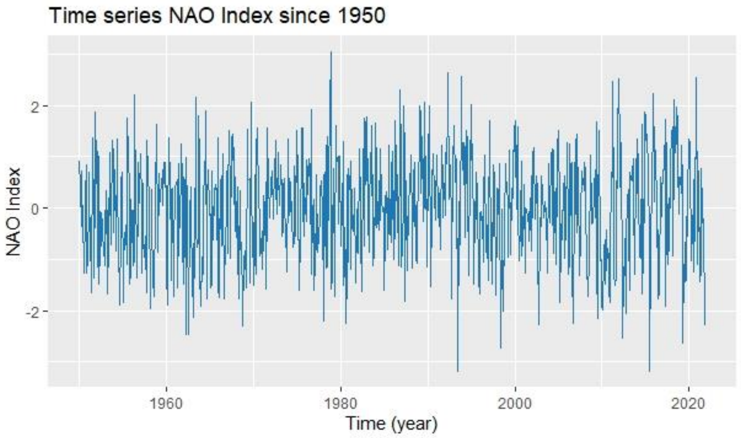


Figure 22 - North Atlantic Oscillation values since 1950.

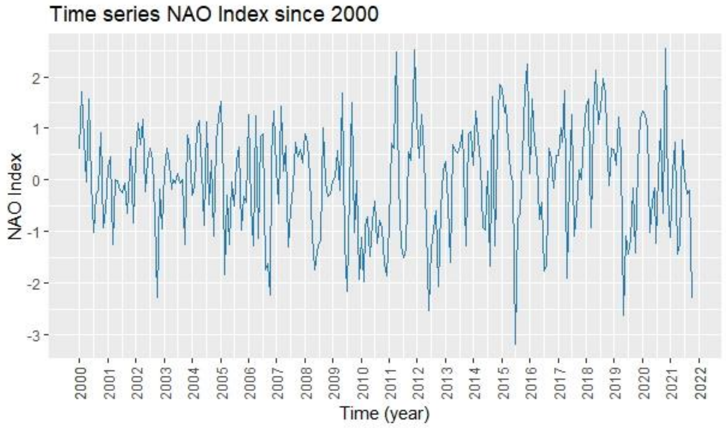
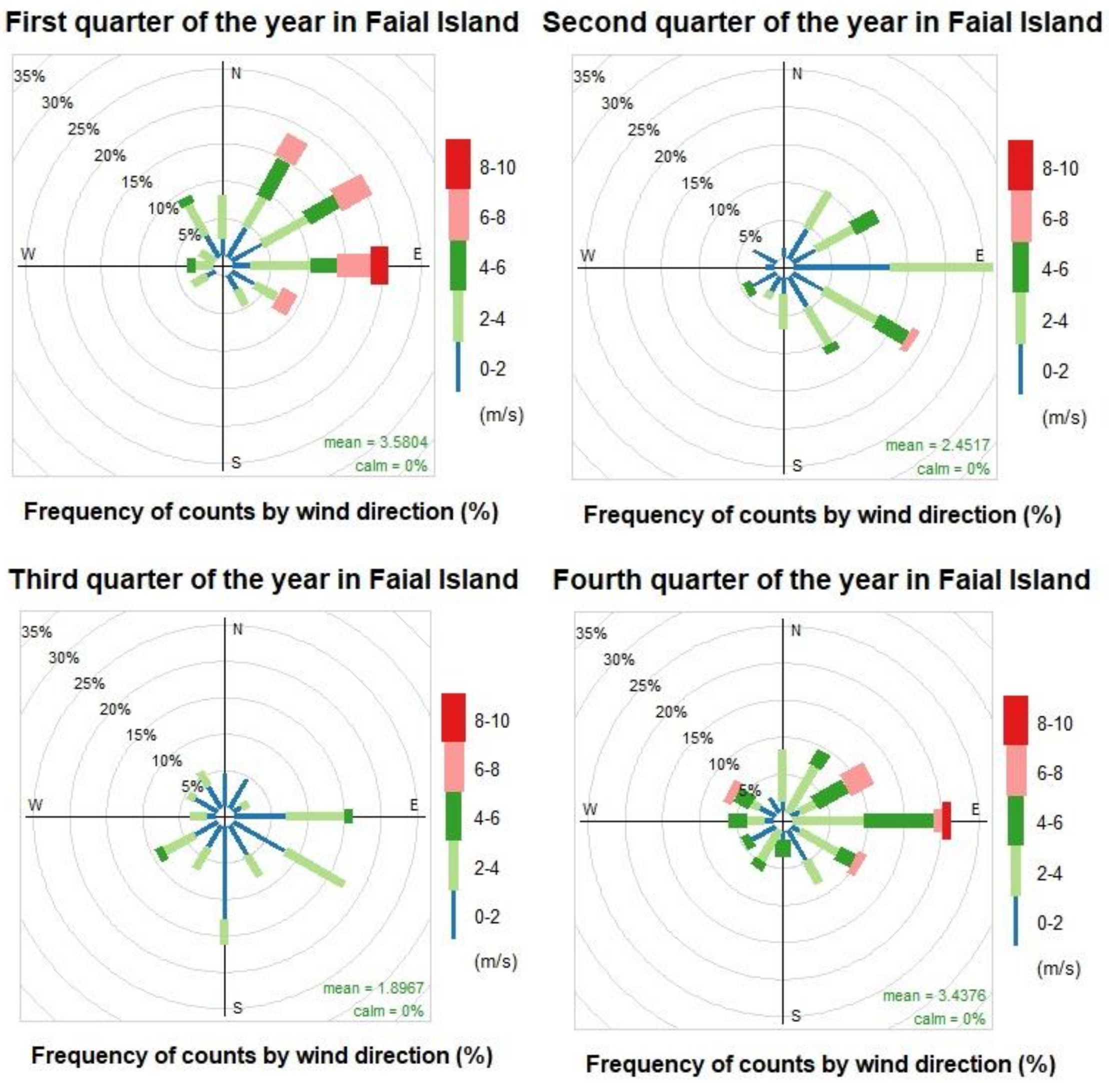


Figure 2.23 - North Atlantic Oscillation values since 2000.

At the beginning of the century, NAO values varied little. Starting in 2008, very low and very high values began to be recorded. 2011, 2012, 2015 and 2020 show very high values and 2012, 2015 and 2019, very low values.

.



First quarter of the year in Faial Island

Second quarter of the year in Faial Island

Third quarter of the year in Faial Island

Fourth quarter of the year in Faial Island

Figure 2.24 - Representation of monthly data divided into quarters on the components of wind direction and speed on Faial Island.

The wind rose shows the wind components U and V (Eastward and Northward respectively) which define wind speed and direction values. The directions taken by the wind are represented by radial lines, the wind frequency by concentric lines, and the wind speed by color-coded bars. In the first quarter of the year on Faial Island, the wind direction predominated North-northeast (22.5º), East-northeast (67.5º), and East (90º), with a maximum wind frequency of approximately 21% northeast. The predominant wind speed was 2-4 m/s and the maximum wind speed was 8-10 m/s (top left panel).

In the second quarter of the year, wind direction predominated to East (90º) and East-southeast (112,5º), with a wind frequency maximum of approximately 26% East. Predominant wind speed was 2-4 m/s and maximum wind speed 6-8 m/s (top right panel).

In the third quarter of the year, wind direction predominated to East (90º), East-southeast (112,5º), and South (180º) with a wind frequency maximum of approximately 17% E. Predominant wind speed was 2-4 m/s and maximum wind speed 4-6 m/s (bottom left panel).

In the fourth quarter of the year, wind direction predominated to East-northeast (67.5º), East (90º), and East-southeast (112,5º) with a wind frequency maximum approximately 22% E. Predominant wind speed was 2-4 m/s and maximum wind speed 8-10 m/s (bottom right panel).

Distribution of records

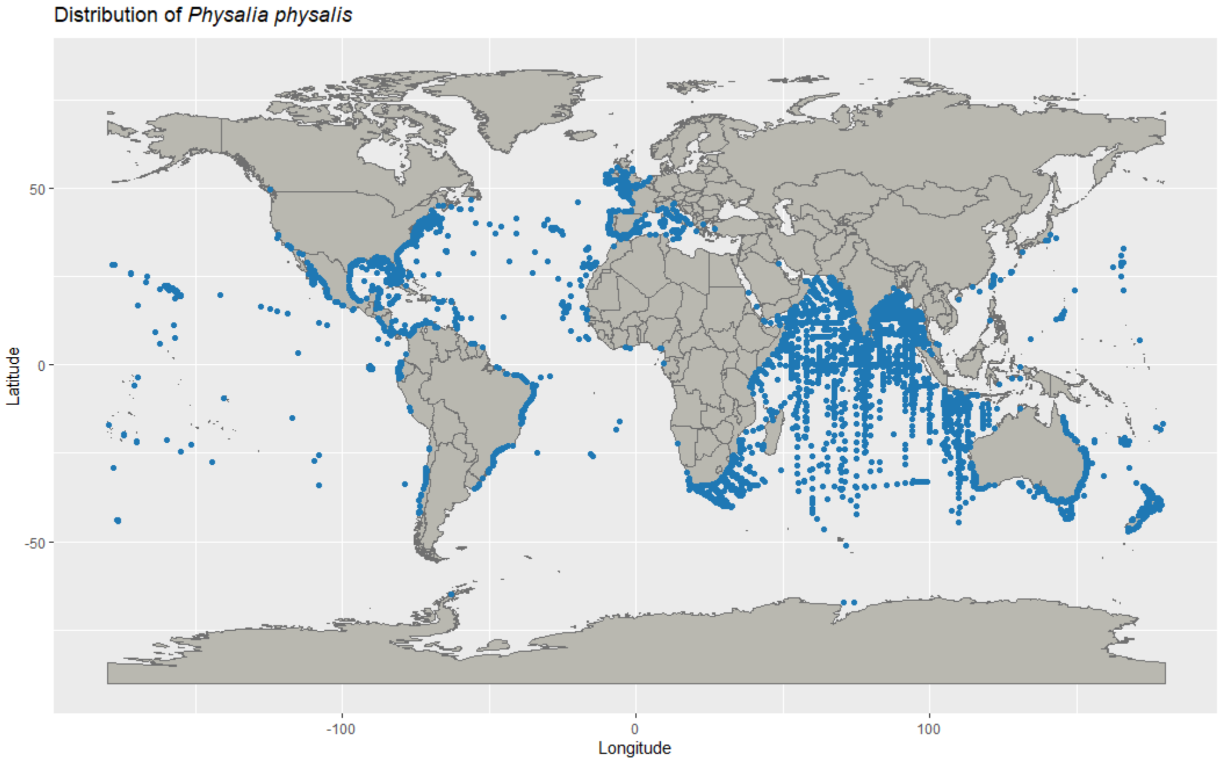


Figure 2.25 – Distribution of records of Physalia physalis *on blue dots.*

P. physalis distribution, was compiled from available literature records (see methods), in one dataset with 16702 presences (Figure 2.25). The region with the most offshore data is the Indian Ocean.

References

Aouititen, M., Bekkali, R., Nachit, D., Luan, X., & Mrhraoui, M. (2019). Predicting jellyfish strandings in the Moroccan North-West mediterranean coastline. *European Scientific Journal*, *15*(2), 72–84. https://doi.org/10.19044/esj.2019.v15n2p72

Araya, J., Aliaga, J., & Araya, M. (2016). On the distribution of Physalia physalis (Hydrozoa: Physaliidae) in Chile. *Marine Biodiversity*, *46*(3), 731–735. https://doi.org/10.1007/s12526-015-0417-6

Assis, J., Berecibar, E., Claro, B., Alberto, F., Reed, D., Raimondi, P., & Serrão, E. (2017). Major shifts at the range edge of marine forests: the combined effects of climate changes and limited dispersal. *Scientific Reports*, *7*(1), 1–10. https://doi.org/10.1038/srep44348

Attrill, M., Wright, J., & Edwards, M. (2007). Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography*, *52*(1), 480–485. https://doi.org/10.4319/lo.2007.52.1.0480

Barbet-Massin, M., Jiguet, F., Albert, C., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, *3*(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Bardi, J., & Marques, A. (2007). Taxonomic redescription of the Portuguese man-of-war, Physalia physalis (Cnidaria, Hydrozoa, Siphonophorae, Cystonectae) from Brazil. *Iheringia, Série Zoologia*, *97*, 425–433. https://doi.org/10.1590/S0073-47212007000400011

Bashmachnikov, I., Lafon, V., & Martins, A. (2004). Sea surface temperature distribution in the Azores region. Part II: space-time variability and underlying mechanisms. *Arquipélago*, *21A*, 19–32.

Bergier, P., Thévenot, M., & Qninba, A. (2013). Notes naturalistes au Sahara Atlantique marocain-5. *Go-South Bulletin*, *10*, 113–197.

Bo, M., Mabruk, S., Balistreri, P., Bariche, M., Batjakas, I., Betti, F., Bilan, M., Canese, S., Cattaneo-Vietti, R., Corsini-Foka, M., Crocetta, F., Deidun, A., Dulčić, J., Grinyo, J., Kampouris, T., Ketsilis-Rinis, V., Kousteni, V., Koutsidi, M., Lubinevsky, H., … Gerovasileiou, V. (2020). New records of rare species in the Mediterranean Sea (October 2020). *Mediterranean Marine Science*, *21*(3), 608–630. https://doi.org/10.12681/mms.23674

Bopp, L., Resplandy, L., Orr, J., Doney, S., Dunne, J., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Seferian, R., Tjiputra, J., & Vichi, M. (2013). Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences*, *10*(10), 6225–6245. https://doi.org/10.5194/bg-10-6225-2013

Bosch-Belmar, M., M'Rabet, C., Dhaouadi, R., Chalghaf, M., Yahia, M., Fuentes, V., Piraino, S., & Yahia, K. (2016). Jellyfish stings trigger gill disorders and increased mortality in farmed Sparus aurata (Linnaeus, 1758) in the Mediterranean Sea. *PLoS One*, *11*(4), 11. https://doi.org/10.1371/journal.pone.0154239

Bosch-Belmar, M., Milisenda, G., Basso, L., Doyle, T., Leone, A., & Piraino, S. (2021). Jellyfish impacts on marine aquaculture and fisheries. *Reviews in Fisheries Science*

& Aquaculture, *29*(2), 242–259. https://doi.org/10.1080/23308249.2020.1806201

Bourg, N., Schaeffer, A., Cetina-Heredia, P., Lawes, J., & Lee, D. (2022). Driving the blue fleet: Temporal variability and drivers behind bluebottle (Physalia physalis) beachings off Sydney, Australia. *PloS One*, *17*(3), 17. https://doi.org/10.1371/journal.pone.0265593

Caldeira, R., & Reis, J. (2017). The Azores confluence zone. *Frontiers in Marine Science*, *4*, 37. https://doi.org/10.3389/fmars.2017.00037

Canepa, A., Purcell, J., Córdova, P., Fernández, M., & Palma, S. (2020). Massive strandings of pleustonic Portuguese Man-of-War (Physalia physalis) related to ENSO events along the southeastern Pacific Ocean. *Latin American Journal of Aquatic Research*, *48*(5), 806–817. https://doi.org/10.3856/vol48-issue5-fulltext-2530

Castriota, L., Falautano, M., Battaglia, P., Maraventano, G., Prazzi, E., Ammendolia, G., & Andaloro, F. (2017). First record of Physalia physalis in the Pelagie Islands (Strait of Sicily) and additional records in the Strait of Messina. *Cahiers de Biologie Marine*, *58*, 1–4. https://doi.org/10.21411/CBM.A.E207E474

Cavalcante, M., Rodrigues, Z., Hauser-Davis, R., Siciliano, S., Junior, H., & Nunes, J. (2020). Health-risk assessment of Portuguese man-of-war (Physalia physalis) envenomations on urban beaches in São Luís city, in the state of Maranhão, Brazil. *Revista Da Sociedade Brasileira De Medicina Tropical*, *53*, 7. https://doi.org/10.1590/0037-8682-0216-2020

Cazorla-Perfetti, D., & Posso, C. (2015). Presencia del Cnidario Hidrozoario Porpita porpita (anthoathecata: porpitidae) en los balnearios de Buchuaco, península de Paraguaná, estado Falcón, Venezuela y su importancia médica. *SABER. Revista Multidisciplinaria Del Consejo de Investigación de La Universidad de Oriente*, *27*(3), 508–510.

Cegolon, L., Heymann, W., Lange, J., & Mastrangelo, G. (2013). Jellyfish stings and their management: a review. *Marine Drugs*, *11*(2), 523–550. https://doi.org/10.3390/md11020523

Condon, R., Duarte, C., Pitt, K., Robinson, K., Lucas, C., Sutherland, K., Mianzan, H., Bogeberg, M., Purcell, J., Decker, M., Uye, S., Madin, L., Brodeur, R., Haddock, S., Malej, A., Parry, G., Eriksen, E., Quiñones, J., Acha, M., … Graham, W. (2013). Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences*, *110*(3), 1000–1005. https://doi.org/10.1073/pnas.1210920110

Condon, R., Graham, W., Duarte, C., Pitt, K., Lucas, C., Haddock, S., Sutherland, K., Robinson, K., Dawson, M., Decker, M., Mills, C., Purcell, J., Malej, A., Mianzan, H., Uye, S., Gelcich, S., & Madin, L. (2012). Questioning the rise of gelatinous zooplankton in the world's oceans. *BioScience*, *62*(2), 160–169. https://doi.org/10.1525/bio.2012.62.2.9

Condon, R., Steinberg, D., Giorgio, P., Bouvier, T., Bronk, D., Graham, W., & Ducklow, H. (2011). Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proceedings of the National Academy of Sciences*, *108*(25), 10225–10230. https://doi.org/10.1073/pnas.1015782108

Costa, A., Marques, F., Hildenbrand, A., Sibrant, A., & Catita, C. (2014). Large-scale catastrophic flank collapses in a steep volcanic ridge: the Pico–Faial Ridge, Azores Triple Junction. *Journal of Volcanology and Geothermal Research*, *272,* 111–125. https://doi.org/10.1016/j.jvolgeores.2014.01.002

Ekwu, S., & Sikoki, F. (2005). Species composition and distribution of zooplankton in the Lower Cross River Estuary. *African Journal of Applied Zoology and Environmental Biology*, *7*, 5–10. https://doi.org/10.4314/ajazeb.v7i1.41137

Elith, J., & Leathwick, J. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40,* 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Faerber, M., & Baird, R. (2010). Does a lack of observed beaked whale strandings in military exercise areas mean no impacts have occurred? A comparison of stranding and detection probabilities in the Canary and main Hawaiian Islands. *Marine Mammal Science*, *26*(3), 602–613. https://doi.org/10.1111/j.1748-7692.2010.00370.x

Fathalli, A., Zaafrane, S., Maatouk, K., Hafi, O., Hamza, A., & Missaoui, H. (2020). First record of the Siphonophore physalia physalis (Linnaeus, 1758) in the gulf of Tunis (Tunisia). *Bulletin de l'Institut National Des Sciences et Technologies de La Mer de Salammbô*, *47,* 203–207.

Fautin, D. (2009). Structural diversity, systematics, and evolution of cnidae. *Toxicon*, *54*(8), 1054–1064. https://doi.org/10.1016/j.toxicon.2009.02.024

Ferrer, L., & González, M. (2021). Relationship between dimorphism and drift in the Portuguese man-of-war. *Continental Shelf Research*, *212*, 104269. https://doi.org/10.1016/j.csr.2020.104269

Ferrer, L., & Pastor, A. (2017). The Portuguese man-of-war: Gone with the wind. *Regional Studies in Marine Science*, *14,* 53–62. https://doi.org/10.1016/j.rsma.2017.05.004

Ferrer, L., Zaldua-Mendizabal, N., Campo, A., Franco, J., Mader, J., Cotano, U., Fraile, I., Rubio, A., Uriarte, A., & Caballero, A. (2015). Operational protocol for the sighting and tracking of Portuguese man-of-war in the southeastern Bay of Biscay: Observations and modeling. *Continental Shelf Research*, *95*, 39–53. https://doi.org/10.1016/j.csr.2014.12.011

Flores-Galicia, L., & Cruz-Francisco, V. (2018). Primeros registros de medusas (cubozoa, scyphozoa), sifonóforos (hydrozoa) y ctenóforos (tentaculata) del sistema arrecifal Lobos-tuxpan, México. *CICIMAR Oceánides*, *33*(1), 25–38. https://doi.org/10.37543/oceanides.v33i1.222

Geetha, S., Kumar, J., Mohapatra, A., & Sornaraj, R. (2019). Occurrence of Portuguese man-of war along Digha coast, West Bengal: a threat to tourists and fisherfolk. *Indian Journal of Geo-Marine Sciences*, *48*(1), 96–98.

Gibbons, M., & Richardson, A. (2008). Patterns of jellyfish abundance in the North Atlantic. In K. Pitt & J. Purcell (Eds.), *Jellyfish Blooms: Causes, Consequences, and Recent Advances* (pp. 51–65). Springer. https://doi.org/10.1007/978-1-4020-9749-2_4

Graham, W., Gelcich, S., Robinson, K., Duarte, C., Brotz, L., Purcell, J., Madin, L., Mianzan, H., Sutherland, K., Uye, S., Pitt, K., Lucas, C., Bøgeberg, M., Brodeur, R., & Condon, R. (2014). Linking human well-being and jellyfish: ecosystem services, impacts, and societal responses. *Frontiers in Ecology and the Environment*, *12*(9), 515–523. https://doi.org/10.1890/130298

Graham, W., & Hamner, W. (2001). A physical context for gelatinous zooplankton aggregations: a review. In J. Purcell, W. Graham, & H. Dumont (Eds.), *Jellyfish blooms: ecological and societal importance* (pp. 199–212). Springer. https://doi.org/10.1007/978-94-010-0722-1_16

Headlam, J., Lyons, K., Kenny, J., Lenihan, E., Quigley, D., Helps, W., Dugon, M., & Doyle, T. (2020). Insights on the origin and drift trajectories of Portuguese man of war (Physalia physalis) over the Celtic Sea shelf area. *Estuarine, Coastal and Shelf Science*, *246*, 107033. https://doi.org/10.1016/j.ecss.2020.107033

Hernández, F. (2020). Ecological discord and the importance of scale in scientific inquiry. *The Journal of Wildlife Management*, *84*(8), 1427–1434. https://doi.org/10.1002/jwmg.21942

Hobbs, N. (2003). Challenges and opportunities in integrating ecological knowledge across scales. *Forest Ecology and Management*, *181*(1–2), 223–238. https://doi.org/10.1016/S0378-1127(03)00135-X

Iosilevskii, G., & Weihs, D. (2009). Hydrodynamics of sailing of the Portuguese man-of-war Physalia physalis. *Journal of the Royal Society Interface*, *6*(36), 613–626. https://doi.org/10.1098/rsif.2008.0457

Jenkins, R. (1983). Observations on the commensal relationship of Nomeus gronovii with Physalia physalis. *Copeia*, *1983*(1), 250–252.

Johnson, D., Perry, H., & Burke, W. (2001). Developing jellyfish strategy hypotheses using circulation models. In J. Purcell, W. Graham, & H. Dumont (Eds.), *Jellyfish Blooms: Ecological and Societal Importance* (pp. 213–221). Springer. https://doi.org/10.1007/978-94-010-0722-1_17

Junior, V., Virga, R., Bechara, A., Silveira, F., & Morandini, A. (2013). An outbreak of Portuguese man-of-war (Physalia physalis-Linnaeus, 1758) envenoming in Southeastern Brazil. *Revista Da Sociedade Brasileira de Medicina Tropical*, *46*(5), 641–644. https://doi.org/10.1590/0037-8682-1518-2013

Kwiatkowski, L., Naar, J., Bopp, L., Aumont, O., Defrance, D., & Couespel, D. (2019). Decline in Atlantic primary production accelerated by Greenland ice sheet melt. *Geophysical Research Letters*, *46*(20), 11347–11357. https://doi.org/10.1029/2019GL085267

Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., Buitenhuis, E., Doney, S. C., Dunne, J., Hashioka, T., Hauck, J., Hirata, T., John, J., Quéré, C., Lima, I., Nakano, H., Seferian, R., Totterdell, I., Vichi, M., & Völker, C. (2015). Drivers and uncertainties of future global marine primary production in marine ecosystem models. *Biogeosciences*, *12*(23), 6955–6984. https://doi.org/10.5194/bg-12-6955-2015

Levin, S. (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, *73*(6), 1943–1967. https://doi.org/10.2307/1941447

Licandro, P., Conway, D., Yahia, M., Puelles, M., Gasparini, S., Hecq, J., Tranter, P., & Kirby, R. (2010). A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters*, *6*(5), 688–691. https://doi.org/10.1098/rsbl.2010.0150

Lopes, A., Baptista, M., Rosa, I., Dionísio, G., Gomes-Pereira, J., Paula, J., Figueiredo, C., Bandarra, N., Calado, R., & Rosa, R. (2016). "Gone with the wind": Fatty acid biomarkers and chemotaxonomy of stranded pleustonic hydrozoans (Velella velella and Physalia physalis). *Biochemical Systematics and Ecology*, *66*, 297–306. https://doi.org/10.1016/j.bse.2016.03.016

Löscher, C., Fischer, M., Neulinger, S., Fiedler, B., Philippi, M., Schütte, F., Singh, A., Hauss, H., Karstensen, J., Körtzinger, A., Künzel, S., & Schmitz, R. (2015). Hidden biosphere in an oxygen-deficient Atlantic open-ocean eddy: future implications of ocean deoxygenation on primary production in the eastern tropical North Atlantic. *Biogeosciences*, *12*(24), 7467–7482. https://doi.org/10.1016/j.bse.2016.03.016

Luana, M. (2017). *Distribuição de caravelas (Physalia physalis) e envenenamentos humanos nas praias urbanas de São Luís, Maranhão-Brasil* [Universidade Federal do Maranhão]. https://tedebc.ufma.br/jspui/bitstream/tede/1355/2/MayanaLuana.pdf

Lucas, C., Jones, D., Hollyhead, C., Condon, R., Duarte, C., Graham, W., Robinson, K., Pitt, K., Schildhauer, M., & Regetz, J. (2014). Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. *Global Ecology and Biogeography*, *23*(7), 701–714. https://doi.org/10.1111/geb.12169

Lynam, C., Gibbons, M., Axelsen, B., Sparks, C., Coetzee, J., Heywood, B., & Brierley, A. (2006). Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology*, *16*(19), R492–R493. https://doi.org/10.1016/j.cub.2006.09.012

Lynam, C., Hay, S., & Brierley, A. (2004). Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography*, *49*(3), 637–643. https://doi.org/10.4319/lo.2004.49.3.0637

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. https://doi.org/10.1016/j.ocecoaman.2021.105810

Mghili, B., Analla, M., & Aksissou, M. (2021). Medusae (Scyphozoa and hydrozoa) from the Moroccan Mediterranean coast: abundance and spatiotemporal dynamics and their economic impact. *Aquatic Ecology*, *56*, 213–226. https://doi.org/10.1007/s10452-021-09910-0

Mills, C. (2001). Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, *451*(1), 55–68. https://doi.org/10.1023/A:1011888006302

Munro, C., Vue, Z., Behringer, R., & Dunn, C. (2019). Morphology and development of the Portuguese man of war, Physalia physalis. *Scientific Reports*, *9*, 1–12. https://doi.org/10.1038/s41598-019-51842-1

Nakamura, Y., & Oka, A. (2019). CMIP5 model analysis of future changes in ocean net primary production focusing on differences among individual oceans and models. *Journal of Oceanography*, *75*(5), 441–462.

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

Pikesley, S., Godley, B., Ranger, S., Richardson, P., & Witt, M. (2014). Cnidaria in UK coastal waters: description of spatio-temporal patterns and inter-annual variability. *Journal of the Marine Biological Association of the United Kingdom*, *94*(7), 1401–1408. https://doi.org/10.1017/S0025315414000137

Pontin, D., & Cruickshank, R. (2012). Molecular phylogenetics of the genus Physalia (Cnidaria: Siphonophora) in New Zealand coastal waters reveals cryptic diversity. *Hydrobiologia*, *686*, 91–105. https://doi.org/10.1007/s10750-011-0994-8

Prieto, L., Macías, D., Peliz, A., & Ruiz, J. (2015). Portuguese Man-of-War (Physalia physalis) in the Mediterranean: A permanent invasion or a casual appearance? *Scientific Reports*, *5*, 11545. https://doi.org/10.1038/srep11545

Purcell, J. (2005). Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom*, *85*(3), 461–476. https://doi.org/10.1017/S0025315405011409

Purcell, J., Uye, S., & Lo, W. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, *350*, 153–174. https://doi.org/10.3354/meps07093

Richardson, A., Bakun, A., Hays, G., & Gibbons, M. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution*, *24*(6), 312–322. https://doi.org/10.1016/j.tree.2009.01.010

Richardson, A., & Gibbons, M. (2008). Are jellyfish increasing in response to ocean acidification? *Limnology and Oceanography*, *53*(5), 2040–2045. https://doi.org/10.4319/lo.2008.53.5.2040

Schuchert, P. (2020). World hydrozoa database. *Cryptospongia Enigmatica*.

Scott-Frías, J., & Jorquera, E. (2020). La Fragata Portuguesa o Aguamala (Physalia physalis): Importancia en la salud pública. *Bionatura*, *5*(4), 1418–1422. https://doi.org/10.21931/RB/2020.05.04.24

Steinacher, M., Joos, F., Frölicher, T., Bopp, L., Cadule, P., Cocco, V., Doney, S., Gehlen, M., Lindsay, K., Moore, J., Schneider, B., & Segschneider, J. (2010). Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences*, *7*(3), 979–1005. https://doi.org/10.5194/bg-7-979-2010, 2010.

Thrush, S., Hewitt, J., Herman, P., & Ysebaert, T. (2005). Multi-scale analysis of species–environment relationships. *Marine Ecology Progress Series*, *302*, 13–26. https://doi.org/10.3354/meps302013

Tiralongo, F., Badalamenti, R., Arizza, V., Prieto, L., & Brutto, S. (2022). The Portuguese Man-of-war, One of The Most Dangerous Marine Species, Has Always Entered The Mediterranean Sea: Strandings, Sightings And Museum Collections. *Frontiers in Marine Science*, *9*(856979), 14. https://doi.org/10.3389/fmars.2022.856979

Torres-Conde, E., Martínez-Daranas, B., & Prieto, L. (2021). The Havana littoral, an area of distribution for Physalia physalis in the Atlantic Ocean. *Regional Studies in Marine Science*, *44*, 101752. https://doi.org/10.1016/j.rsma.2021.101752

Wiens, J. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*(4), 385–397. https://doi.org/10.2307/2389612

Woodcock, A. (1944). A theory of surface water motion deduced from the wind-induced motion of the Physalia. *Journal of Marine Research*, *5*(3), 196–205.