Jellyfish of the Spanish Mediterranean coast: effects of environmental factors on their spatio-temporal dynamics and economic impacts

Antonio Jesús Canepa Oneto

Aquesta tesi doctoral està subjecta a la llicència ***Reconeixement- NoComercial – SenseObraDerivada 3.0. Espanya de Creative Commons***.

Esta tesis doctoral está sujeta a la licencia ***Reconocimiento - NoComercial – SinObraDerivada 3.0. España de Creative Commons.***

This doctoral thesis is licensed under the ***Creative Commons Attribution-NonCommercial-NoDerivs 3.0. Spain License.***

Jellyfish of the Spanish Mediterranean coast:

effects of environmental factors on their spatio-temporal dynamics and economic impacts

ANTONIO J. CANEPA ONETO

Barcelona, 2014

ANTONIO J. CANEPA ONETO

Jellyfish of the Spanish Mediterranean coast:
effects of environmental factors on their spatio-temporal dynamics and economic impacts

Jellyfish of the Spanish Mediterranean coast: effects of environmental factors on their spatio-temporal dynamics and economic impacts

Memòria presentada per Antonio Jesús Canepa Oneto per optar al grau de doctor per la Universitat de Barcelona.

Programa de Doctorat en Ecologia Fonamental i Aplicada

Antonio J. Canepa Oneto
Barcelona, julio 2014

Directors:

Dr. Josep-Maria Gili Sardá
Research Professor
Dept. of Marine Biology and Oceanography
Institute of Marine Science (ICM-CSIC)

Dra. Verónica L. Fuentes
Postdoctoral Scientist
Dept. of Marine Biology and Oceanography
Institute of Marine Science (ICM-CSIC)

Tutor:

Dra. Isabel Muñoz Gracia
Professor
Ecology Department
Faculty of Biology, University of Barcelona (UB)

2014

"Jellyfish of the Spanish Mediterranean coast: effects of environmental factors on their spatio-temporal dynamics and economic impacts"

The author was funded by the Chilean Government through the National Commission for Scientific and Technological Research (CONICYT) - BECASCHILE Scholarship Program (PFCHA/Doctorado al Extranjero 4ª Convocatoria, 72120016).

This work has been carried out in the framework of the following research projects:

- **LIFE-CUBOMED**: development and demonstration, eradication and control methods for an invasive species: *Carybdea marsupials* (Cubozoa), Spanish Mediterranean. 2010-2014. Project Funding Agency: The LIFE Programme (LIFE/NAT/ES/64), Ministerio de Medio Ambiente y Medio Rural y Marino y la Conselleria de Medio Ambiente de la Generalitat Valenciana. Project Executing Agency: Multidisciplinary Institute for Environmental Studies "Ramon Margalef", University of Alicante (UA) and the Institute of Marine Science, Spanish National Research Council (ICM–CSIC).

- **Projecte MEDUSA**: realització dels treballs de recerca i seguiment de les proliferacions de meduses a les aigües lltorals de Catalunya. Project Funding Agency: Catalan Water Agency (ACA) and Departament de Medi Ambient i Habitatge de la Generalitat de Catalunya. Project Executing Agency: Institute of Marine Science, Spanish National Research Council (ICM–CSIC).

- **VECTORS**: Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors. Project Funding Agency: European Commission, contract agreement no. 266445.

CONTENTS (Índex)

A Patricia y Álvaro por ser las mejores personas y el mejor apoyo que uno pueda tener en la vida.

A mi Familia, para todos ellos los que están más cerca y más lejos, por haberse esforzado en que las distancias y el añoro no fuese un impadimento, sino una motivación.

AGRADECIMIENTOS

Esta tesis doctoral representa el fin de un largo camino, lleno de emociones y aventuras, por lo que en esta sección no creo poder ser justo; es mucha la gente a la que le estoy agradecido y resumirlo aquí generará inequívocamente una subestimación de la ayuda recibida. No puedo dejar de agradecer a los Doctores José Luis Pelegrí, Miriam Fernández y Stefan Gelcich quienes a través de su trabajo y apoyo permitieron que el financiamiento a esta tesis tuviera lugar. A mis directores Josep-Maria Gili y Verónica Fuentes, que desde un principio me abrieron las puertas y me motivaron para embarcarme en esta propuesta doctoral, apoyándome en todo momento. Al Sr. César Bordehore y a las personas que por su trabajo voluntario en terreno permitieron abordar el tema de la proliferación de *Carybdea marsupialis* en la costa de Denia. A Mar Bosch y Melissa Acevedo con las que establecimos una amistad que perdura hasta ahora y que hicieron de los muestreos y de la estancia en la estación Montgò uno de los mejores momentos que he vivido. A todo el grupo Medusas por la ayuda recibida en todos los momentos, en los buenos y en los no tan buenos. En especial a Miriam, Maca, Mely, Mar, Uxue, Elena, Maria y Alejandro, por su paciencia y apoyo y por todos los momentos que compartimos en esta etapa de mi vida. Al Sr. Eduardo Obis y al projecto Med-Jellyrisk por permitirme utilizar su material audiovisual. A los co-autores de los trabajos que forman mi tesis, muchas gracias a cada uno de ustedes. He aprendido muchísimo de vuestra experiencia y sin duda han sido una parte importante de mi preparación doctoral. A la Dra. Jennifer Purcell, por su esfuerzo, dedicación y guía durante este proceso y quien sin su ayuda esta tesis no sería la que es. Finalmente y quizá el más importante, agradecer el amor, tiempo, dedicación y paciencia que he recibido de Patricia y Álvaro (mi familia más cercana) que me han permitido terminar este hermoso proceso lleno de aprendizaje y que nos embarca en una nueva aventura.

ABSTRACT

During recent years, jellyfish blooms have become in a passionate issue among marine scientists with a series of studies and reviews. The main concern about this blooms are related with ecosystem and socio-economic impacts and lately with the possibility of a global increase in these blooms. Jellyfish populations are known to follow periodic fluctuations in occurrence, abundance (biomass), where some regions, like the Mediterranean Sea, appear to sustain a long-term increase. Several causes have been hypothesized as drivers of jellyfish blooms that may contribute to a future "jelly-world"; however, long-term data are generally lacking to test if we are (or not) approaching this state. Even when data can not reveal a unique global long-term increase, there are several human-related threats to oceans that intuitively will be beneficial for jellyfishes and may be responsible for the increases where the trend is clear, e.g. the Mediterranean Sea.

The Mediterranean Sea has been largely and historically affected with blooms of several jellyfish species. Among them *Pelagia noctiluca* is the most abundant and the most problematic jellyfish species in the Western Mediterranean. Along the Catalan coast evidence for a jellyfish increase are not conclusive with signals of an increase in Jellyfish aggregations, duration of the bloom and number of species that form these blooms. Beside this, little information about the environmental restriction on the spatio-temporal dynamics is available.

In order to address these needs, this thesis has been structured covering two geographical areas reflecting two different approaches to understanding jellyfish spatio-temporal dynamics, bloom formation, impacts and analytical procedures. The first part of the thesis (Papers 1-3) deals with the outbreaks of the cubozoan *Carybdea marsupialis* along the coast of Denia (Alicante), including innovative work to develop experimentally based tools and analyses to generate scientifically-based recommendations for stakeholders. The second part of this thesis was done on the northern Mediterranean Spanish coast (Catalan coast) (Papers 4-6). This work is mostly based on stranded jellyfish data collected by the MEDUSA project in association with the Catalan Water Agency (ACA). The data analyzed covered a four year range (2007-2010), where more than 240

beaches were monitored daily during the spring-summer season (May-September).

The general objective of the Thesis was to understand the spatio-temporal dynamics of the jellyfish along the Spanish Mediterranean coast and the economic impacts of their blooms. To answer this general objective several specific objectives were defined: 1) To characterize the effects of salinity variation on the asexual reproduction of a coastal box jellyfish (paper 1); 2) To develop and test a new system for experimenting with jellyfish polyps using continuous seawater renewal and testing the effects of pH reduction (paper 2); 3) To characterize the annual cycle of a coastal box jellyfish and the effects of environmental variables on its spatio-temporal dynamics (paper 3); 4) To understand the ecological context of blooms of the mauve stinger *Pelagia noctiluca* throughout the Mediterranean Sea, with implications for the socio-ecological ecosystems (paper 4); 5) To determine the importance of stochastic versus deterministic drivers of jellyfish outbreaks along the Catalan Coast (paper 5) and 6)To understand the beach recreationists' preferences and to characterize the economic impact of jellyfish outbreaks along the Catalan Coast (paper 6).

First Part: outbreaks of the cubozoan *Carybdea marsupialis* along the coast of Denia (Alicante) (Papers 1-3).

On the central Spanish Mediterranean coast, along the coast of Denia (Alicante), the coastal box jellyfish *Carybdea marsupialis* has caused major concern due to its painful sting and high abundances since 2008. A positive association of this species with river mouths suggested an important role of salinity changes in its biology. Salinity reduction significantly shortened the time required by *Carybdea* sp. to complete metamorphosis. Thus, late winter-early spring runoff of low salinity hastens jellyfish production. Conversely, high salinity extended the days to metamorphosis allowing the polyps to produce more buds and increase population size. We hypothesize that *Carybdea sp. polyps metamorphose into medusae in early spring when salinity decreases from high rain and terrestrial runoff and they benefit from high levels of primary and secondary* *production in the coastal water column generated by the nutrient-rich runoff. The importance of freshwater runoff and other environmental conditions for the distribution of C. marsupialis along the coast of Denia were further demonstrated by* non-normal distribution models. The effects of environmental variables on the local (~ tens of kilometres) abundance of the cubomedusae showed that sea surface temperature (SST) and salinity were the main environmental variables, followed by those related to primary and secondary production and local retention or transportation to the coast. This conclusion led to our management recommendation that, to reduce the blooms of *C. marsupialis,* crop fertilizers and sewage discharges should be reduced in highly populated or industrialized areas. Most importantly, high amounts of nutrients reaching the coast (by rivers or ground water discharges) should be prevented, especially in early spring. In order to decrease the amount of sewage water, solutions are possible with improvement in technology adding tertiary biological treatment to the sewage plants and by relocating the submarine pipeline further from the coast where the currents will spread the effluents.

Other major issue concerning anthropogenic influences in the marine realm is ocean acidification. Our new system was shown to be accurate and stable for experimentation on jellyfish polyps. It is also easy to maintain, and therefore, suitable for long-term studies on the responses of these organisms to environmental stressors such as ocean acidification. The mortality rate of polyps during our experiment was very low compared with other studies. Overall, this study presents a relatively simple and affordable system that can greatly improve the results obtained from testing the effects of a range of environmental pressures on the eco-physiology of jellyfish polyps.

Second Part: outbreaks of *Pelagia noctiluca* and other jellyfish along the Catalan coast and their economical impacts (Papers 4-6).

The mauve stinger *Pelagia noctiluca* is the most common jellyfish in the Mediterranean Sea. Its records began in the 1700s, motivated by its high numbers and painful stings. In the

Mediterranean Sea, this species is known to form dense aggregations offshore that reach the coast when favored by winds and surface currents.

From The Medusa Project along the Catalan Coast some characteristic species of spring time were *Chrysaora hysoscella*, *Aurelia aurita*, *Aequorea forskalea* and *Velella velella*. During the summer, the most frequent jellyfish species recorded was the scyphozoan *Rhizostoma pulmo*. Finally, in late summer, the scyphozoan *Cotylorhiza tuberculata* arrived and dominated the records. Stranded *P. noctiluca* medusae occurred throughout the sampling period (May-September), but with highest abundances in spring. The stability of the shelf-slope front and its duration in time and space have been proposed to be responsible for the massive arrival of medusae to the coast. Many sightings (high abundances) of *P. noctiluca* were spatially correlated with canyons along the Catalan coast. That phenomenon also occurs in other places in the Western Mediterranean, which led to a new hypothesis about the seasonal vertical migration and overwintering behavior of this species.

Bayesian analysis of the importance of stochastic versus deterministic drivers of jellyfish outbreaks along the Catalan Coast showed that jellyfish outbreaks were more frequent in May and June, particularly in the years 2009 and 2010. Outbreaks were negatively associated with SST and distance to canyons, and positively associated with the onshore current transport force. This model was largely influenced by the abundance of *P. noctiluca*, the most common jellyfish along the Catalan coast and elsewhere in the Western Mediterranean, and the environmental factors reflect the conditions in which *P. noctiluca* reaches the coast. Our results indicated that deterministic processes were more important than the stochastic component of environmental variation, suggesting that extreme events, visualized as the compound effects of environmental variables, did not affect the probability of an outbreak along the Catalan Coast. Nevertheless, SST and the onshore current transport force were significant time-varying predictors, but their signal was not strong enough to overwhelm deterministic effects.

From a stated-choice questionnaire and a Random Utility Model, which estimated how much respondents were willing to spend, in terms of reported extra travel time to a bathing beach with lower risk of jellyfish outbreaks, we tested the impact of the risk of jellyfish outbreaks on beach recreationists along the Catalan coast. The visitors were willing to spend an additional 23.8% of their travel time to enjoy beach recreation where risk of a jellyfish outbreak was lower. We calculated that the well-being gains associated with a reduction of jellyfish outbreaks in this area would range between €312 and €322 million annually, corresponding approximately to 19% of the tourism expenditures of the Catalan population in 2012. Nevertheless, improvement in the beach water quality was, by far, the most valuable attribute for all types of respondents. Improvement in the beach infrastructure was ranked second and reduction in the risk of jellyfish outbreaks, third. This study confirms the urgency to provide daily information by use of the wide set of social media applications. The current lack of public knowledge about jellyfish suggests that providing such information to beach recreationists is the only effective policy instrument to minimize the impact of jellyfish outbreaks.

GENERAL INTRODUCTION

Jellyfish concept

The term “jellyfish” includes several phylogenetically unrelated organisms that have evolved under different selective pressures (Boero et al. 2008; Boero 2013; Pitt and Lucas 2014). One common characteristic of this polyphyletic group is its watery constitution with a low carbon/water content ratio and low energy densities (Doyle et al. 2007, Lucas et al. 2011), which has let them to be collectively known as gelatinous (macro) zooplankton (Hamner et al. 1975). The gelatinous plankters have evolved several times within the Metazoa (Fig. 1), gathering taxa as disparate as the Phyla Mollusca, Urochordata, Cnidaria, Ctenophora, Echinodermata, Annelida and Nemertea (Fig. 2). Based on their trophic similarity, the term jellyfish was first (mid-1800s) attributed to various medusae and later (1990s) applied to other groups, including ctenophores and siphonophores (Mills 1995). This definition has been widely accepted in order to refer the planktonic stages of three Classes (Classes Hydrozoa, Scyphozoa and Cubozoa) of the Phylum Cnidaria, the “true” jellyfish plus the Phylum Ctenophora (Purcell 2012, Boero 2013; Pitt and Lucas 2014). This definition will be used throughout this manuscript.

Trends of jellyfish

Jellyfish, as for other planktonic marine species, show cyclical patterns of high biomass that lead to sequential pulses of phyto- and zooplankton (Boero 1994). These pulses are mostly driven by good environmental conditions and zooplankton predators like jellyfish respond with high abundances during the highly productive conditions (Boero 1994). This last condition is particularly important in species like jellyfish that have a metagenetic life cycle (alternation of a sexually reproducing medusa in the pelagic realm and an asexually reproducing benthic polyp; Fig. 3). The scyphozoan benthic polyps can increase their numbers through asexual reproduction (budding), they posses greater longevity than the medusa phase, they can withstand bad environmental conditions through resistant cyst or podocyst and can produce several free-swimming ephyrae in each strobilation process. If good environmental conditions are coupled with this asexual process occurs, a bloom is triggered (Lucas et al. 2012). Thus, high numbers of jellyfish as part of their biological cycle can be seen as a normal phenomenon (Boero et al. 2008), referred as a "true" bloom (Graham et al. 2001). But many individuals or high biomass does not always represent an increase in reproduction and/or growth (i.e. a consequence of their life cycle), because planktonic organisms can drift by wind and surface currents and accumulate elsewhere, leading to conditions that resemble a jellyfish bloom. This last condition is referred to as an *accumulation* or *mass occurrence* depending on the magnitude of the event. For a review and detailed suggested nomenclature see Box 2.2 in Lucas and Dawson (2014).

During recent years, jellyfish blooms have become in a passionate issue among marine scientists with a series of studies and reviews (Brodeur et al. 2008; Brotz et al. 2012; Mianzan et al. 2012; Purcell 2012; Condon et al. 2012). The main concern about this blooms are related with ecosystem and socio-economic impacts (reviewed in Purcell et al. 2007) and lately with the possibility of a global increase in these blooms (Mills 2001; Purcell 2005; Brotz et al. 2012; Purcell 2012; Condon et al. 2012). Jellyfish populations are known to follow periodic (circa-decadal) fluctuations in occurrence, abundance (biomass) (Goy et al. 1989, Purcell 2005; Brotz et al. 2012; Condon et al. 2013), where some regions, like the Mediterranean Sea, appear to sustain a long-term increase (Condon et al. 2013).

Environmental restriction on jellyfish and outbreak formation

Several causes have been hypothesized as drivers of jellyfish blooms that may contribute to a future "jelly-world" (Richardson et al. 2009); however, long-term data are generally lacking to test if we are (or not) approaching this state. Evidence showed that climatic cycles (e.g., the North Atlantic Oscillation, El Niño Southern Oscillation; Purcell et al. 2007, Brodeur et al. 2008, Kogovšek et al. 2010) and the effects of over-fishing (Pauly et al. 2003, Lynam et al. 2006) are responsible for the deviation from natural oscillations of some gelatinous zooplankton on their ecosystem-specific baselines (reviewed in Purcell et al. 2007; Purcell 2012). Even when data can not reveal a unique global long-term increase, there are several human-related threats to oceans that intuitively will be beneficial for jellyfishes and may be responsible for the increases where the trend is clear, e.g. the Mediterranean Sea (Purcell et al. 2007; Brotz et al. 2012; Purcell 2012).

The over-harvesting of fish could be beneficial for jellyfish populations through the removal of their predators and competitors (the fishing down described by Pauly et al. (1998)) that has been occurring since ancient times (reviewed in Purcell 2012). Other important factors are those related to the human intervention in coastal areas. Different human-made transformations on the shoreline can increase the available free substrata needed for the benthic stage (polyps) of many jellyfishes and the building rate of these structures is increasing, favoring jellyfish populations (Lo et al. 2008; Bulleri and Chapman 2010; Duarte et al. 2013). Coastal pollution like eutrophication generate high N:P ratios, altering the plankton community structure with shifts from large diatoms to small flagellates, allowing for short trophic chains with small zooplankton that favor jellyfish feeding over fish (Parsons and Lalli 2002; Purcell et al. 2007). Also, eutrophication generates high turbidity conditions that can lead to competitive feeding advantages of jellyfish (tactile predators) compared with fishes (visual predators), increasing the role of coastal eutrophication on the relative effect of jellyfish predation (Ohata et al. 2011; Purcell 2012). For zooxanthellate species, where a direct uptake of inorganic nutrients occurs, the coastal eutrophication was shown to increase the size and density of jellyfish populations (Stoner et al. 2011). Counterintuitively, the jellyfish predatory effects on herbivorous zooplankton and the subsequent release of inorganic nutrients (*e.g.* NH_4^+) and dissolved organic compounds (*e.g.* free amino acids) can increase the levels of Chl-a in a top-down stimulation of primary production (Møller and Riisgård 2007; Kideys et al. 2008; Pitt et al. 2008). Additionally, the deposition of dead jellyfish, "jelly-falls", accelerate the biological pump and benthopelagic coupling (Lebrato et al. 2012) and increase the effect of coastal eutrophication, because many of the jelly-falls happen in coastal areas.

Associations with environmental variables showed a general pattern of positive relationships of jellyfish abundance with SST and salinity, e.g. in the North Sea (*Aurelia aurita* and *Cyanea* spp.), the Northern Adriatic Sea (*Pelagia noctiluca*, *A. aurita* and *Rhizostoma pulmo*), Chesapeake Bay *(Chrysaora quinquecirrha*) and the Humboldt Current System (*Chrysaora plocamia*) among others (Goy et al. 1989; Purcell 2005; Decker et al. 2007; Quiñones et al. 2010; Kogovšek et al. 2010; Lynam et al. 2011). These population correlations agree with the results of controlled increased temperature experiments that show an increase in survival and asexual reproduction (e.g. Purcell et al. 1999, 2012). As seen for other zooplankton taxa, the effects of the long-term sea surface temperature increase globally as a consequence of global climate change, will trigger a pole-ward migration (Richardson 2008; Klein et al. 2014), with negative impacts expected for species living at their upper thermal limit (e.g. *Mastigias* sp. in Palau, Dawson et al. 2001) and affecting the biogeography of several species. Other important variables related to jellyfish biogeography are primary production (PP) and apparent oxygen utilization (AOU) (Lucas et al. 2014). This last variable reveals an advantage to jellyfish in low dissolved oxygen (DO) environments. Their ability is related to outstanding asexual reproduction even in low oxygen concentrations, a general tolerance of low oxygen and their ability to use of the intragel as an oxygen reservoir (Condon et al. 2001; Rutherford and Thuesen 2005; Thuesen et al. 2005; Stramma et al. 2010), resulting in a jellyfish increased competitive advantage over their prey items and fish (reviewed in Purcell et al. 2001). Finally ocean acidification has been addressed as a driver of jellyfish populations with contrasting conclusions (Attrill et al. 2007; Richardson and Gibbons 2008); however, experimental results suggest a lack of detrimental effects (Winans and Purcell 2010; Yang et al. 2011; Klein et al. 2014). Thus, as ocean acidification increases and detrimental effects arise for several marine species (Doney et al. 2009; 2012), competitive advantages for jellyfish may occur.

Spatio-temporal dynamics of common jellyfish in the Mediterranean Sea and along the Catalan coast

The Mediterranean Sea has been largely and historically affected with blooms of several jellyfish species, with 12 species of scyphomedusae forming dense blooms (Axiak et al, 1991; Gili and Pagès 2005). Among them the most conspicuous scyphozoans are *Pelagia noctiluca* (Forskål, 1775), *Rhizostoma pulmo* (Macri 1778), *Aurelia aurita* (Linnaeus, 1758), *Cotylorhiza tuberculata* (Macri, 1778), and *Chrysaora hysoscella* (Linnaeus, 1767), and among the hydromedusae, *Aequorea forskalea* (Forskål, 1775) and *Velella velella* (Linnaeus, 1758) (Mariottini and Pane 2010; Fuentes et al. 2011; Purcell et al. 2012b). All of them are large and easy to detect, with *P.*

noctiluca being the most abundant and the most problematic jellyfish species in the Western Mediterranean (Mariottini and Pane 2010; Ferraris et al. 2012).

Recently, Bordehore et al. (2011) showed a recent outbreak of another painful stinger, the cubozoan *Carybdea marsupialis* (Linnaeus, 1758), along the southwest Mediterranean (Alicante coast). Its outbreak negatively affected the local tourism due to its painful stings and high abundances in very shallow coastal areas. This species also is important in southern Italy, being the third most important jellyfish species in stinging people and causing important economic losses (De Donno et al. 2014).

Along the Catalan coast evidence for a jellyfish increase are not conclusive, Atienza et al. (2010) showed no obvious trend for any species over the last decade, nevertheless Calvo et al. (2011) pointed out that since 2000, and especially the last five years, an increase in Jellyfish aggregations (swarm in her study), duration of the bloom and number of species that form these blooms can be observed. Beside this, little information about the environmental restriction on the spatio-temporal dynamics is available. In the case of *P. noctiluca*, Sabatés et al. (2010) highlights the role of oceanographic structures like shelf-slope front in explaining the accumulation and feeding performance of jellyfish associated with this structure on a limited spatio-temporal scale (one transect in one year). Thus, there are clear needs for longer spatio-temporal analyses on the dynamics of jellyfish along the Mediterranean Spanish coast and evaluation of the effects of jellyfish blooms.

In order to address these needs, this thesis has been structured covering two geographical areas reflecting two different approaches to understanding jellyfish spatio-temporal dynamics, bloom formation, impacts and analytical procedures. The first part of the thesis (Papers 1-3) deals with the outbreaks of the cubozoan *C. marsupialis* along the coast of Denia (Alicante), including innovative work to develop experimentally based tools and analyses to generate scientifically-based recommendations for stakeholders. The second part of this thesis was done on the northern Mediterranean Spanish coast (Catalan coast) (Papers 4-6). This work is mostly based on stranded jellyfish data collected by the MEDUSA project in association with the Catalan Water Agency (ACA) (http://www.icm.csic.es/bio/medusa/Castellano/CastProyecto.html). The data analyzed covered a four year range (2007-2010), where more than 240 beaches were monitored daily during the spring-summer season (May-September).

Carybdea marsupialis **in Alicante**

The outbreak of the cubozoan *Carybdea marsupialis* (Linnaeus, 1758) in 2008 along the coast of Denia (Alicante) negatively affected as many as 185 people day^{-1}, with consequences on local tourism (Bordehore et al. 2011). A positive association of this species with river mouths suggested an important role of salinity changes in its biology. Thus, the first step for testing salinity effects on *C. marsupialis* was to conduct a controlled experiment on the asexual reproduction of its polyps. Because the genus *Carydea* is under revision and the polyps from the Mediterranean cubomedusae (*C. marsupialis*) were not found, we tested the effects of salinity changes on the asexual reproduction on polyps from the congener, *Carybdea* sp. (Paper 1) (Canepa et al. 2014b). After running this experiment, the need for an specially designed experimental system for jellyfish polyps was apparent. Thus, a new system was developed to keep polyps individually under controlled temperature and salinity with continuous water renewal and testing, in this case, the differences in pH levels for insights into ocean acidification (Paper 2) (Olariaga et al. 2014).

Due to the urgent need to understand the unusual outbreak of *C. marsupialis,* the LIFE CUBOMED project (http://www.lifecubomed.eu/es/) was conducted to explain the environmental restrictions of cubomedusae presence and abundance along the coast of Denia. Six sites were selected to cover a gradient in environmental variables along the coast, where weekly sampling was done over a year. The abundance and size of medusae and the associated environmental variables were collected. Non-normal distribution models were applied to understanding the role of the environmental variables in *C. marsupialis* medusa distribution and zero-inflated models also were used to evaluate the conditions of false zero captures. As a result, some highlights and recommendations about monitoring and coastal management could be given to deal with outbreaks of this species (Paper 3).

Pelagia noctiluca and other jellyfish along the Catalan coast

The massive occurrences of *Pelagia noctiluca* have stimulated research since the 1980s, mostly by its massive occurrences in the Eastern Mediterranean Sea, the North Adriatic Sea, and subsequently the western Mediterranean Sea. Its temporal dynamics was first evaluated by Goy et al. (1989), who reconstructed a time series of the occurrences of *P. noctiluca* dating back to 1775. In her analysis, Goy et al. (1989) determined a periodicity of blooms of about 12 years that was related to climatic fluctuations. More recently, an increasing frequency of blooms has been suggested for the Balearic Islands (Daly Yahia et al. 2010), the North Adriatic Sea (Kogovšek et al. 2010) and the Ligurian Sea in the western Mediterranean Sea (Bernard et al. 2011). Despite its importance due to its painful sting, high numbers and broad distribution, information on *P. noctiluca* bloom conditions and consequences on a Mediterranean Basin scale was unavailable. Thus, in the framework of a global overview of jellyfish blooms in the book "Jellyfish Blooms" (Pitt and Lucas 2014), Paper 4 of this thesis deals with *P. noctiluca* blooms throughout the Mediterranean Sea (Canepa et al. 2014a). In this chapter, all the information about the blooming behavior, environmental restrictions, human interactions and costs for the Mediterranean Sea are summarized. In addition, new information was analyzed from stranded jellyfish data collected by the MEDUSA project between 2007 and 2010 along the Catalan coast. Thus, the spatio-temporal variability of the most important jellyfish species along the Catalan coast was analyzed with emphasis on *P. noctiluca*. A model for the arrival of *P. noctiluca* to the coast was presented considering drift associated variables. From the distributional data gathered, and in agreement with observations from other co-authors, a new hypothesis about the role of marine canyons in the overwintering and seasonal vertical migration of the species was proposed. Finally, analysis of the number of stings recorded by the Red Cross and medusae abundance showed that *P. noctiluca* was the species mainly responsible for these stings.

From this medium-term database, a relatively new statistical approach (environmental bootstrapping) was used to evaluate short- to medium-term temporal data. This analysis tested the deterministic versus stochastic environmental variables that can lead to jellyfish blooms (outbreaks) (Paper 5). Additionally, the importance of deterministic features, like coastal morphology, for *P. noctiluca* blooming periodicity is highlighted.

Finally, Paper 6 examined beach users' perceptions about jellyfish blooms and their preferences in different scenarios of jellyfish presence along the Catalan coast. To do this, at-beach questionnaires were conducted for more than 300 people, from which results from a stated-choice experiment enabled conclusions about the economic importance of jellyfish blooms along the Catalan coast.

OBJECTIVES

General Objective:

To understand the spatio-temporal dynamics of the jellyfish along the Spanish Mediterranean coast and the economic impacts of their blooms.

Specific objectives:

To characterize the effects of salinity variation on the asexual reproduction of a coastal box jellyfish.

To develop and test a new system for experimenting with jellyfish polyps using continuous seawater renewal and testing the effects of pH reduction.

To characterize the annual cycle of a coastal box jellyfish and the effects of environmental variables on its spatio-temporal dynamics.

To understand the ecological context of blooms of the mauve stinger *Pelagia noctiluca* throughout the Mediterranean Sea, with implications for the socio-ecological ecosystems.

To determine the importance of stochastic versus deterministic drivers of jellyfish outbreaks along the Catalan Coast.

To understand the beach recreationists' preferences and to characterize the economic impact of jellyfish outbreaks along the Catalan Coast.

DIRECTORS’ REPORT

Dr. Josep-Maria Gili Sardá and Dra. Verónica Fuentes, advisors of the PhD thesis entitled *“Jellyfish of the Spanish Mediterranean coast: effects of environmental factors on their spatio-temporal dynamics and economic impacts”*, certify that the dissertation presented here has been carried out by Mr. Antonio J. Canepa Oneto in its totally, participating in all the task: conceiving and performing the experiments, field sampling, analysing the data and writing the manuscripts. As advisors we inform that the results and conclusions achieved in his PhD thesis have been organised in 6 chapters which correspond to 3 publications and 3 manuscripts ready to be submitted to the corresponding journals. We have participated in designing, guiding and correcting the manuscripts written by the PhD candidate.

LIST OF THE MANUSCRIPTS PUBLISHED AND IN PREPARATION

PAPER 1: **Antonio Canepa**, Jennifer E. Purcell, Mar Bosch Belmar, Melisa Acevedo, Miriam Gentile and Veronica Fuentes (2014) Salinity effects on asexual reproduction of *Carybdea* sp. (Cnidaria: Cubozoa). Journal of Plankton Research, 36:585–590. *Impact factor*: 2.435

PAPER 2: Alejandro Olariaga, Elisa F. Guallart, Verónica Fuentes, Àngel López-Sanz, **Antonio Canepa**, Juancho Movilla, Mar Bosch, Eva Calvo and Carles Pelejero. 2014. Polyp flats, a new system for experimenting with jellyfish polyps, with insights into the effects of ocean acidification . Limnology and Oceanography: Methods, 12: 210–220 . *Impact factor*: 1.95

PAPER 3: **Antonio Canepa**, Verónica Fuentes, Mar B. Belmar, Melissa Acevedo, Kilian Toledo-Guedes, Antonio Ortiz, Elia Durá, César Bordehore, Josep-Maria Gili. Environmental factors that influence the distribution of *Carybdea marsupialis* (Lineo, 1978, Cubozoa), in south-western Mediterranean coasts. Marine Ecology Progress Series. *In preparation*. Impact factor: 2.55

PAPER 4 **Antonio Canepa**, Verónica Fuentes, Ana Sabatés, Stefano Piraino, Ferdinando Boero, Josep-Maria Gili (2014) *Pelagia noctiluca* in the Mediterranean Sea. In: Jellyfish Blooms (eds Pitt, K. & Lucas, C.), Chapter 11, pages 237-266. Springer Netherlands.

PAPER 5: Lisandro Benedetti-Cecchi, **Antonio Canepa**, Veronica Fuentes, Laura Tamburello, Pat Halpin, Stefano Piraino, Jennifer E. Purcell and Jason Roberts. Extreme ecological events: The importance of deterministic and stochastic drivers of jellyfish outbreaks. Global Change Biology. *In preparation*. Impact factor: 6.91

PAPER 6: Paulo A.L.D Nunes, Maria Loureiro, Laia Piñol, Sergio Sastre, Louinord Voltaire and **Antonio Canepa**. Beach recreationists' preferences for lower risk of jellyfish outbreaks: economic results from a stated-choice experiment in Catalonia, Spain. Environmental Science & Policy. *Submitted*. Impact factor: 2.978

CONTRIBUTION OF THE AUTHORS:

PAPER 1: Conceived and designed the experiments: **AC**, JEP, VF. Performed the Experiment: **AC**, MBB, MA, MG. Analyzed the Data: **AC**, MA, MBB. Wrote the paper: **AC**, JEP, VF.

PAPER 2: Conceived and designed the experiments: AO, VF, AL-S, **AC**, JM, EC, CP. Performed the Experiment: EFG, AL-S, JM, **AC**, MB. Analyzed the Data: AL-S, **AC**, JM. Wrote the paper: CP, EC, VF, JM, **AC**, AL-S, AO.

PAPER 3: Conceived and designed the field sampling: CB, VF, **AC**, KT-G, J-MG. Performed the sampling: **AC**, MBB, MA, KT-G, AO, ED. Analyzed the Data: **AC**. Wrote the paper: **AC**, J-MG.

PAPER 4: Conceived and designed the idea and review: **AC**, J-MG, VF. Performed the review: **AC**, AS, SP. Analyzed the Data: **AC**, AS, SP. Wrote the paper: **AC**, AS, SP, FB, VF.

PAPER 5: Conceived and designed the work: LB-C, **AC**, LT, VF. Analyzed the Data: LB-C, **AC**, LT. Wrote the manuscript: LB-C, **AC**, JEP.

PAPER 6: Conceived and designed the experiments: PALDN, ML, LP, SS, LV, **AC**. Performed the Experiment: **AC**, SS, LP. Analyzed the Data: PALDN, ML, LV. Wrote the paper: PALDN, ML, LP, SS, LV, **AC**.

Dr. Josep-Maria Gili Sardá
Research Professor
Dept. of Marine Biology and Oceanography
Institute of Marine Science (ICM-CSIC)

Dra. Verónica L. Fuentes
Postdoctoral Scientist
Dept. of Marine Biology and Oceanography
Institute of Marine Science (ICM-CSIC)

GENERAL DISCUSSION

Despite the popular view that we are approaching a "jelly world" and the dramatic increase in the number of papers on jellyfish blooms published during the last decade (Condon et al. 2012), there are not enough data to sustain this suggestion on a global scale, with only some places indicating a significant increase (Brotz et al. 2012; Condon et al. 2013). Rather than arguing against the possibility of our ecological footprint being favourable for jellyfish blooms (reviewed in Purcell et al. 2007; Purcell 2012; Duarte et al. 2013), the lack of data should stimulate increased studies. Many places face blooms of gelatinous organisms annually and have in common highly perturbed marine ecosystems (Purcell 2012). Unfortunately, our increasing impacts in the socio-ecological marine ecosystem may lead to more problems associated with the positive phases of decadal oscillations of gelatinous zooplankton populations. Thus, it is a pressing need to understand which extrinsic factors relevant to the modern seas and near-future scenarios, coupled with the intrinsic functional biological traits of this polyphyletic group, can interact to trigger jellyfish blooms (Gibbons and Richardson 2013; Lucas and Dawson 2014).

The present work highlights the environmental drivers of the spatio-temporal dynamics of jellyfish along the Spanish Mediterranean coast. Also addressed are some differences associated with their geographical location and life cycle strategies (meroplanktonic versus holoplanktonic) in the relationship to both stochastic and deterministic environmental factors that modulate the abundance and spatial dynamics of jellyfish along the Spanish Mediterranean coast.

The importance of environmental conditions to jellyfish distributions

On the central Spanish Mediterranean coast, along the coast of Denia (Alicante), the coastal box jellyfish *Carybdea marsupialis* has caused major concern due to its painful sting and high abundances since 2008. Previous field based observations have shown that medusae were associated geographically with places near river mouths. The results of the salinity reduction experiment revealed the importance of this location for *Carybdea*. Salinity reduction significantly shortened the time required by *Carybdea* sp. to complete metamorphosis. Thus, late winter-early spring runoff of low salinity hastens jellyfish production. Conversely, high salinity extended the days to metamorphosis allowing the polyps to produce more buds and increase population size. Thus, the importance of salinity changes may be related to the habitat of some species living where salinity changes occur seasonally (i.e. mangroves, estuaries) (Studebaker 1972; Kingsford et al. 2012). Thus, the population of *Carybdea* sp. responds to changes in salinity by transforming into medusae at low salinity regimes and by increasing polyp population size with asexual budding at high salinity conditions. We hypothesize that *Carybdea* sp. polyps metamorphose into medusae in early spring when salinity decreases from high rain and terrestrial runoff and they benefit from high levels of primary and secondary production in the coastal water column generated by the nutrient-rich runoff.

The importance of freshwater runoff and other environmental conditions for the distribution of *C. marsupialis* along the coast of Denia were further demonstrated by non-normal distribution models. The effects of environmental variables on the local (~ tens of kilometres) abundance of the cubomedusae showed that sea surface temperature (SST) and salinity were the main environmental variables, followed by those related to primary and secondary production and local retention or transportation to the coast.

Temperature and salinity showed sudden changes (increases and decreases, respectively) during the spring period, at the same time small medusae were captured in samples, suggesting a relationship between changing environmental variables and the metamorphosis of *C. marsupialis* cubopolyps, as seen for jellyfish of other species (reviewed in Lucas et al. 2012; Purcell et al. 2012a). Salinity changes also signaled high coastal production, as hypothesized by Canepa et al. (2014b). In addition, the abundance of small *C. marsupialis* medusae was significantly correlated with Chl a, nitrate and phosphate along the coast of Denia. Thus, reduction of salinity with associated increases in nutrients and coastal production may be increasing the production of *C. marsupialis* medusae.

The distribution of *C. marsupialis* medusae seems to reflect the dispersion of the small and medium size classes by the onshore transport due to surface currents and by the high levels of primary and secondary production associated with the bottom type (sandy bottom and algae/sea grass meadows). Those factors allow *C. marsupialis* medusae to thrive where high densities were also recorded previously (Bordehore et al. 2011). Synergistic effects of fresh water discharge and processes related to artificial beach replenishment (Sardá et al. 2000) and locally nutrient rich water discharges seemed to occur. We speculate that the local industries add high nitrate and other crop fertilizers loads in freshwater, as commonly found in Spain where there is traditional farming and agricultural industry (Sebastiá et al. 2012; Gadea et al. 2013). Although, *C. marsupialis* has been recorded several places in the Mediterranean Sea, it rarely generates blooms (reviewed in Acevedo et al. 2013). Along the coast of Denia, high abundances of *C. marsupialis* were associated with variables indicating high local productivity.

This conclusion led to our management recommendation that, to reduce the blooms of *C. marsupialis,* crop fertilizers and sewage discharges should be reduced in highly populated or industrialized areas. Most importantly, high amounts of nutrients reaching the coast (by rivers or ground water discharges) should be prevented, especially in early spring. In order to decrease the amount of sewage water, solutions are possible with improvement in technology adding tertiary biological treatment to the sewage plants and by relocating the submarine pipeline further from the coast where the currents will spread the effluents. The idea behind this recommendation is to diminish the local secondary production, especially where habitats are good for *C. marsupialis*, *i.e.* soft bottom, sandy to gravel-sandy beaches and sea grass meadows.

Further investigation on the effects of increased coastal production on the fitness and cubopolyp metamorphosis is needed. Because *in situ* experimental research is difficult to conduct, with only a few studies following natural established polyp populations (Purcell et al. 2009; Malej et al. 2012), asexual reproduction of polyps has been mostly studied in controlled experiments. For this, a specialized experimental setup is needed. A number of experiments to determine the effects of different environmental parameters (especially temperature and salinity) on jellyfish polyps have been conducted in the past (reviewed in Lucas et al. 2012; Purcell et al. 2012). In all of these studies, the jellyfish polyps (1 to 2 mm high) were placed in small containers, from 5 to 160 mL volume, with periodic seawater renewal. That method might lead to unfavorable conditions for experimentation (Connor and Wilson 1972); the physico-chemical conditions of the seawater changed during the experiment, due to accumulation of waste products, depletion of dissolved oxygen, changes in pH, and growth of bacterial communities, which could alter the outcome of the experiment.

One major issue concerning anthropogenic influences in the marine realm is ocean acidification (Doney et al. 2009). Several studies on the effects of pH on different organisms have shown that maintain pH levels constant is a major challenge (Winans and Purcell 2010). Our new system was shown to be accurate and stable for experimentation on jellyfish polyps. It is also easy to maintain, and therefore, suitable for long-term studies on the responses of these organisms to environmental stressors such as ocean acidification. The mortality rate of polyps during our experiment was only 0.05% d^{-1} over 278 days, a very low mortality rate compared with other studies (Purcell et al. 2012a). This prototype contributes a unique design to the new devices (e.g., Fangue et al. 2010; McGraw et al. 2010; Hoffmann et al. 2013; Bockmon et al. 2013) aimed at providing better tools for testing the effects of acidification and other environmental stressors in marine organisms, a discipline that recently was ranked as the top research front in Ecology and Environmental Sciences (King and Pendlebury 2013). Overall, this study presents a relatively simple and affordable system that can greatly improve the results obtained from testing the effects of a range of environmental pressures on the eco-physiology of jellyfish polyps.

The mauve stinger *Pelagia noctiluca* is the most common jellyfish in the Mediterranean Sea. Its records began in the 1700s, motivated by its high numbers and painful stings. Because it has a holoplanktonic life cycle without polyps, this species has a global distribution (Purcell 2004) and reaches up to 4° north in European waters (Doyle et al. 2008; Bastian et al. 2011). In the Mediterranean Sea, this species is known to form dense aggregations offshore that reach the coast when favored by winds and surface currents. Along the Catalan coast, the abundances of *P. noctiluca* and other planktonic cnidarians were highest at the shelf-slope front (Sabatés et al. 2010). The stability of the front and its duration in time and space have been proposed to be responsible for the massive arrival of medusae to the coast (Rubio and Muñoz 1997).

Nevertheless, the vertical migration, swimming activity and abundance of prey that enhance its survival, will ultimately determine the time spent in the column water affected by surface transport (reviewed in Canepa et al. 2014a). Thus, coastal morphology and local hydrodynamics explain its massive presence in enclosed coastal habitats like ports, beaches and coves.

Recently, a citizen science-based monitoring program along the Catalan coast (see section 11.5.1 "The Medusa Project" in Canepa et al. 2014a), revealed the fact that many sightings (high abundances) of *P. noctiluca* were spatially correlated with canyons along the Catalan coast. That phenomenon also occurs in other places in the Western Mediterranean, which led to a new hypothesis about the seasonal vertical migration and overwintering behavior of this species (Fig. 11.5a-d in Canepa et al. 2014a). In summer, warm temperatures and the reduction of zooplankton prey make surface waters unfavorable for *P. noctiluca* and their records along shorelines become increasingly rare. Boero (in Sacchetti 2012) hypothesized that, during summer, jellyfish migrate down to cooler mid-water depths, possibly along canyon corridors. Thus, *P. noctiluca* may spend the warmer months at deeper habitats along the continental slope with abundant food sources like euphausiid shrimps maintained in part by the high amount of the coastal surface primary production that is swept down by the canyons net downward particle flux (Palanques et al. 2005). At depth, *P. noctiluca* can invest more energy towards future sexual reproduction. During the late autumn and early winter, massive numbers of *P. noctiluca* appear at localities along the coastline nearest the upper margins of marine canyons and upwelling areas, such as around the Aeolian archipelago and the Strait of Messina, NE Sicily, the Island of Elba, Tuscany, and the continental platform of the Ligurian Sea. In late autumn-winter, large *P. noctiluca* can be found in surface waters even in daytime, where they also exhibit an uncommon swimming behavior, with frequent formation of couples (Fig. 11.6 in Canepa et al. 2014a), which may be associated with sexual reproduction and lead to a new cohort of planulae and ephyrae. Indeed, swarms of juvenile jellyfish are encountered throughout winter. During the following months, the juvenile medusae will feed in surface waters on the spring zooplankton and ichthyoplankton. After the increase of sea surface temperatures and water mass stratification, *P.*

noctiluca will leave the surface waters, starting a new annual migratory cycle.

From The Medusa Project along the Catalan Coast some characteristic species of spring time were *Chrysaora hysoscella*, *Aurelia aurita*, *Aequorea forskalea* and *Velella velella*. During the summer, the most frequent jellyfish species recorded was the scyphozoan *Rhizostoma pulmo*, whose occurrence seemed to increase over time, especially in 2011 and 2012 (Fuentes et al. 2011). Finally, in late summer, the scyphozoan *Cotylorhiza tuberculata* arrived and dominated the records. Stranded *P. noctiluca* medusae occurred throughout the sampling period (May-September), but with highest abundances in spring (Fig. 11.3 in Canepa et al. 2014a).

Our Bayesian analysis of the importance of stochastic versus deterministic drivers of jellyfish outbreaks along the Catalan Coast showed that jellyfish outbreaks were more frequent in May and June, particularly in the years 2009 and 2010. Outbreaks were negatively associated with SST and distance to canyons, and positively associated with the onshore current transport force. This model was largely influenced by the abundance of *P. noctiluca*, the most common jellyfish along the Catalan coast and elsewhere in the Western Mediterranean, and the environmental factors reflect the conditions in which *P. noctiluca* reaches the coast. The model results agreed with other data that *P. noctiluca* is more abundant during spring and summer months (Morand et al. 1992; Licandro et al. 2010; Berline et al. 2013). This result gives empirical support to the hypothesis proposed by Canepa et al. (2014a) that canyons funnel blooms of *P. noctiluca* to the coast during upwelling of cold water masses.

Our results indicated that deterministic processes were more important than the stochastic component of environmental variation, suggesting that extreme events, visualized as the compound effects of environmental variables, did not affect the probability of an outbreak along the Catalan Coast. Nevertheless, SST and the onshore current transport force were significant time-varying predictors, but their signal was not strong enough to overwhelm deterministic effects. These results are in accord with the relationship of the distribution of gelatinous zooplankton at the shelf-slope front and with the signal of frontal mesoscale activity; specifically, when the front weakens, jellyfish are able to reach the coast (Gili et al. 1988; Rubio and Muñoz

1997; Sabatés et al. 2010).

Return time values from the model indicated that the frequency of jellyfish outbreaks should not increase in the study region as a consequence of environmental fluctuations. This return time (~ 6.5 years) is more similar to that predicted by (Kogovšek et al. 2010) for 1960s onwards (< 8 years) than 12 years previously calculated by Goy et al. (1989). Shorter return times also have been predicted for the Western Mediterranean, averaging 3-4 years (Goy et al. 1989; Daly Yahia et al. 2010). These results highlight the necessity to better understand how environmental factors affect population and demographic processes in jellyfish species. By doing this, we can greatly improve our ability to anticipate their outbreaks in the future.

The increasing importance of jellyfish interactions with humans

In this thesis, I have addressed the problem of jellyfish – human interactions in three main ways. The first focus was to provide recommendations for dealing with proliferation of stinging *Carybdea marsupialis* cubomedusae along the coast of Denia. In addition to the recommendation to reduce nutrient supplies to the coast (see Discussion section 'The importance of environmental conditions to jellyfish distributions' and paper 3), the results from our study suggested two steps. First, in order to detect the presence and estimate the abundance of *C. marsupialis*, coastal sampling should start in mid-spring and use ~ 500 µm mesh size to collect the small medusae. Sampling during rough sea conditions should be avoided to minimize underestimation and false negative records. Once the population is established and the presence of medium size is confirmed, the large medusae should be sampled with greater mesh size (~ 4 mm) to collect the most, large stinging individuals. In this case, sampling should be restricted to popular beaches with sandy bottom associated with three dimensional structures like sea grass/algae meadows, new breakwaters or other artificial substrata. Similarly, sampling for large individuals should start earlier at beaches with low wave dynamics and higher temperature due to shallow profiles.

The problems for humans from jellyfish have increased many places around the world (Purcell et al. 2007, Purcell 2012). Jellyfish blooms appear to be increasing in parts of the world, including the Mediterranean Sea (Brotz et al. 2012; Condon et al. 2013). This trend is supported by relatively few existing long-term data sets due to the earlier lack of recognition of the importance of jellyfish and to the expense and scarcity of long-term monitoring programs. A solution to such problems has arisen recently. Citizen science, in which the public participates in scientific research mostly by collecting of data, has proven to be a positive and economical source of data (reviewed in Conrad & Hilchey 2011). One of the principal benefits of these activities is that many minimally-trained people can make simple sampling with much greater spatial and temporal coverage and lower costs than limited scientific studies. Citizen scientists are involved in many topics, including climate change, invasive species, conservation biology, ecological restoration, water quality and species monitoring and population ecology (Silvertown 2009). Jellyfish citizen science programs along the Mediterranean Sea have resulted in efforts to understand epidemiology, jellyfish sting treatments and socio-economic impacts (De Donno et al. 2014) and have led to new sightings of non-native species like the ctenophore *Mnemiopsis leidyi* off the NW Mediterranean Spanish coast (Fuentes et al. 2009), the scyphozoan *Rhopilema nomadica* in Maltese waters (Deidun et al. 2011), and a new species in Venice Lagoon (Piraino et al. 2014). My second focus is based on a citizen science based monitoring program that lead to key information on the importance of jellyfish to local beach tourism (Canepa et al. 2014a). During the summer season, *Pelagia noctiluca*, *Rhizostoma pulmo*, *Olindias phosphorica*, and *Carybdea marsupialis* (in decreasing order of abundance) were responsible for stings that required first aid attention. But importantly, among the jellyfish species associated with painful stings, *P. noctiluca* was the only species positively correlated with the number of stings, which in 2006 totaled 9,155 cases in the northern province (Girona) of Catalonia and contributed to the total of 22,655 assistances due to jellyfish stings for the Catalan coast (Fig. 11.10 in Canepa et al. 2014a).

Citizen Science contributed even more value. Papers 4 and 5 relied on those data from the Catalan coast, which in turn, provided critical insights into the locations and times that jellyfish arrive at the coast and affect tourism. The citizen science program also provides a key educational tool to increase public understanding of jellyfish, which in turn reduces their economic damage to tourism.

Finally the third focus of my thesis sought to characterize the public perception of jellyfish outbreaks and to determine their importance to tourism in economic value. From a stated-choice questionnaire and a Random Utility Model, which estimated how much respondents were willing to spend, in terms of reported extra travel time to a bathing beach with lower risk of jellyfish outbreaks, we tested the impact of the risk of jellyfish outbreaks on beach recreationists along the Catalan coast. The visitors were willing to spend an additional 23.8% of their travel time to enjoy beach recreation where risk of a jellyfish outbreak was lower. We calculated that the well-being gains associated with a reduction of jellyfish outbreaks in this area would range between €312 and €322 million annually, corresponding approximately to 19% of the tourism expenditures of the Catalan population in 2012. Nevertheless, improvement in the beach water quality was, by far, the most valuable attribute for all types of respondents. Improvement in the beach infrastructure was ranked second and reduction in the risk of jellyfish outbreaks, third. From the econometric view point, the difference in ranking between improved infrastructure and jellyfish risk was not statistically significant, meaning that these attributes were seen as equally important by the respondents of this study. This study confirms the urgency to provide daily information by use of the wide set of social media applications. The current lack of public knowledge about jellyfish suggests that providing such information to beach recreationists is the only effective policy instrument to minimize the impact of jellyfish outbreaks.

REFERENCES

Acevedo MJ, Fuentes VL, Olariaga A, et al. (2013) Maintenance, feeding and growth of *Carybdea marsupialis* (Cnidaria : Cubozoa) in the laboratory. J Exp Mar Bio Ecol 439:84–91.

Acuña JL, López-Urrutia Á, Colin S (2011) Faking giants: the evolution of high prey clearance rates in jellyfishes. Science 333:1627–9. doi: 10.1126/science.1205134

Atienza D, Lewinsky I, Fuentes V, Tilves U, Gentile M, Olariaga A, Gili JM, & De Torres M (2010) Nine years of jellyfish observations in Catalonia, Spain (NW Mediterranean). Third International Jellyfish Blooms Symposium, Mar del Plata, Argentina.

Attrill MJ, Wright J, Edwards M (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnol Oceanogr 52:480–485. doi: 10.4319/lo.2007.52.1.0480

Axiak V, Galea C, Schembri PJ (1991) Coastal aggregations of the jellyfish *Pelagia noctiluca* (Scyphozoa) in Maltese coastal waters during 1980–1986. UNEP: Jellyfish blooms in the Mediterranean. In: Proceedings of the II workshop on jellyfish in the Mediterranean Sea. MAP Tech Rep Ser, 47. UNEP, Athens, pp 32–40

Bastian T, Stokes D, Kelleher JE, et al. (2011) Fisheries bycatch data provide insights into the distribution of the mauve stinger (*Pelagia noctiluca*) around Ireland. ICES J Mar Sci 68:436–443.

Berline L, Zakardjian B, Molcard A, et al. (2013) Modeling jellyfish *Pelagia noctiluca* transport and stranding in the Ligurian Sea. Mar Pollut Bull 70:90–99. doi: 10.1016/j.marpolbul.2013.02.016

Bernard P, Berline L, Gorsky G (2011) Long term (1981-2008) monitoring of the jellyfish *Pelagia noctiluca* (Cnidaria, Scyphozoa) on Mediterranean Coasts (Principality of Monaco and French Riviera). J Oceanogr Res Data 4:1–10.

Bockmon EE, Frieder CA, Navarro MO, et al. (2013) Technical Note: Controlled experimental aquarium system for multi-stressor investigation of carbonate chemistry, oxygen saturation, and temperature. Biogeosciences 10:5967–5975. doi: 10.5194/bg-10-5967-2013.

Boero F (2013) Review of jellyfish blooms in the Mediterranean and Black Sea. Stud Rev Gen Fish Comm Mediterr FAO, Rome, p 53.

Boero F (1994) Fluctuations and variations in coastal marine environments. PSZN I Mar Ecol 15:3–25.

Boero F, Bouillon J, Gravili C, et al. (2008) Gelatinous plankton : irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299–310. doi: 10.3354/meps07368.

Bordehore C, Fuentes VL, Atienza D, et al. (2011) Detection of an unusual presence of the cubozoan *Carybdea marsupialis* at shallow beaches located near Denia, Spain (south-western Mediterranean). Mar Biodivers Rec 4:1–6. doi: 10.1017/S1755267211000650.

Brodeur RD, Decker MB, Ciannelli L, et al. (2008) Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Progr Oceanogr 77:103–111. doi: 10.1016/j.pocean.2008.03.017

Brotz L, Cheung WWL, Kleisner K, et al. (2012) Increasing jellyfish populations : trends in Large Marine Ecosystems. Hydrobiologia 690:3–20. doi: 10.1007/s10750-012-1039-7 Brotz L, Pauly D (2012) Jellyfish populations in the Mediterranean Sea. Acta Adriat 53:211–230.

Bulleri F, Chapman MG (2010) The introduction of coastal infrastructure as a driver of change in marine environments. J Appl Ecol 47:26–35. doi: 10.1111/j.1365-2664.2009.01751.x

Calvo E, Simó R, Coma R, et al. (2011) Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. Clim Res 50:1–29. doi: 10.3354/cr01040

Canepa A, Fuentes V, Sabatés A, et al. (2014a) *Pelagia noctiluca* in the Mediterranean Sea. In: Pitt KA, Lucas CH (eds) Jellyfish Bloom. Springer Netherlands, pp 237–266.

Canepa A, Purcell JE, Belmar MB, et al. (2014b) Salinity effects on asexual reproduction of *Carybdea* sp. (Cnidaria: Cubozoa). J Plankton Res 36:585–590. doi: 10.1093/plankt/fbt124

Condon RH, Decker MB, Purcell JE (2001) Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (*Chrysaora quinquecirrha*). Hydrobiologia 451:89–95.

Condon RH, Graham WM, Duarte CM et al. (2012) Questioning the rise of gelatinous zooplankton in the world’s oceans. Bioscience 62:160–169. doi: 10.1525/bio.2012.62.2.9

Condon RH, Duarte CM, Pitt K a, et al. (2013) Recurrent jellyfish blooms are a consequence of global oscillations. Proc Natl Acad Sci U S A 110:1000–1005. doi: 10.1073/pnas.1210920110.

Connor PM, Wilson KW (1972) A continuous-flow apparatus for assessing the toxicity of substances to marine animals. J Exp Mar Biol Ecol 9:209–215. doi:http://dx.doi.org/10.1016/0022-0981(72)90033-0.

Conrad CC & Hilchey KG (2011) A review of citizen science and community-based environmental monitoring: issues and opportunities. Environ Monit Assess 176:273–291. doi: 10.1007/s10661-010-1582-5.

Daly Yahia NM, Batistic M, Lucic D, et al. (2010) Are the outbreaks of *Pelagia noctiluca* (Forsskål, 1775) more frequent in the Mediterranean basin? ICES Coop Rep 300:8–14.

Dawson MN, Martin LE, Penland LK (2001) Jellyfish swarms, tourists, and the Christ-child. Hydrobiologia 451:131–144.

Decker MB, Brown CW, Hood RR, et al. (2007) Development of habitat models for predicting the distribution of the scyphomedusa *Chrysaora quinquecirrha* in Chesapeake Bay. Mar Ecol Prog Ser 329:99–113. doi: 10.3354/meps329099

Deidun A, Arrigo S, Piraino S (2011) The westernmost record of *Rhopilema nomadica* (Galil, 1990) in the Mediterranean – off the Maltese Islands. Aquatic Invasions 6: S99–S103. doi: 10.3391/ai.2011.6.S1.023

Doney SC, Fabry VJ, Feely R a., Kleypas J a. (2009) Ocean Acidification: The Other CO2 Problem. Ann Rev Mar Sci 1:169–192. doi: 10.1146/annurev.marine.010908.163834

Doney SC, Ruckelshaus M, Emmett Duffy J, et al. (2012) Climate change impacts on marine ecosystems. Ann Rev Mar Sci 4:11–37. doi: 10.1146/annurev-marine-041911-111611

De Donno A, Idolo A, Bagordo F, et al. (2014) Impact of stinging jellyfish proliferations along south Italian Coasts: Human health hazards, treatment and social costs. Int J Environ Res Public Health 11:2488–2503. doi: 10.3390/ijerph110302488.

Doyle TK, Houghton JDR, McDevitt R, Davenport J, Hays GC (2007) The energy density of jellyfish: Estimates from bomb-calorimetry and proximate-composition. J Exp Mar Biol Ecol 343: 239–252. doi:10.1016/j.jembe.2006.12.010

Doyle TK, De Haas H, Cotton D, et al. (2008) Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. J Plankton Res 30:963–968. doi: 10.1093/plankt/fbn052

Duarte CM, Pitt KA, Lucas CH, et al. (2013) Is global ocean sprawl a cause of jellyfish blooms? Front Ecol Environ 11:91–97. doi: 10.1890/110246

Fangue NA, O'Donnell MJ, Sewell MA, et al. (2010) A laboratory-based, experimental system for the study of ocean acidification effects on marine invertebrate larvae. Limnol Oceanogr Methods 8:441–452. doi: 10.4319/lom.2010.8.441

Ferraris M, Berline L, Lombard F, et al. (2012) Distribution of *Pelagia noctiluca* (Cnidaria, Scyphozoa) in the Ligurian Sea (NW Mediterranean Sea). J Plankton Res 34:874–885. doi: 10.1093/plankt/fbs049

Fuentes V, Atienza D, Gili J-M, Purcell JE (2009) First records of *Mnemiopsis leidyi* A. Agassiz 1865 off the NW Mediterranean coast of Spain. Aquatic Invasions 4: 671–674. doi:10.3391/ai.2009.4.4.12

Fuentes V, Straehler-Pohl I, Atienza D, et al. (2011) Life cycle of the jellyfish *Rhizostoma pulmo* (Scyphozoa: Rhizostomeae) and its distribution, seasonality and inter-annual variability along the Catalan coast and the Mar Menor (Spain, NW Mediterranean). Mar Biol 158:2247–2266. doi: 10.1007/s00227-011-1730-7

Gadea I, Rodilla M, Sospedra J, et al. (2013) seasonal dynamics of the phytoplankton community in the gandia coastal area , southern gulf of valencia. Thalassia 29:35–58.

Gibbons MJ, Richardson AJ (2013) Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. J Plankton Res 35:929–938. doi: 10.1093/plankt/fbt063

Gili J-M, Pagès F (2005) Les proliferacions de meduses. Bolletí la Soc d'Historia Nat les Balear 48:9–22.

Gili JM, Pagès F, Sabatés A, Ros JD (1988) Small-scale distribution of a cnidarian population in the western Mediterranean. J Plankton Res 10:385–401.

Goy J, Morand P, Etienne M (1989) Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. Deep Sea Res Part A Oceanogr Res Pap 36:269–279. doi: 10.1016/0198-0149(89)90138-6

Graham WM, Pagès F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451: 199–212.

Hamner WM, Madin LP, Alldredge AL, Gilmer RW, Hamner PP (1975) Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. Limnol Oceanogr 20:907–917

Hoffmann LJ, Breitbarth E, McGraw CM, et al. (2013) A trace-metal clean, pH-controlled incubator system for ocean acidification incubation studies. Limnol Oceanogr Meth 11:53–61. doi: 10.4319/lom.2013.11.53

Kideys AE, Roohi A, Eker-Develi E, et al. (2008) Increased chlorophyll levels in the southern Caspian Sea following an invasion of jellyfish. Res Lett Ecol 2008:1–4. doi: 10.1155/2008/185642

King C, Pendlebury DA (2013) Research Fronts 2013: 100 top-ranked specialties in the sciences and social sciences. Thomson Reuters 1–32.

Kingsford MJ, Seymour JE, O'Callaghan MD (2012) Abundance patterns of cubozoans on and near the Great Barrier Reef. Hydrobiologia 690:257–268. doi: 10.1007/s10750-012-1041-0

Klein SG, Pitt KA, Rathjen KA, Seymour JE (2014) Irukandji jellyfish polyps exhibit tolerance to interacting climate change stressors. Glob Change Biol 20:28–37. doi: 10.1111/gcb.12408

Kogovšek T, Bogunović B, Malej A (2010) Recurrence of bloom-forming scyphomedusae: wavelet analysis of a 200-year time series. Hydrobiologia 645:81–96. doi: 10.1007/s10750-010-0217-8

Lebrato M, Pitt KA, Sweetman AK, et al. (2012) Jelly-falls historic and recent observations: a review to drive future research directions. Hydrobiologia 690:227–245. doi: 10.1007/s10750-012-1046-8

Licandro P, Conway DVP, Daly Yahia MN, et al. (2010) A blooming jellyfish in the northeast Atlantic and Mediterranean. Biol Lett 6:688–691. doi: 10.1098/rsbl.2010.0150

Lo W-T, Purcell JE, Hung J-J, et al. (2008) Enhancement of jellyfish (*Aurelia aurita*) populations by extensive aquaculture rafts in a coastal lagoon in Taiwan. ICES J Mar Sci 65:453–461.

Lo WT, Chen IL (2008) Population succession and feeding of scyphomedusae, *Aurelia aurita*, in a eutrophic tropical lagoon in Taiwan. Estuar Coast Shelf Sci 76:227–238. doi: 10.1016/j.ecss.2007.07.015

Lucas CH, Dawson MN (2014) What Are jellyfishes and thaliaceans and why do they bloom? In: Pitt KA, Lucas CH (eds) Jellyfish Bloom. Springer Netherlands, pp 9–44

Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories：Role of polyps in forming and maintaining scyphomedusa populations. Adv Mar Biol 63:133–196

Lucas CH, Jones DOB, Hollyhead CJ, et al. (2014) Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. Glob Ecol Biogeogr in press. doi: 10.1111/geb.12169

Lucas CH, Kylie AP, Purcell JE, Lebrato M, Condon RH (2011) What's in a jellyfish? Proximate and elemental composition and biometric relationships for use in biogeochemical studies. Ecology 92:1704-1704.

Lynam CP, Gibbons MJ, Axelsen BE, et al. (2006) Jellyfish overtake fish in a heavily fished ecosystem. Curr Biol 16:R492

Lynam CP, Lilley MKS, Bastian T, et al. (2011) Have jellyfish in the Irish Sea benefited from climate change and overfishing? Glob Change Biol 17:767–782. doi: 10.1111/j.1365-2486.2010.02352.x

Malej A, Kogovšek T, Ramšak A, Catenacci L (2012) Blooms and population dynamics of moon jellyfish in the northern Adriatic. Cah Biol Mar 53:337–342.

Mariottini GL, Pane L (2010) Mediterranean jellyfish venoms：A review on scyphomedusae. Mar Drugs 8:1122–1152. doi: 10.3390/md8041122

McGraw CM, Cornwall CE, Reid MR, et al. (2010) An automated pH-controlled culture system for laboratory-based ocean acidification experiments. Limnol Oceanogr Meth 8:686–694. doi: 10.4319/lom.2010.8.686

Mianzan H, Purcell JE, Frost JR (2012) Preface：Jellyfish blooms：interactions with humans and fisheries. 1–2. doi: 10.1007/s10750-012-1050-z

Mills CE (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451:55–68. doi: 10.1023/a:1011888006302

Mills CE (1995) Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES J Mar Sci 52:575–581.

Møller LF, Riisgård HU (2007) Impact of jellyfish and mussels on algal blooms caused by seasonal oxygen depletion and nutrient release from the sediment in a Danish fjord. J Exp Mar Bio Ecol 351:92–105. doi: 10.1016/j.jembe.2007.06.026

Morand P, Goy J, Dallot S (1992) Recrutement et fluctuations à long terme de *Pelagia noctiluca* (Cnidaria, Scyphozoa). Ann L'institut océanographique 68:151–158.

Ohata R, Masuda R, Yamashita Y (2011) Ontogeny of antipredator performance in hatchery-reared Japanese anchovy *Engraulis japonicus* larvae exposed to visual or tactile predators in relation to turbidity. J Fish Biol 79:2007–18. doi: 10.1111/j.1095-8649.2011.03141.x

Olariaga A, Guallart EF, Fuentes V, et al. (2014) Polyp flats, a new system for experimenting with jellyfish polyps, with insights into the effects of ocean acidification. Limnol Oceanogr Methods 12:210–220. doi: 10.4319/lom.2014.12.210

Palanques A, García-Ladona E, Gomis D, et al. (2005) General patterns of circulation, sediment fluxes and ecology of the Palamós (La Fonera) submarine canyon, northwestern Mediterranean. Prog Oceanogr 66:89–119. doi: 10.1016/j.pocean.2004.07.016

Parsons TR, Lalli CM (2002) Jellyfish population explosions: Revisiting a hypothesis of possible causes. La Mer 40:111–121.

Pauly D, Christensen V, Dalsgaard J et al. (1998) Fishing down marine food webs. Science (80-) 279:860–863. doi: 10.1126/science.279.5352.860

Pauly D, Alder J, Bennett E, Christensen V, Tyedmers P, Watson R. 2003. The future of fisheries. Science 302: 1359–1361.

Piraino S, Aglieri G, Martell L et al. (2014) *Pelagia benovici* sp. nov. (Cnidaria, Scyphozoa): a new jellyfish in the Mediterranean Sea. Zootaxa 3794 (3): 455–468

Pitt KA, Welsh DT, Condon RH (2008) Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. Hydrobiologia 616:133–149. doi: 10.1007/s10750-008-9584-9

Pitt KA, Lucas CH (2014) Jellyfish Blooms. Springer. 308 pp. doi: 10.1007/978-94-007-7015-7

Purcell JE (2004) Class Scyphozoa. Pp. 153-168 In Grzimek’s Animal Life Encyclopedia 2nd Edition Vol. 1 Lower Metazoans and Lesser Deuterostomes. M Hutchins, D.A. Thoney & N. Schlager (eds). Farmington Hills, MI: Gale Group.

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms：a review. J Mar Biol Assoc UK 85:461–476.

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Ann Rev Mar Sci 4:1.1–1.27. doi: 10.1146/annurev-marine-120709-142751

Purcell JE, White JR, Nemazie DA, Wright DA (1999) Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. Mar Ecol Prog Ser 180:187-196.

Purcell JE, Breitburg DL, Decker MB, et al. (2001) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: A review. In: Rabalais NN, Turner RE (eds) Coastal Hypoxia Consequences Living Resources and Ecosystems American Geophysical Union, Washington, D. C., Coast Estuar Stud 58:77–100.

Purcell JE, Uye S, Lo W-T (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans：a review. Mar Ecol Prog Ser 350:153–174. doi: 10.3354/meps07093

Purcell JE, Hoover RA, Schwarck NT (2009). Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions in situ. Mar Ecol Progr Ser *375*:139–149. doi:10.3354/meps07785

Purcell JE, Atienza D, Fuentes V, et al. (2012a) Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. Hydrobiologia 690:169–180. doi: 10.1007/s10750-012-1047-7

Purcell JE, Clarkin E, Doyle TK (2012b) Foods of *Velella velella* (Cnidaria: Hydrozoa) in algal rafts and its distribution in Irish seas. Hydrobiologia 690: 47-55.

Quiñones J, González Carman V, Zeballos J, et al. (2010) Effects of El Niño-driven environmental variability on black turtle migration to Peruvian foraging grounds. Hydrobiologia 645:69–79. doi: 10.1007/s10750-010-0225-8

Richardson AJ (2008) In hot water: zooplankton and climate change. ICES J Mar Sci 65:279–295.

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol Evol 24:312–322. doi: 10.1016/j.tree.2009.01.010

Richardson AJ, Gibbons MJ (2008) Are jellyfish increasing in response to ocean acidification? Limnol Oceanogr 53:2040–2045.

Rubio P, Muñoz JMH (1997) Predicción estival del riesgo de blooms de *Pelagia noctiluca* (litoral central catalán). In: Novau JC (ed) Situaciones riesgo climático en España. Instituto Pirenaico de Ecología, Jaca (Huesca), pp 281–287

Rutherford LDJ, Thuesen E V. (2005) Metabolic performance and survival of medusae in estuarine hypoxia. Mar Ecol Prog Ser 294:189–200.

Sabatés A, Pagès F, Atienza D, et al. (2010) Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. Hydrobiologia 645:153–165. doi: 10.1007/s10750-010-0221-z

Sardá R, Pinedo S, Gremare A, Taboada S (2000) Changes in the dynamics of shallow sandy-bottom assemblages due to sand extraction in the Catalan Western Mediterranean Sea. ICES J Mar Sci 57:1446–1453. doi: 10.1006/jmsc.2000.0922

Sacchetti F (2012) Il ritorno di MeteoMedusa. Focus 237:92–94

Sebastiá MT, Estornell J, Rodilla M, et al. (2012) Estimation of chlorophyll «A» on the Mediterranean coast using a QuickBird image. Rev Teledetección 37:23–33.

Silvertown J (2009) A new dawn for citizen science. Trends Ecol Evol 24: 467-471.

Stoner EW, Layman CA, Yeager LA, Hassett HM (2011) Effects of anthropogenic disturbance on the abundance and size of epibenthic jellyfish *Cassiopea* spp. Mar Pollut Bull 62:1109–14. doi: 10.1016/j.marpolbul.2011.03.023

Stramma L, Schmidtko S, Levin LA, Johnson GC (2010) Ocean oxygen minima expansions and their biological impacts. Deep Sea Res Part I Oceanogr Res Pap 57:587–595. doi: 10.1016/j.dsr.2010.01.005

Studebaker JP (1972) Development of the cubomedusa, *Carybdea marsupialis*. Master Thesis, University of Puerto Rico, Department of Marine Sciences. 86pp.

Thein H, Ikeda H, Uye S (2012) The potential role of podocysts in perpetuation of the common jellyfish *Aurelia aurita* s.l. (Cnidaria: Scyphozoa) in anthropogenically perturbed coastal waters. Hydrobiologia 690:157–167. doi: 10.1007/s10750-012-1045-9

Thuesen E V, Rutherford LD, Brommer PL, et al. (2005) Intragel oxygen promotes hypoxia tolerance of scyphomedusae. J Exp Biol 208:2475–82. doi: 10.1242/jeb.01655

Winans AK, Purcell JE (2010) Effects of pH on asexual reproduction and statolith formation of the scyphozoan, *Aurelia labiata*. Hydrobiologia 645:39–52. doi: 10.1007/s10750-010-0224-9

Yang W, Guo L, Zhao W, et al. (2011) The effect of pH, salinity and food organism species on survival and growth of larval jellyfish *Chrysaora melanaster*. J Dalian Ocean Univ 26:223–226.

FIGURES

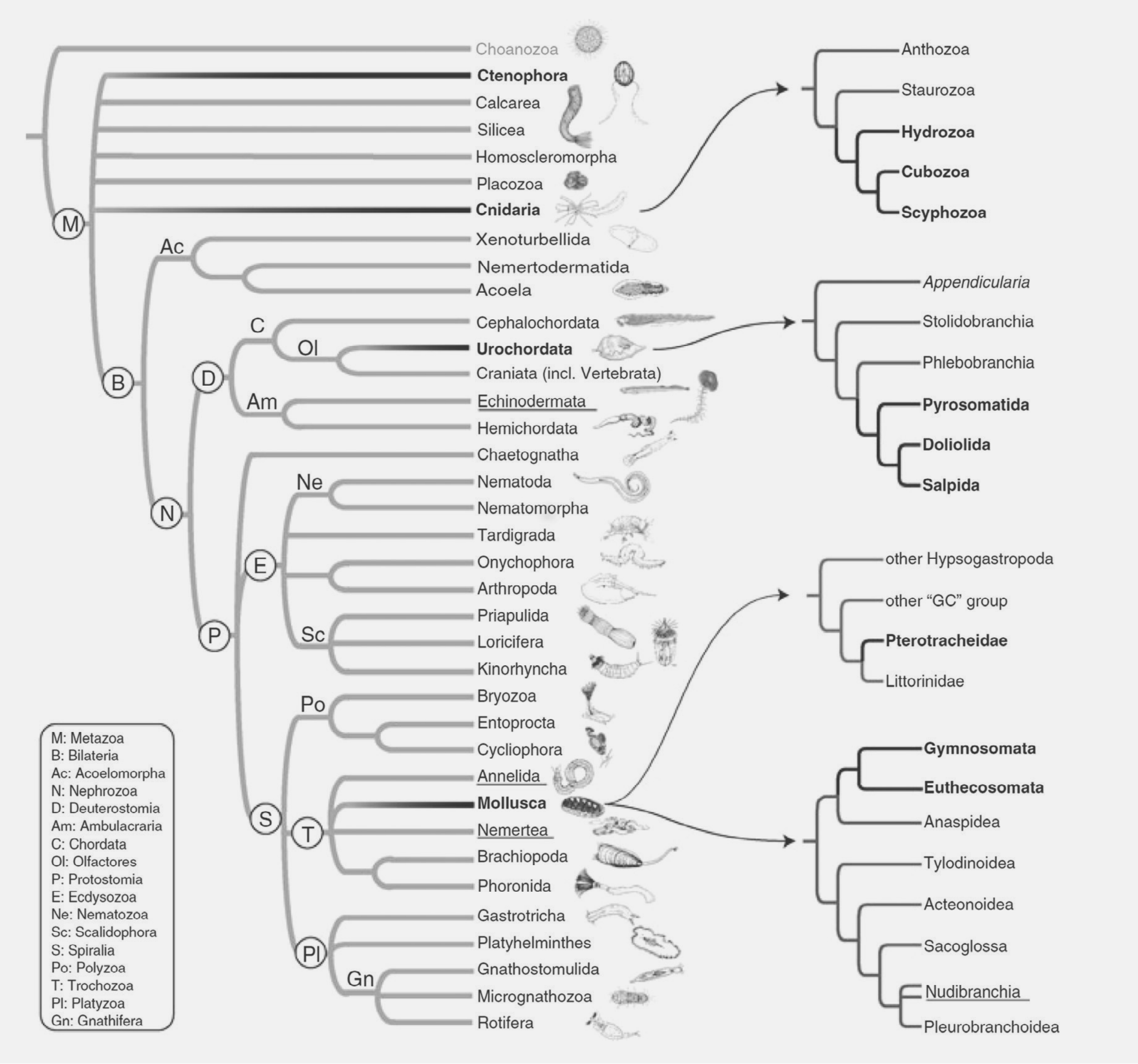


Figure 1. The gelatinous planktonic ecotype arose at least nine separate times within Metazoa. Phylogeny of the metazoans (*left*) indicating the principal gelatinous zooplanktonic phyla (*black branches*, *bold*) and also other phyla in which there are occasional gelatinous zooplanktonic taxa (*underlined*). Relationships within the principal gelatinous zooplanktonic taxa are shown for Cnidaria (*right top*), for Urochordata (*right upper middle*) and within Mollusca (*bottom*). Appendicularia is highlighted (italics) because, although their body is not gelatinous, the large mucous net they secrete conveys many of the functional attributes of other gelatinous zooplankton. (Fig. 2.1; Pitt and Lucas 2014).

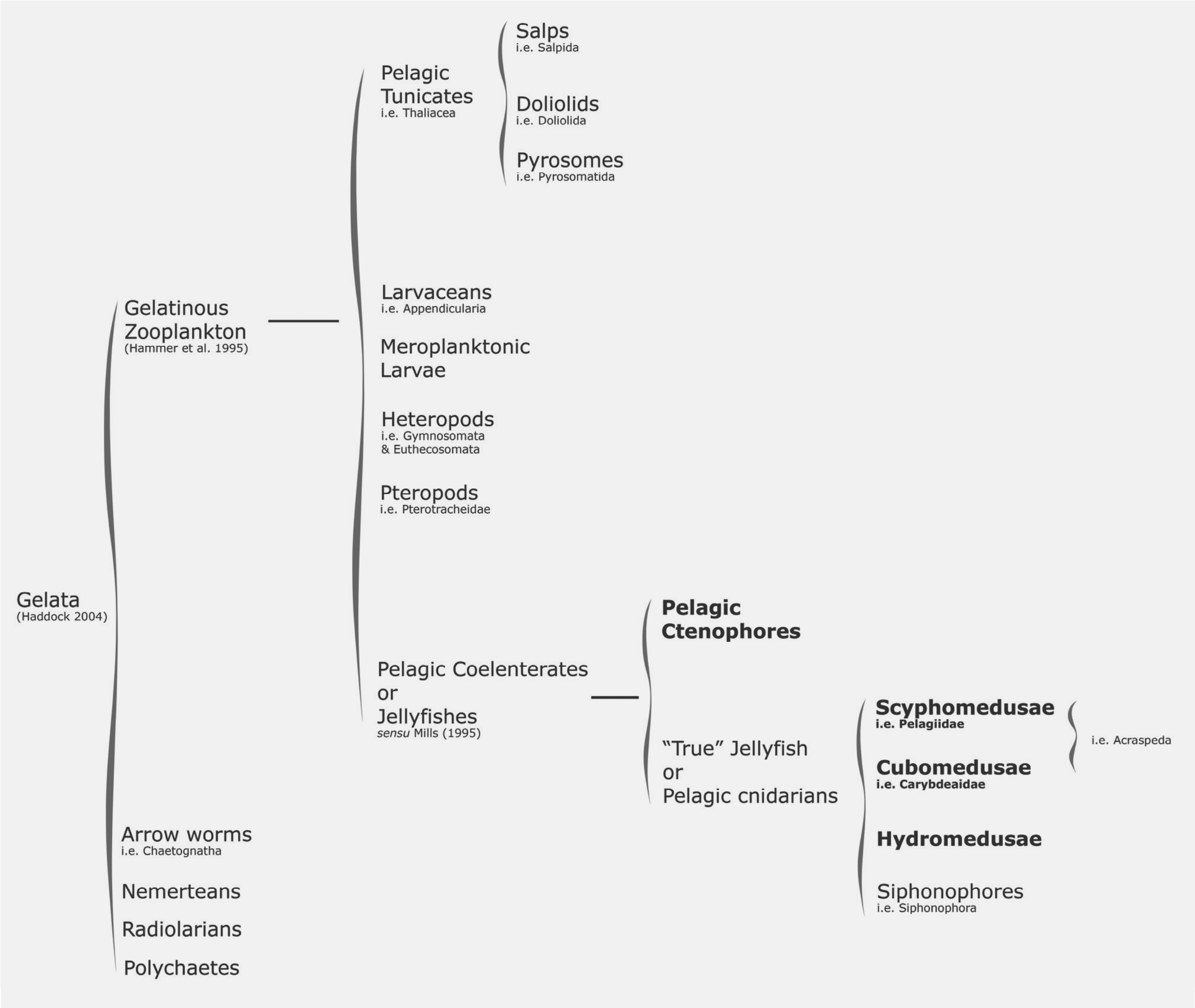


Figure 2. Schematic view of the gelatinous plankton ecotype and several nested taxa. Groups that are in bold are those defined as jellyfish (common names equivalent with clades are marked 'i.e.'). (Re-drawn from Box 2.1; Pitt and Lucas 2014).

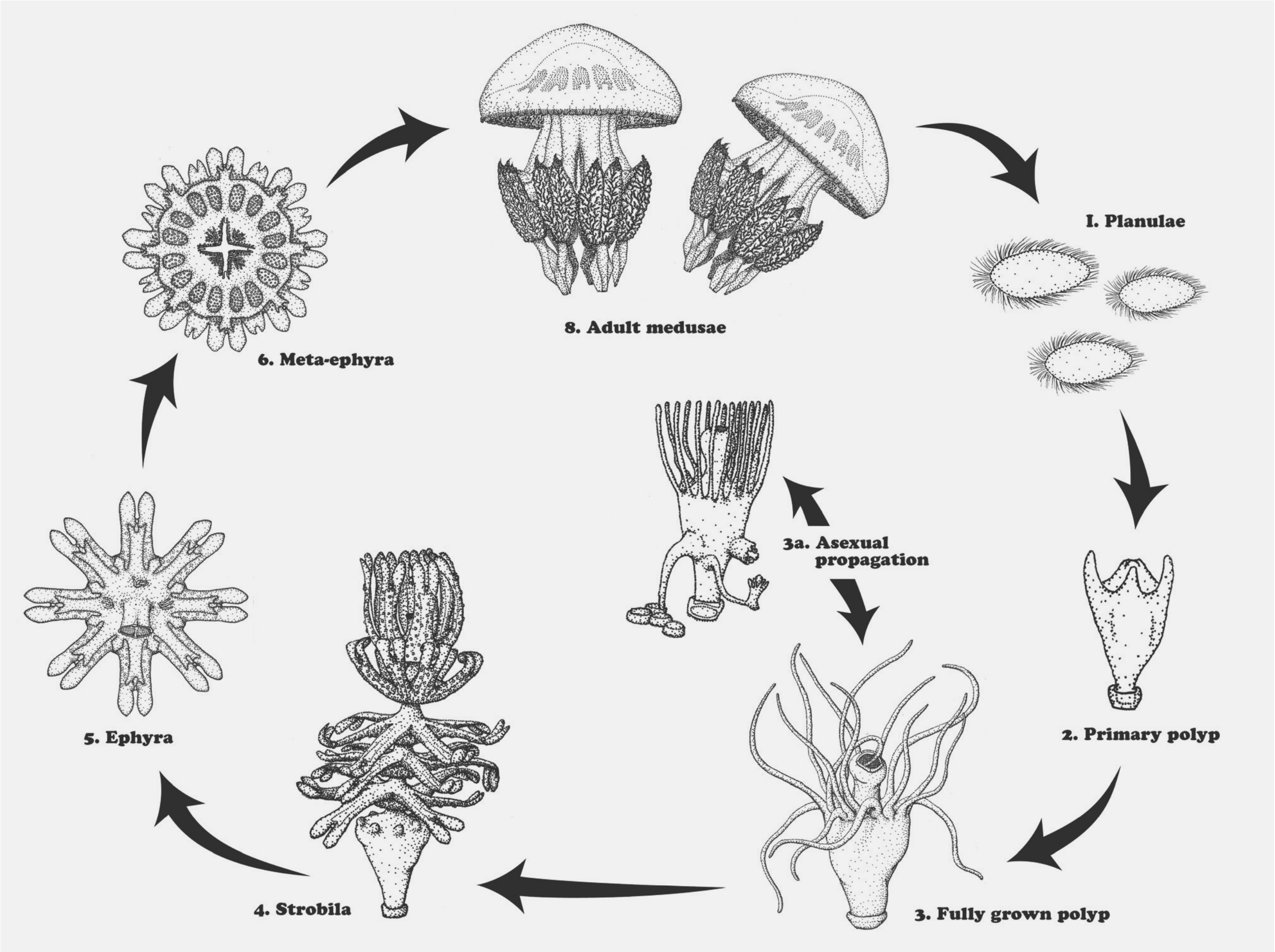


Figure 3. The life cycle of the scyphozoan Rhizostoma pulmo, which is typical for most scyphozoans. (From Fuentes et al. 2011).

GENERAL CONCLUSIONS (*addendum*)

First Part: outbreaks of the cubozoan *Carybdea marsupialis* along the coast of Denia, Alicante (Papers 1-3)

Environmental restriction on box-jellyfish *Carybdea* spp.

Salinity changes affected the asexual reproduction of *Carybdea* sp., by hastily transforming into medusae at low salinity regimes and by increasing polyp population size through asexual budding at high salinity conditions.

Metamorphosis of *Carybdea marsupialis* polyps into medusae along the coast of Denia seemed not to be one synchronized event and possible related with a sudden increase in temperature and decrease in salinity.

The distribution and high abundance of *C. marsupialis* medusae along the coast of Denia was associated with springtime salinity changes and increased primary and secondary production due to anthropogenic activities, in association with the availability of free substrata and type of sea bed.

Methodologies to study environmental restriction on jellyfish polyps

A new methodological device was designed and tested demonstrating its efficiency to evaluate the effects of environmental variables on jellyfish polyp biology.

Second Part: outbreaks of *Pelagia noctiluca* and other jellyfish along the Catalan coast and their economical impacts (Papers 4-6)

Spatio-temporal dynamics of jellyfish in the Catalan coast

The spatio-temporal analysis of a citizen science-based monitoring program along the Catalan coast showed that the characteristic species of springtime were *Chrysaora hysoscella*, *Aurelia aurita*, *Aequorea forskalea* and *Velella velella*. During the summer and late summer, the most frequent jellyfish species recorded were the scyphozoans *Rhizostoma pulmo* and *Cotylorhiza tuberculata*, respectively. Abundance of *Pelagia noctiluca* medusae was highest in spring and was spatially correlated with the location of marine canyons along the Catalan coast, suggesting a new hypothesis about the seasonal vertical migration and overwintering behaviour of this species.

For those species with a benthic phase the arrival and coastal proliferations of jellyfish are related with anthropogenic activities like habitat transforming and coastal eutrophication, offering new substrata and elevated primary and secondary production. In contrast, the spatio-temporal dynamics of jellyfish arrivals to the coast, for holoplanktonic species, will be determined by oceanographic characteristics like shelf-slope front and geostrophic currents modelled by the presence of canyons near the coast.

Along the Catalan coast sea surface temperature (SST) and the onshore current transport force were significant time-varying predictors of the distribution of stranded jellyfish, in accord with the relationship of the distribution of gelatinous zooplankton at the shelf-slope front and with the signal of frontal mesoscale activity; specifically, when the front weakens, jellyfish are able to reach the coast.

The effect of deterministic processes were more important than the stochastic component of environmental variation in order to explain the spatio-temporal distribution of jellyfish, suggesting that alignment in space and time of the environmental variables selected had little influence on the spatial distribution of jellyfish outbreaks.

We demonstrated the usefulness of a citizen science-based monitoring program to characterize and understand the spatio-temporal dynamics and the underlying environmental restriction of jellyfish blooms along the Catalan Coast.

Socio-economical impact of jellyfish in the Catalan coast

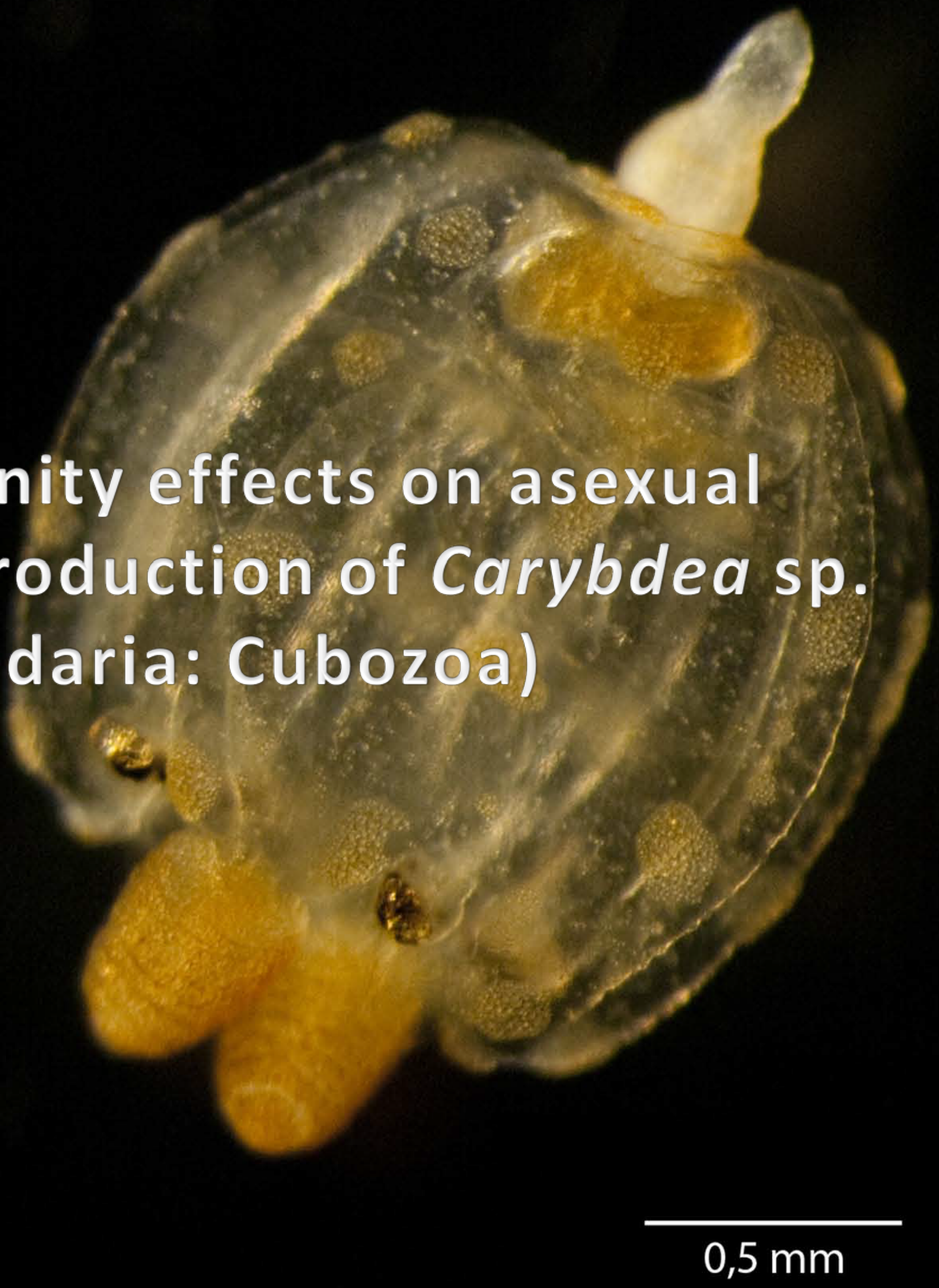
Along the Catalan coast jellyfish outbreaks were the third most important factor for beach users when choosing a beach and visitors were willing to spend an additional 23.8% of their travel time to enjoy beach recreation where the risk of a jellyfish outbreak was lower.

We calculated that the well-being gains associated with a reduction of jellyfish outbreaks in this area corresponded, approximately, to 19% of the tourism expenditures of the Catalan population in 2012, highlighting the necessity of preventive and adaptive policy measures associated with jellyfish outbreaks.

Jellyfish blooms in coastal areas are heterogeneous in space and time and will differ from the species involved. Thus, providing species-specific predictive tools and increasing the effort in prevention and information at local scale are the most efficient mechanism to minimize their impacts.

PUBLICATIONS

Salinity effects on asexual reproduction of *Carybdea* sp. (Cnidaria: Cubozoa)



© Eduardo OBIS

Journal of
Plankton Research

plankt.oxfordjournals.org

J. Plankton Res. (2014) 36(2): 585–590. *First published online December 10, 2013 doi:10.1093/plankt/fbt124*

SHORT COMMUNICATION

Salinity effects on asexual reproduction of *Carybdea* sp. (Cnidaria: Cubozoa)

ANTONIO CANEPA[1]*, JENNIFER E. PURCELL[2], MAR BOSCH BELMAR[1], MELISA ACEVEDO[1], MIRIAM GENTILE[1] AND VERÓNICA FUENTES[1]

[1]ICM-CSIC, INSTITUT DE CIENCIES DEL MAR. PASSEIG MARÍTIM DE LA BARCELONETA, BARCELONA 37-49.08003, SPAIN AND [2]SHANNON POINT MARINE CENTER, WESTERN WASHINGTON UNIVERSITY, 1900 SHANNON POINT ROAD, ANA CORTES, WA 98221, USA

*CORRESPONDING AUTHOR: canepa@icm.csic.es

Received September 16, 2013; accepted November 17, 2013

Corresponding editor: Roger Harris

Medusa production in cubozoans may be associated with reduced-salinity waters. Asexual reproduction of *Carybdea* sp. differed at different salinities. The metamorphosis of *Carybdea* sp. polyps into medusae was accelerated at low salinity (32), while more polyps were budded from the original polyp at the highest salinity (38), probably due to prolonged metamorphosis. High-nutrient river discharge may provide favorable conditions for *Carybdea* sp. blooms.

KEYWORDS: box jellyfish; budding; jellyfish bloom; metamorphosis; mixed models; survival analysis

Jellyfish blooms have been increasingly reported in recent decades (Brotz *et al.*, 2012; Condon *et al.*, 2012; Purcell, 2012). The main concerns about blooms are due to their ecosystem and socio-economic impacts (reviewed in Purcell *et al.*, 2007) and possible long-term increases of such blooms (Brotz *et al.*, 2012; Condon *et al.*, 2012; Purcell, 2012; Gibbons and Richardson, 2013). Several authors report the appearance or increased abundance of cubomedusae after seasonal rains (Gordon *et al.*, 2004; Bordehore *et al.*, 2011). Among jellyfish, the Class Cubozoa is particularly interesting due to its visual ecology, mating behavior and toxicity (Bentlage *et al.*, 2010), but the ecology of cubozoans is poorly known and understanding their life cycle and seasonal dynamics of

Downloaded from http://plankt.oxfordjournals.org/ at CSIC on March 23, 2014

available online at www.plankt.oxfordjournals.org

© The Author 2013. Published by Oxford University Press. All rights reserved. For permissions, please email: journals.permissions@oup.com

all life history stages with controlled experiments is urgently needed (Kingsford *et al.*, 2012). Cubozoans have a metagenetic life cycle, characterized by a benthic polyp that can asexually produce more polyps by budding, each of which then can metamorphose into a single medusa (Werner *et al.*, 1971). Most cubozoan species inhabit coastal habitats in tropical to subtropical and even temperate waters of many parts of the world (Kraeuter and Setzler, 1975; Bentlage *et al.*, 2010; Kingsford *et al.*, 2012).

The early life cycle of *Carybdea marsupialis* (von Linné, 1758) was described from polyps found on shells of dead bivalves on the bottom of mangrove channels in Puerto Rico (Studebaker, 1972; Cutress and Studebaker, 1973; Stangl *et al.*, 2002; Fischer and Hofmann, 2004; Straehler-Pohl and Jarms, 2005). Nevertheless, some differences were found between medusae of *C. marsupialis*, from the Mediterranean, and those from Puerto Rico (Acevedo *et al.*, unpublished data), supporting the hypothesis based on molecular data that *Carybdea* in Caribbean waters might not be *C. marsupialis* (Bentlage *et al.*, 2010). The identity of the polyps herein is uncertain and currently under review (Acevedo *et al.*, unpublished data); therefore, we refer to it as *Carybdea* sp.

In the present study, we tested the null hypothesis that different salinity levels do not affect the asexual reproduction of the polyps of *Carybdea* sp. As far as we know, no previous data exist on the effects of salinity on the asexual reproduction of *Carybdea* sp.

Stock cultures of polyps established by Werner in 1971 from south western Puerto Rico (La Parguera) were kindly provided by the laboratory of Ass. Prof. Dr Anders Garm (University of Copenhagen). The polyps were maintained at the Marine Science Institute (Barcelona, Spain) in glass dishes containing 500 mL of 5-μm-filtered ambient seawater at 23°C and salinity of 35.

The salinity treatment simulated seawater conditions in Puerto Rico: (i) low rainfall (high salinity level = 38), (ii) the annual average salinity throughout the known polyp area (35) (Otero, 2009) and (iii) high rainfall (low salinity = 32), following Hertler (Hertler, 2002). Before the experiment, polyps were transferred and acclimated to salinity changes by increases or decreases of 15% per day, resulting in a "Rapid Dilution" scheme, following Hartwick (Hartwick, 1991).

At each salinity level, 18 polyps were kept individually in 3 6-well polycarbonate culture plates with 10 mL of 5-μm-filtered seawater. The polyps were fed *ad libitum* twice weekly with newly hatched *Artemia salina* nauplii, resulting in equal feeding in all levels of the treatment and were kept in dark conditions and at a constant temperature of 23°C. After the polyps were fed for 1.5 h, the water was replaced with clean filtered sea water of the appropriate salinity and temperature.

Every second day each individual was checked for bud production and metamorphosis state following Straehler-Pohl and Jarms (2005). Detached buds and medusae produced were counted and removed from each well. Parameters evaluated to quantify the asexual reproduction of *Carybdea* sp. were budding index = BI (buds cubopolyp^{-1} day^{-1}); accumulated buds produced during the experiment = AB (buds salinity^{-1}); accumulated medusae produced during the experiment = AM (medusa salinity^{-1}); days to metamorphosis = DTM (days) and metamorphosis development = MD. For our analyses, the metamorphosis stages given in Straehler-Pohl and Jarms (Straehler-Pohl and Jarms, 2005) were simplified to: metamorphosis stages a–c = early, stages d–f = mid, and stages g and medusa = late. The experiment ran for 74 days.

Comparisons of the BI among salinities were made using one-way ANOVA. For AB and AM, the effects of repeated measurements on the same individuals were assessed using random slope for each polyp through the generalized linear mixed models (GLMM) with the package lme4 (Bates *et al.*, 2011) setting a Poisson error family and a log link. The DTM was treated as a survival analysis because, after a polyp metamorphosed, it was no longer part of the experiment (i.e. the distribution of remaining polyps followed a Kaplan–Meier survivor function) and the transformation to medusa was considered as "death" data. The survival analysis was done using censored data, because all polyps had not metamorphosed into medusae by the end of the experiment. To do this the *Survival* package (Therneau, 2012) fitting a parametric model using the *survreg* (accelerated failure-time models) function was used to estimate the total number of days to become a medusa for the un-metamorphosed polyps using a GLM with an exponential error distribution. Differences in MD were compared using the Pearson's χ^2 test and the *P*-values obtained by Monte Carlo simulation (number of simulations = 2000). All analyses and figures were made using the free statistical software R, version 2.15.0. Data are presented as mean ± standard error.

Survival of *Carybdea* sp. polyps was 100% at all salinities and the polyps began budding new polyps on the eighth day (Fig. 1A). The BI (buds cubopolyp^{-1} day^{-1}) showed no differences between tested (32 and 38) and the control (35) salinities (Table I). The AB (buds salinity^{-1}) during the experiment did not differ among salinities (Table I), but the interaction between the days of the experiment and salinity was significant at $P < 0.01$. After Day 43, polyps at low salinity (32) had accumulated fewer buds than those at the control salinity (35) ($t = -4.1$, $P < 0.0001$). In contrast, polyps at high salinity (38) after Day 43 had accumulated more buds than in the control (*t*-value -6.36, *P*-value < 0.0001) (Fig. 1A).

Downloaded from http://plankt.oxfordjournals.org/ at CSIC on March 23, 2014

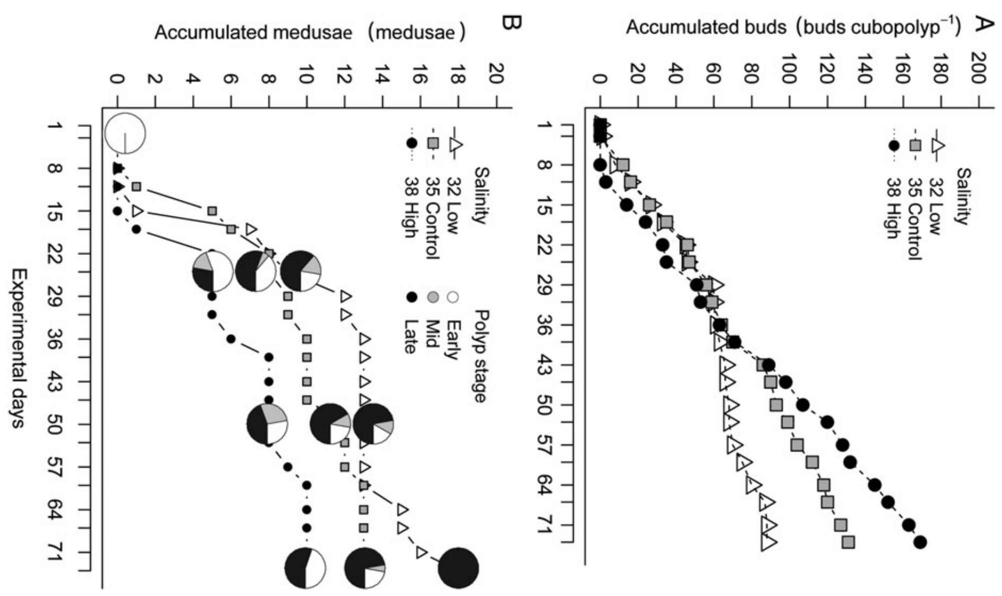


Fig. 1. Accumulated buds (**A**) and medusae (**B**) produced by 18 polyps of *Carybdea* sp. during the 74-day experiment at three salinities (low = 32, control = 35, high = 38) at 23°C. The pie charts in (**B**) represent the proportion of polyps in three metamorphosis states (early, mid and late) at the beginning of the experiment and at 25-day intervals thereafter.

It is important to note that both budding and metamorphosis into medusae occurred simultaneously during each metamorphosis phase (except "a") at all salinities (Supplementary data, Fig. S1).

Metamorphosis of polyps into medusae was significantly ($P < 0.05$) affected by the salinity treatment. The average number of medusae produced was higher at low salinity (0.89 ± 0.07 medusae salinity^{-1} day^{-1}) than at the control and high salinities (0.72 ± 0.1 and 0.56 ± 0.1 medusae salinity^{-1} day^{-1}, respectively) (Fig. 1B). The AM (medusae salinity^{-1}) also differed among salinities, showing a negative trend with the increase in salinity (Table I). DTM (days) clearly increased with increasing salinity (Fig. 2A). Survival analysis showed that polyps at high salinity took significantly ($P < 0.01$) longer to

Table I: Salinity effects on asexual reproduction of Carybdea *sp.*

	Polyp production				Medusa production							
	BI (buds cubopolyp^{-1} day^{-1})		AB (buds salinity^{-1})		AM (medusae salinity^{-1})		DTM (days)		*MD* (Early/mid/late)			
Salinity									*Day 1* *E/M/L*	*Day 25* *E/M/L*	*Day 50* *E/M/L*	*Day 74* *E/M/L*
Low (32)	0.12 ± 0.014	88	18	35.6 ± 5.3	18/0/0	4/3/11	3/2/13	0/0/18				
Control (35)	0.15 ± 0.016	131	13	40.4 ± 5.9	18/0/0	7/1/10	4/2/12	4/1/13				
High (38)	0.16 ± 0.017	169	10	51.6 ± 5.5	18/0/0	10/3/5	5/5/8	8/0/10				
Comparisons	35 vs. 32	35 vs. 38	35 vs. 32	35 vs. 38	35 vs. 32	35 vs. 38	35 vs. 32	35 vs. 38	All	All	All	All
Statistical test (df)	$F = -1.23$ (2)	$F = 0.41$ (2)	$t = 0.23$ (51)	$t = -1.26$ (51)	$t = 2.56$ (42)	$t = -5.87$ (42)	$z = 1.25$ (2)	$z = 2.79$ (2)	$\chi^2 = 1$ (4)	$\chi^2 = 6.1$ (4)	$\chi^2 = 3.8$ (4)	$\chi^2 = 12.4$ (4)
Significance (*P*)	0.23 ns	0.69 ns	0.82 ns	0.21 ns	0.014[a]	<0.001[c]	0.21 ns	0.005[b]	1 ns	0.22 ns	0.44 ns	0.004[c]
Code	32 = 35 = 38	32 = 35 = 38	32 > 35 > 38	32 = 35 < 38	32 = 35 = 38	32 = 35 = 38	32 = 35 = 38	32 ≠ 35 ≠ 38				

ns, non-significant; BI, budding index (buds cubopolyp^{-1} d^{-1}); AB, accumulated buds produced (buds salinity^{-1}) and effects on medusa production: AM, accumulated medusae produced (medusae salinity level^{-1}); DTM, days to metamorphosis (days); MD, metamorphosis development (early/mid/late). Means ± standard error.

[a]0.05, [b]0.01 and [c]0.001.

Downloaded from http://plankt.oxfordjournals.org/ at CSIC on March 23, 2014

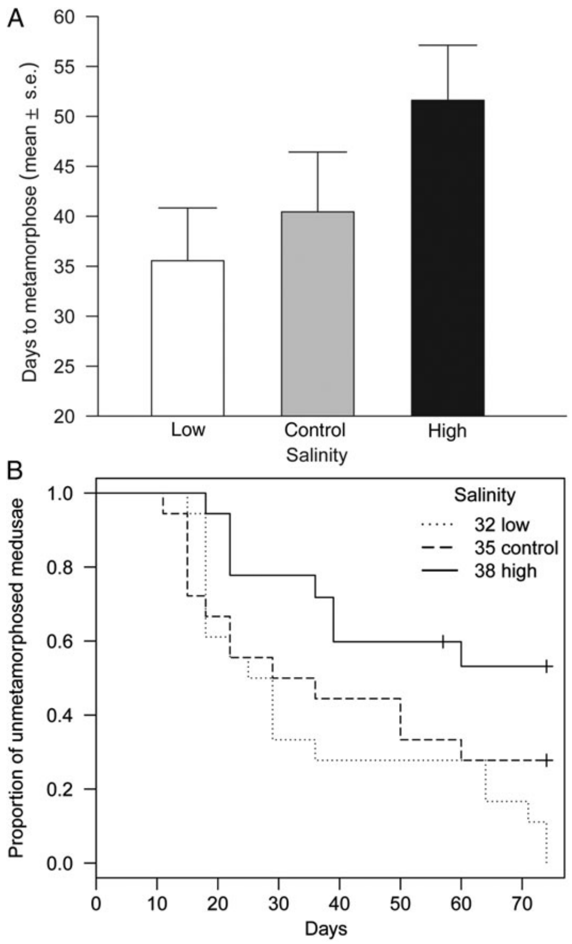


Fig. 2. Effects of salinity on the days to metamorphosis for *Carybdea* sp. (**A**) Number of days until metamorphosis in each salinity and (**B**) the survival model in which the decay rates of the curves are proportional to the numbers of polyps that transformed into a medusa.

metamorphose than at the low and control salinities (Fig. 2B). The survival model with censored data estimated times for all polyps to metamorphose into medusae to be 36, 56 and 116 days for the low, control and high salinities, respectively (Table I). Differences in the medusa development stage (MD) among salinities were obvious and significant ($P < 0.01$) at the end of the experiment (Fig. 1B, Table I).

Our results show that salinity significantly affects the asexual reproduction of the cubozoan *Carybdea* sp. Salinity variability along the coast of La Parguera (SW Puerto Rico), where the polyps live (Studebaker, 1972), is governed mostly by weather conditions; thus clear weather conditions can increase salinity to 37.7, comparable to our high salinity of 38, and rain storms can reduce salinity <31, even in bottom waters (Otero, 2009). These and the annual average coastal salinity (35) as the control (Hertler, 2002; Otero, 2009) provided realistic levels for our experiment.

Carybdea sp. polyps produced medusae more rapidly at low salinity than at control and high salinities. Significant effects of salinity on medusa production have also been shown in hydrozoans (Ma and Purcell, 2005) and scyphozoans (Rippingale and Kelly, 1995; Purcell, 2007; Holst and Jarms, 2010).

The budding index (BI) of *Carybdea* sp. showed no significant differences among salinities (Table I). This BI reflects the numbers of buds produced per polyp before metamorphosis, comparable to the budding rate commonly measured for scyphozoan polyps (Purcell, 2007). The lack of differences among salinities for BI suggests that salinity does not change the budding process; however, salinity affected the time span in which a bud was produced, as reflected by the significant interaction between days and treatment levels in AB, which resulted in a lower proportion of accumulated buds after Day 43 at low (32) salinity.

Salinity affected the time required by *Carybdea* sp. to complete metamorphosis. High salinity extended the days to metamorphosis (DTM). In previous studies, metamorphosis of *Carybdea* sp. polyps was induced by increasing the temperature above a critical threshold (24°C) and by suspension of feeding (Stangl *et al*., 2002). Gordan *et al*. (Gordon *et al*., 2004) found young medusae of *Chiropsalmus* sp. (= *Chiropsella bronzie*; Gershwin, 2006) after rain events, suggesting enhanced metamorphosis at low salinity conditions. The opposite may be true for the sea wasp (*Chironex fleckeri*; Southcott, 1956), for which small (<2 mm) medusae appeared when river waters were >25°C and at the annual salinity peak (>40) (Hartwick, 1991). Kingsford *et al*. (Kingsford *et al*., 2012) similarly suggested that high rainfall may negatively affect this species. In contrast, polyps of *Alatina* nr *mordens* budded at all combinations of temperature (18–31°C) and salinity (22–40); however, metamorphosis was not induced in any of the temperature–salinity combinations over 6 weeks, even when polyps were returned to pre-experimental conditions (25°C and 32.6) (Courtney and Seymour, 2013). Thus, the importance of salinity changes may be related to the habitat of some species living where salinity changes occur seasonally (i.e. mangroves, estuaries) (Studebaker, 1972; Kingsford *et al*., 2012).

The effect of salinity seemed to be most important for the rate of metamorphosis of *Carybdea* sp. This idea is supported by both (i) the results of the survival model and (ii) the results from MD. The survival model showed that the DTM at high salinity (38) was more than three times longer than at low (32) salinity (116 vs. 36 d). Although all polyps followed the stages of metamorphosis described for *Carybdea* sp. (Straehler-Pohl and Jarms, 2005), those at

Downloaded from http://plankt.oxfordjournals.org/ at CSIC on March 23, 2014

the low salinity completed metamorphosis in significantly fewer days and, consequently, were in a significantly different stage at the end of the experiment (Fig. 1B, Table I). Furthermore, metamorphosis reversed in high salinity (38) during the last week of the experiment; between Days 57 and 67, three of five remaining polyps reverted from mid- to early metamorphosis stage. The other two polyps continued metamorphosis to late stage.

Our results clearly show that salinity affected the asexual reproduction of *Carybdea* sp., mainly modifying the rate of metamorphosis, but also the total numbers of buds and medusae accumulated. Moreover, if we use the total days predicted by the survival model, the numbers of buds generated at the three salinities would be 78, 151 and 334 for the low, control and high salinities, respectively. Thus, the population of *Carybdea* sp. responds to changes in salinity by transforming into medusae at low salinity regimes and by increasing polyp population size with asexual budding at high salinity conditions.

For some cubozoans, salinity changes may be an important signal for metamorphosis. Kingsford *et al.* (Kingsford *et al.*, 2012) noted that planktonic food abundance as well as polyp substrates and retention areas for medusae ultimately may be related to cubozoan abundance. In tropical waters, salinity changes in coastal areas are correlated with rains and river run-off and, consequently, increased coastal productivity (Rippingale and Kelly, 1995; Hertler, 2002; Otero, 2009). As part of the natural seasonal cycle in Puerto Rican coastal surface waters, zooplankton abundance increases in July, following the peak of Chl *a* and the decline in salinity (Yoshioka *et al.*, 1985). In a similar context, Bordehore *et al.* (Bordehore *et al.*, 2011) described an unusually high abundance of *C. marsupialis* associated with low salinity of natural freshwater discharges with increased Chl *a* due to the enhancement of nutrients from anthropogenic (agricultural, sewage discharges) activities along the coast of Denia (Alicante, Spain). Thus, *Carybdea* sp. polyps metamorphose in the wet season and release medusae that benefit from high levels of production in the coastal water column.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

FUNDING

This work was funded by the LIFE Programme of the European Commission, the Ministry of the Environment of Spain and the Conselleria de Medi Ambient from the Generalitat Valenciana CUBOMED project (LIFE08 NAT ES64). A.C. was supported by a doctoral fellowship from the Chilean National Commission for Scientific and Technological Research (CONICYT – PFCHA/ Doctorado al Extranjero 4^{a} Convocatoria, 72120016).

REFERENCES

Bates, D., Maechler, M. and Bolker, B. (2011) lme4: linear mixed-effects models using S4 classes. R package version 0.999375-42. http://CRAN.R-project.org/package=lme4 (accessed on 6 December 2012).

Bentlage, B., Cartwright, P., Yanagihara, A. A. *et al.* (2010) Evolution of box jellyfish (Cnidaria: Cubozoa), a group of highly toxic invertebrates. *Proc. R. Soc. B*, **1707**, 1–9.

Bordehore, C., Fuentes, V. L., Atienza, D. *et al.* (2011) Detection of an unusual presence of the cubozoan *Carybdea marsupialis* at shallow beaches located near Denia, Spain (south-western Mediterranean). *Mar. Biodivers. Records*, **4**, 1–6.

Brotz, L., Cheung, W. W. L., Kleisner, K. *et al.* (2012) Increasing jellyfish populations: trends in large marine ecosystems. *Hydrobiologia*, **690**, 3–20.

Condon, R. H., Duarte, C. M., Pitt, K. A. *et al.* (2012) Recurrent jellyfish blooms are a consequence of global oscillations. *P Natl Acad. Sci.*, **110**, 1000–1005.

Courtney, R. J. and Seymour, J. (2013) Seasonality in polyps of a tropical cubozoan: *Alatina* nr *mordens*. *PLoS One*, **8**, e69369.

Cutress, C. E. and Studebaker, J. P. (1973) Development of the cubomedusae, *Carybdea marsupialis*.*Proc. Ass. Is. Mar. Lab. Caribb.*, **9**, 1.

Fischer, A. B. and Hofmann, D. K. (2004) Budding, bud morphogenesis, and regeneration in *Carybdea marsupialis*; Linnaeus, 1758 (Cnidaria: Cubozoa). *Hydrobiologia*, **530/531**, 331–337.

Gershwin, L. A. (2006) Comments on *Chiropsalmus* (Cnidaria: Cubozoa: Chirodropida): a preliminary revision of the Chiropsalmidae, with descriptions of two new genera and two new species. *Zootaxa*, **1231**, 1–42.

Gibbons, M. J. and Richardson, A. J. (2013) Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. *J. Plankton Res.*, **35**, 929–938.

Gordon, M., Hatcher, C. and Seymour, J. (2004) Growth and age determination of the tropical Australian cubozoan *Chiropsalmus* sp. *Hydrobiologia*, **530/531**, 339–345.

Hartwick, R. F. (1991) Distributional ecology and behaviour of the early life stages of the boxjellyfish *Chironex fleckeri*. *Hydrobiologia*, **216/217**, 181–188.

Hertler, H. (2002) The implications of resource management in La Parguera, Puerto Rico. PhD Thesis. Drexel University, Philadelphia, USA, 143 pp.

Holst, S. and Jarms, G. (2010) Effects of low salinity on settlement and strobilation of Scyphozoa (Cnidaria): is the lion's mane *Cyanea capillata* (L.) able to reproduce in the brackish Baltic Sea? *Hydrobiologia*, **645**, 53–68.

Kingsford, M. J., Seymour, J. E. and O'Callaghan, M. D. (2012) Abundance patterns of cubozoans on and near the Great Barrier Reef. *Hydrobiologia*, **690**, 257–268.

Kraeuter, J. N. and Setzler, E. M. (1975) The seasonal cycle of Scyphozoa and Cubozoa in Georgia estuaries. *Bull. Mar. Sci.*, **25**, 66–74.

Downloaded from http://plankt.oxfordjournals.org/ at CSIC on March 23, 2014

Ma, X. and Purcell, J. E. (2005) Temperature, salinity, and prey effects on polyp versus medusa bud production by the invasive hydrozoan *Moerisia lyonsi*. *Mar. Biol.*, **147**, 225–234.

Otero, E. (2009) Spatial and temporal patterns of water quality indicators in reef systems of southwestern Puerto Rico. *Caribb. J. Sci.*, **45**, 168–180.

Purcell, J. E. (2007) Environmental effects on asexual reproduction rates of the scyphozoan, *Aurelia labiata*. *Mar. Ecol. Prog. Ser.*, **348**, 183–196.

Purcell, J. E. (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu. Rev. Marine Sci.*, **4**, 209–235.x

Purcell, J. E., Uye, S.-I. and Lo, W.-T. (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar. Ecol. Prog. Ser.*, **350**, 153–174.

Rippingale, R. J. and Kelly, S. J. (1995) Reproduction and survival of *Phyllorhiza punctata* (Cnidaria: Rhizostomeae) in a seasonally fluctuating salinity regime in Western Australia. *Mar. Freshwater Res.*, **46**, 1145–1151.

Southcott, R. V. (1956) Studies on Australian cubomedusae, including a new genus and species apparently harmful to man. *Aust. J. Mar. Fresh. Res.*, **7**, 254–280.

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

Straehler-Pohl, I. and Jarms, G. (2005) Life cycle of *Carybdea marsupialis* Linnaeus, 1758 (Cubozoa, Carybdeidae) reveals metamorphosis to be a modified strobilation. *Mar. Biol.*, **147**, 1271–1277.

Studebaker, J. P. (1972) Development of the cubomedusa, *Carybdea marsupialis*. Masters Thesis. Department of Marine Sciences, University of Puerto Rico College of Agriculture and Mechanical Arts Mayaguez, Puerto Rico, pp. 1–60.

Therneau, T. (2012) A package for survival analysis in S. R package version 2.36-12. http://CRAN.R-project.org/package=survival (accessed on 6 February 2013).

von Linné, C. (1758) Systema Naturae, Edit. 10, reformata (2 vols). Holmiae, 1758–1759, pp. 659–660.

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

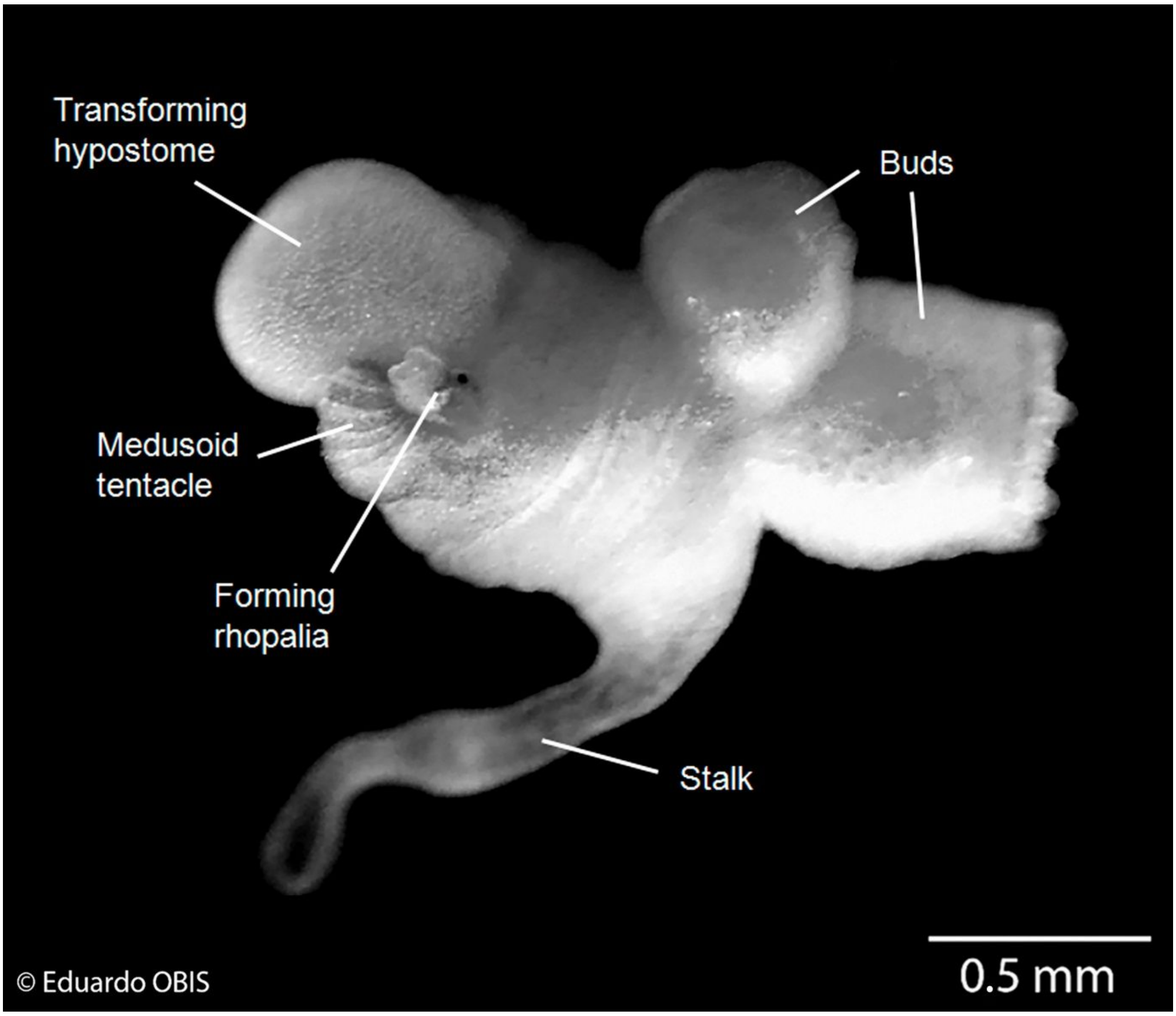
Yoshioka, P. M., Owen, G. P. and Pesante, D. (1985) Spatial and temporal variations in Caribbean zooplankton near Puerto Rico. *J. Plankton Res.*, **7**, 733–751.

Downloaded from http://plankt.oxfordjournals.org/ at CSIC on March 23, 2014

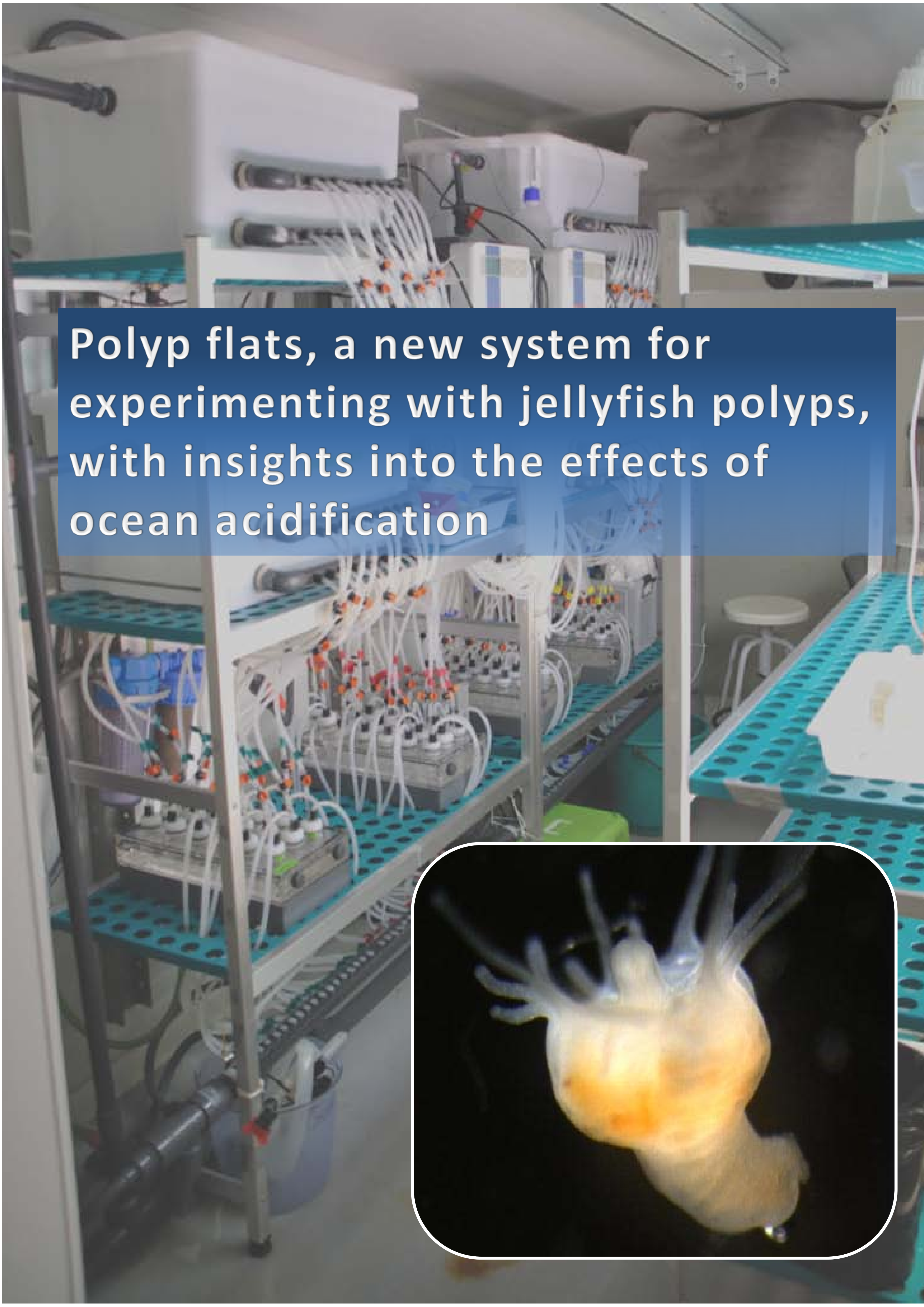
Salinity effects on asexual reproduction of Carybdea sp. (Cnidaria: Cubozoa)

Supplementary Data

Fig. S1. *Carybdea* sp. polyp in state “g” of metamorphosis (following Straehler-PohlandJarms, 2005) showing simultaneously two buds in stage “5 and 6” (following Fischer and Hofmann, 2004)



Polyp flats, a new system for experimenting with jellyfish polyps, with insights into the effects of ocean acidification



LIMNOLOGY
and
OCEANOGRAPHY: METHODS

Limnol. Oceanogr.: Methods 12, 2014, 210–220
© 2014, by the American Society of Limnology and Oceanography, Inc.

Polyp flats, a new system for experimenting with jellyfish polyps, with insights into the effects of ocean acidification

Alejandro Olariaga[1]*, *Elisa F. Guallart*[1], *Verónica Fuentes*[1], *Àngel López-Sanz*[1], *Antonio Canepa*[1], *Juancho Movilla*[1], *Mar Bosch*[1], *Eva Calvo*[1], *and Carles Pelejero*[1,2]
[1]Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta 08003, Barcelona, Catalonia, Spain
[2]Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Catalonia, Spain

Abstract

Research interest on jellyfish has grown exponentially over the last years and studies focusing on the biology and ecology of the jellyfish polyp stage are being recognized as crucial in understanding jellyfish proliferations. Due to the difficulty of conducting in situ work with jellyfish polyps, laboratory experiments are the most used approach. Here, we describe the design and successful testing of a new system that allows continuous seawater renewal while keeping constant the selected physicochemical conditions of the water throughout the experiment in contrast to closed systems used previously. As a first test, we started an experiment to assess the effects of ocean acidification on the growth and development of jellyfish polyps of *Aurelia* sp. This new design demonstrated high precision in maintaining constant conditions (pH, temperature, and flow rates) among the replicates of each treatment, and ensured excellent conditions for jellyfish polyp survival. All together it has shown to be an effective platform to assess the effect of environmental variables on the growth and development of jellyfish polyps.

In recent years, reports of jellyfish blooms are increasing worldwide (Brotz et al. 2012; Purcell 2012), and there are reasons to believe that oceans are facing a more gelatinous future (Richardson et al. 2009; Purcell et al. 2012). Many anthropogenic stressors are likely to impact jellyfish development, including global warming, overfishing, nutrient additions, invasion and translocation of species or global ocean sprawl (Purcell et al. 2007, 2012; Duarte et al. 2012). Ocean acidification, the decrease in seawater pH due to the marine absorption of atmospheric CO_2 (Pelejero et al. 2010 and references therein), could also play an important role. However, the very few published studies attempting to assess the possible effect of acidification on jellyfish are still inconclusive, and it is unknown whether this group of animals will be benefited or harmed by such pressure. Even though one study has suggested increasing jellyfish population due to ocean acidification (Attrill et al. 2007), the conclusions are still unclear and even contradictory results had been shown in other studies (Richardson and Gibbons 2008).

The term jellyfish includes several taxonomic groups, but scyphozoans are the most known group that produces jellyfish blooms. Most scyphozoans have a metagenetic life cycle that includes planktonic medusa and benthic polyp generations (Fig. 1). Polyps produced from the settlement and metamorphosis of planktonic planulae larvae can increase the population by asexual reproduction, contributing to the development of jellyfish blooms (Boero et al. 2008). Monitoring and testing these polyps in the field is notoriously difficult due to their small sizes and the lack of knowledge regarding the settlement preferences of the planulae (Holst and Jarms 2007; Holst 2012). Thus, laboratory experimentation is still the most feasible approach to study the response of jellyfish polyps to natural environmental conditions and to detect the factors that might affect their survival, reproduction, and other developmental parameters (see references in Table 1). In all these studies, however, results were obtained from incubation experiments under non- or discontinuous renewal of seawater. In such conditions, it is very difficult to maintain the

---

*Corresponding author: E-mail: olariaga@icm.csic.es

Acknowledgments

We would like to thank Miriam Gentile for her assistance during the laboratory experiments. The construction of the system was funded by the European Commission through the LIFE + program CUBOMED project, by the Spanish Ministry of Economy and Competitiveness through projects ACDC (CTM2009-08849) and MANIFEST (CTM2012-32017) and by Generalitat de Catalunya through the Marine Biogeochemistry and Global Change research group (grant 2009SGR142). E.F. Guallart was funded by CSIC through a JAE-Pre grant, and A. Canepa was funded by CONICYT (PFCHA/Doctorado al Extranjero 4ª Convocatoria, 72120016) All developmental work in this study was performed at the Experimental Aquaria Zone (ZAE) of Institut de Ciències del Mar (ICM-CSIC).

DOI 10.4319/lom.2014.12.210

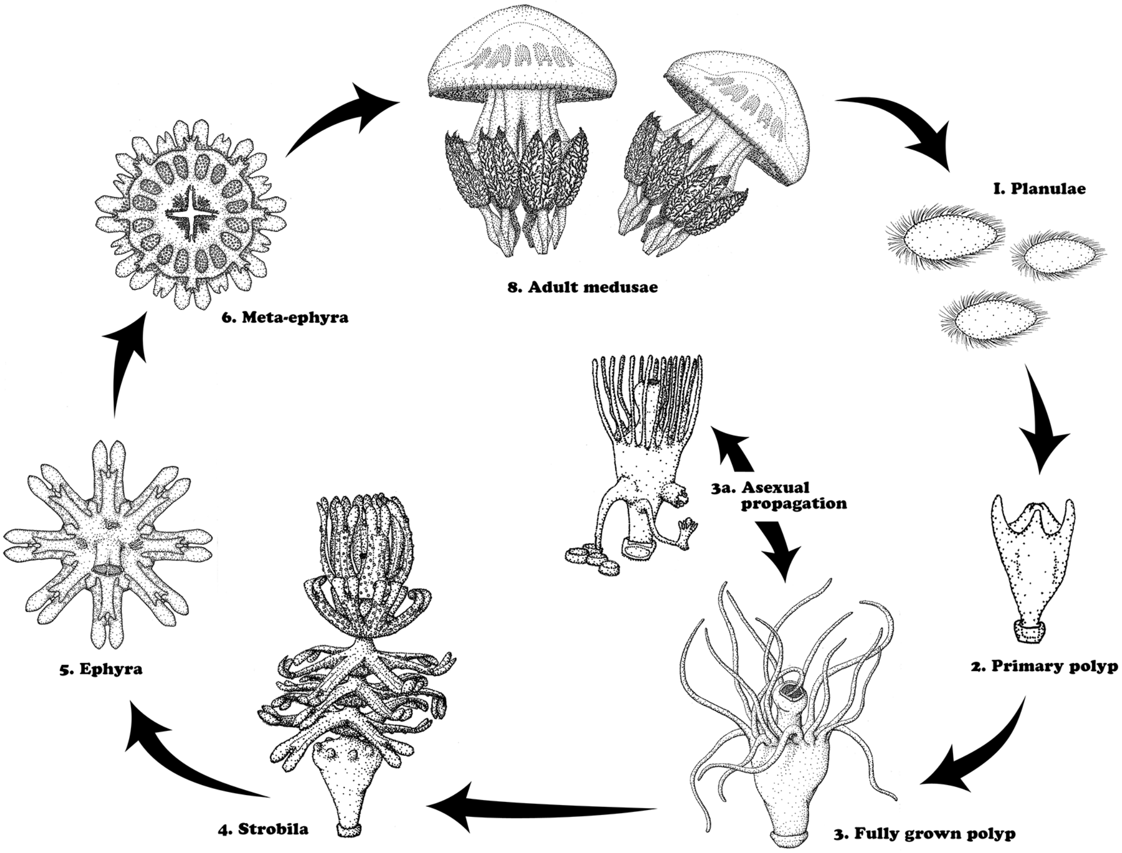


Fig. 1. The life cycle of the scyphozoan *Rhizostoma pulmo*, which is typical for most scyphozoans, including *Aurelia* sp. (adapted from Fuentes et al. 2011), with kind permission of Springer Science+Business Media

different physicochemical parameters at the desired constant levels, making complex the assessment of possible environmental effects from specific stressors. Therefore, improving the available methodology towards continuously seawater renovation systems is of special interest.

In this context, we provide details on a newly developed experimental set-up that allows the manipulation of environmental parameters in individual containers with continuous water renewal. They are designed to host single jellyfish polyps under a continuous seawater flow, guaranteeing a good reproducibility amongst all containers in each treatment. Given the recently recognized potential threat of ocean acidification, this set-up has been focused on pH manipulation, but it could be well adapted to modify other relevant parameters (e.g. nutrients, salinity, temperature, oxygen, among others). This new set-up represents an important step forward in experimental research on jellyfish, with the potential to provide new information on the fate of these species in the future changing ocean.

Materials and procedures

System overview

In this article, we describe a new system that we call "polyp flats" specially designed to conduct experiments with jellyfish polyps. As a first test of its performance and suitability, we have used this system for assessing the effect of ocean acidification on jellyfish proliferations. In the following, we provide full details on the design of this system and the specific configuration that allows changing and maintaining the pH conditions of the polyp flats associated to each treatment.

Incubation chambers and main containers

The polyp flats system was designed to supply a constant flow of seawater in 18 replicates for each level of the experimental treatment, whose parts and components are depicted in Fig. 2.

A transparent acrylic closed box (40 cm long, 23 cm wide, 5 cm high; A in Fig. 2) was built and 18 circular holes (4 cm diameter each) were sawed in the upper surface of it to allow fitting the individual incubation chambers. The distribution of the holes in the box is shown in Fig. 2. In one of the vertical sides, two small circular holes are used as water inlet/outlet (B in Fig. 2) allowing the connection of several boxes to the same water bath line. This recirculating water through the acrylic boxes acts only to homogenize temperature between all the individual incubation chambers, and there is no contact between the water in the bath with that inside the incubation chambers.

Table 1. Synthesis of methods used in experimental studies conducted on jellyfish polyps. T = temperature; Temperature regulation: Water Bath (W-B), Constant running water (C-R-W), Incubators (I), not mentioned (NM); Type of chambers: Glass bowls (G-B), Culture plates (C-P), Glass Jars (G-J), Flasks (F), Better Square Dishes (S-D) and add Acrylic plates (A-P) afterwards, Acrylic Incubation Chamber (A-I-CH), Glass Bottle (G-BT); Controlled parameters: T = temperature, DO = Dissolved oxygen, F = Flow rate, L (Light), N = Nutrients, FS = Food supply.

	Methods							
Species	T regulation	Type of chamber	Nr of polyps per chamber	Volume of chambers (mL)	Water renewal	Controlled parameters	Exp. duration (weeks)	Reference
Aurelia aurita	I	C-P	1	10	NM	T*, Salinity*, DO*, FS*	4-8	Thein et al. 2012
Cotylorhiza tuberculata	I	G-B	22	150	Once a week	T*, Salinity, Photoperiod	2	Astorga et al. 2012
A. aurita, Cyanea capilata, Cyanea lamarckii, Chrysaora hizsoscella	I	G-B	bulk of polyps	150	Once a week	T*, Salinity	40-80	Holst 2012
A. aurita, Rhizostoma pulmo, C. tuberculata	W-B	C-P	1	10	Every 2-4 days	T*	11-14	Purcell et al. 2012
C. tuberculata	I; W-B	F	20 to 50	NM	Once a week	T*, salinity*, L*, N*, FS*	8-10	Prieto et al. 2010
A. aurita	NM	C-P	1	5	NM	T. FS*		Kamiyama 2011
Aurelia labiata	I	G-J	1	125	Every 2-4 days	T*, pH*	17	Winans and Purcell 2010
A. aurita	I	S-D	3	160	NM	T*, FS*	4	Han and Uye 2010
A. aurita	I	C-P	1	50	Every 2-3 days	T*, L*	11	Liu et al. 2009
A. aurita	NM	G-BT	3	100	NM	DO*, T		Ishii et al. 2008
A. labiata	I	C-P	1	10	Every 2-3 days	T*, S*, L*	29	Purcell 2007
Aurelia sp.	W-B	A-P	30	NM	Every 2 days	T*, Salinity*	5	Willcox et al. 2007
Aurelia sp.	C-R-W	A-I-CH	1	35	Every minute, continuous flow	T*, pH*, F*	38	This study

*Parameters manipulated/controlled in the experiments.

The acrylic box containing the incubation chambers was constructed on top of a PVC box of the same size (C in Fig. 2). This PVC box has a transparent lid and contains 18 MSD light-emitting diodes (LED), located on the perpendicular axis of each incubation chamber. The LEDs are connected to an adjustable external power supply that allows for regulation of the light's duration and intensity, which are important factors to be considered depending on the jellyfish species under study. For example, the Mediterranean jellyfish *Cotylorhiza tuberculata* has symbiotic zooxanthellae and, therefore, light conditions are critical. In this experiment, light was used to facilitate the polyp's feeding. The LEDs were located at the bottom of the polyp flat, where the polyps are fixed. The polyps were fed with live *Artemia salina* nauplii that have positive phototaxis, facilitating their capture by the polyps.

Each incubation chamber (Fig. 3) consists of a 6 cm high transparent acrylic cylinder (1 cm thick) with an external diameter of 4 cm and an internal volume of 35 cm^3. Nylon lids were made using a mechanical lathe and an O-ring assured the sealed connection with the acrylic cylinder. Two holes were drilled in the lids to house the inlet and outlet water tubes, ensuring water renewal, and a small 60 μm mesh covered the water outlet, acting as a filter to avoid losses of organisms (food, polyp buds, or even small polyps). The specifically designed cover of the incubation chamber is shown in detail in Fig. 4.

Positioning and maintenance of the jellyfish polyps in the polyp flat

Polyps of the scyphozoan species *Aurelia* sp. (NW Mediterranean sea population) were used on this first experiment to test the performance of the new system. The polyps were obtained from the jellyfish cultures maintained at the Experimental Aquaria Zone (ZAE) of Institut de Ciències del Mar (ICM-CSIC), which are kept at a salinity of 38 and a temperature of 21°C to ensure the typical natural strobilation in spring.

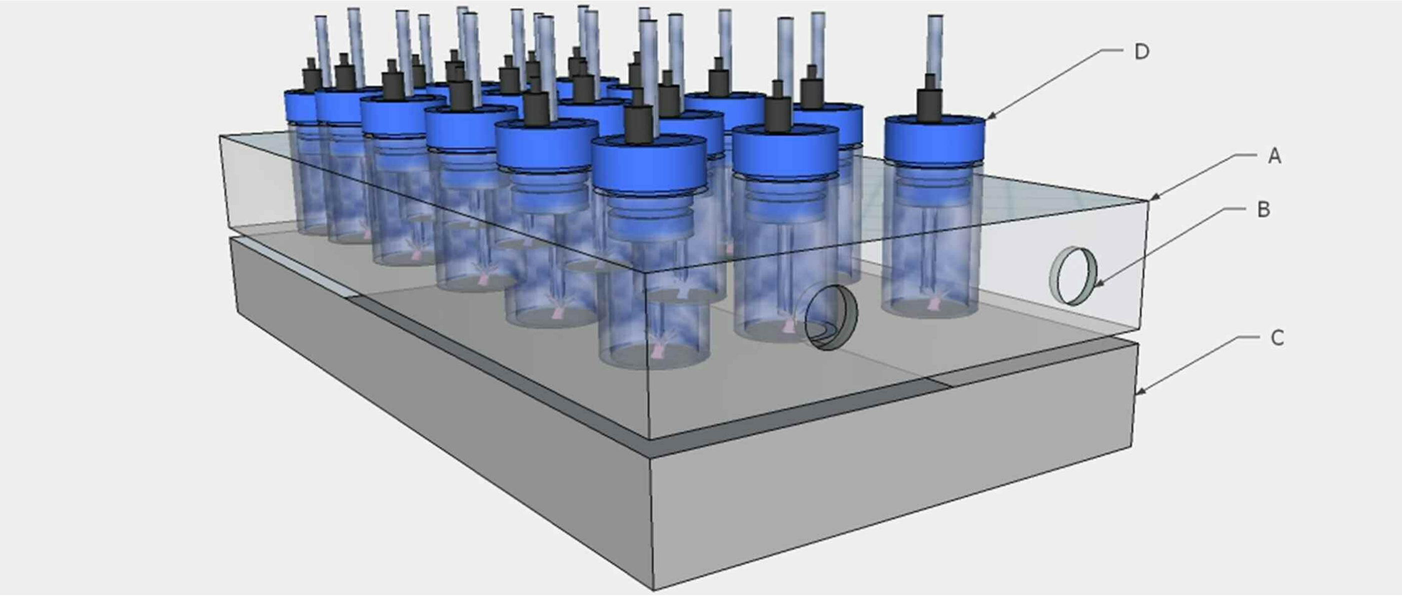


Fig. 2. Complete polyp flat for one treatment consisting in 18 individual incubation chambers submerged in a temperature controlled water bath. A) Acrylic box, B) holes for the bath water inlet and outlet, C) PVC box with a transparent lid containing the LED lights, D) incubation chambers.

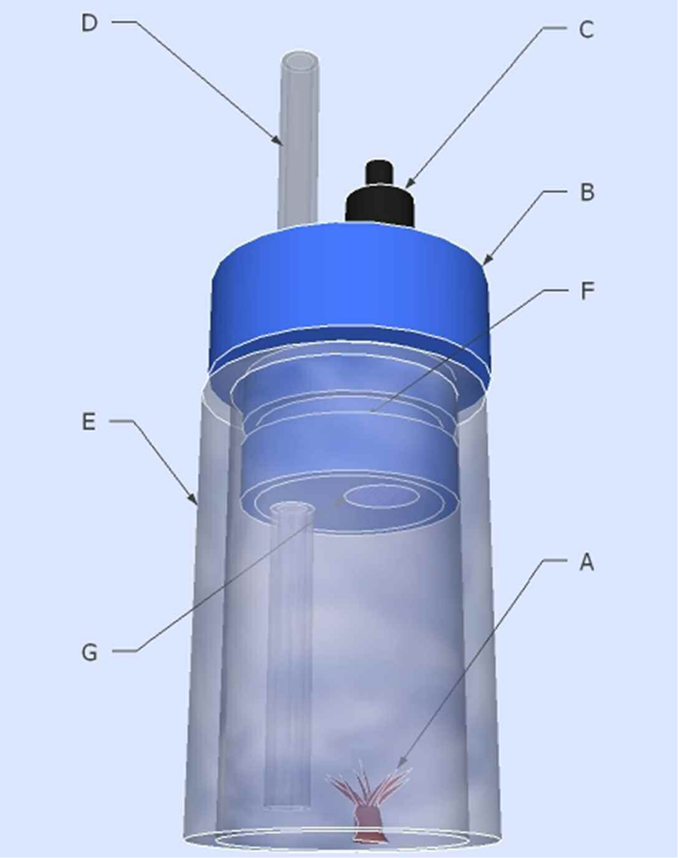


Fig. 3. Detail of an incubation chamber. A) Jellyfish polyp, B) Nylon lid, C) Water outlet, D) Water inlet, E) Incubation chamber, F) "o"-ring slot housing, G) 60 μm mesh.

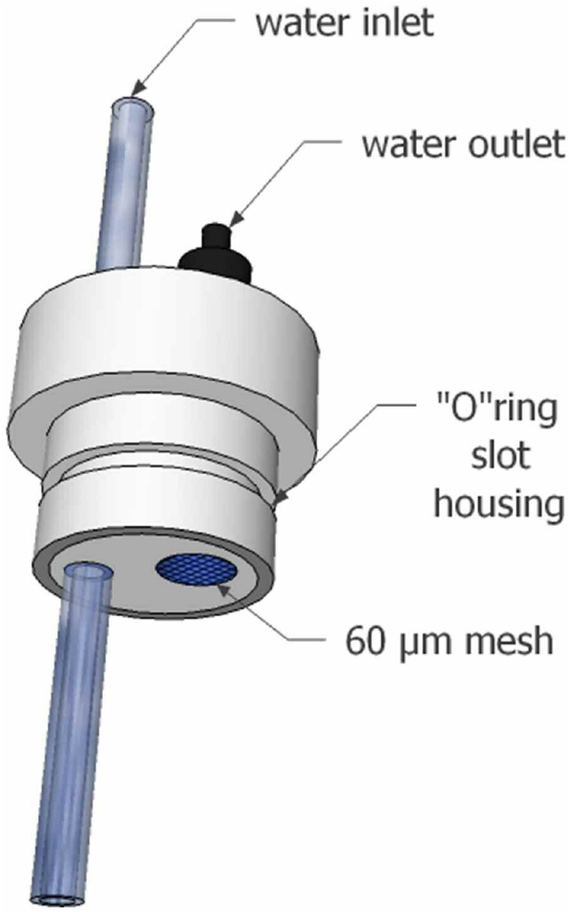


Fig. 4. Detail of the designed lid of each incubation chamber.

Single polyps of similar sizes were selected from these cultures and positioned at the base of each incubation chamber (Fig. 3). Before starting the experiment, all polyps were kept in their chambers with a very low water flow to ensure and facilitate their proper attachment. Once the polyps were totally attached, the water flow was increased to achieve a proper water renewal (~30 mL/min) so approximately the whole volume of the chamber was renewed every minute.

Once a week, the polyps were checked for survival, asexual reproduction (production of buds), and strobilation (production of ephyrae) following Purcell et al. (2012). The produced buds were removed periodically while maintaining the original polyp in the incubation chamber, allowing the tracking of individual specimens. The polyps were fed twice a week with newly hatched *A. salina* nauplii by closing the seawater flow-through during one hour to ensure a proper feeding. After feeding, the chambers were cleaned using a fine brush to gently scrap away all dirt and food remains.

Experimental setup and CO_2 system manipulation

Filtered seawater (through a 20 μm cartridge filter) was continuously supplied to four 150 L tanks (A in Fig. 5), and their pH was gradually adjusted to four selected values of ~8.10, ~7.80, ~7.50, and ~7.20 units (total scale). To achieve these pH levels, seawater in each tank was bubbled with CO_2 (99.9% purity; C in Fig. 5) or CO_2-free air (using a filter filled with soda lime absorber, Sigma Aldrich; F in Fig. 5). Seawater pH was monitored continuously by glass electrodes (LL Ecotrode plus –Metrohm; K in Fig. 5) connected to two pH controllers (Consort R316, Topac Inc.; E in Fig. 5), which automatically opened and closed the solenoid valves of CO_2 or CO_2-free air when needed (J and G in Fig. 5, respectively). To avoid drifts in the pH measurements, glass electrodes were calibrated on a daily basis with a Tris buffer, following standard procedures (SOP6a of Dickson et al. 2007). In addition, small volumes of water were taken periodically to analyze total alkalinity (TA) by potentiometric titration (Perez and Fraga, 1987; Perez et al. 2000) and pH using spectrophotometry (Clayton and Byrne 1993), which provides better precision than glass electrodes. Water from the 150 L tanks flowed continuously (1.8 L per hour) by means of individual silicone tubing (not shown) through each incubation chamber where organisms were maintained. The pH-manipulative experimental set-up was installed inside a thermostatic room, ensuring constant temperature values during the whole experiment.

The objective of this manipulation experiment, whose scientific results and implications will be published elsewhere,

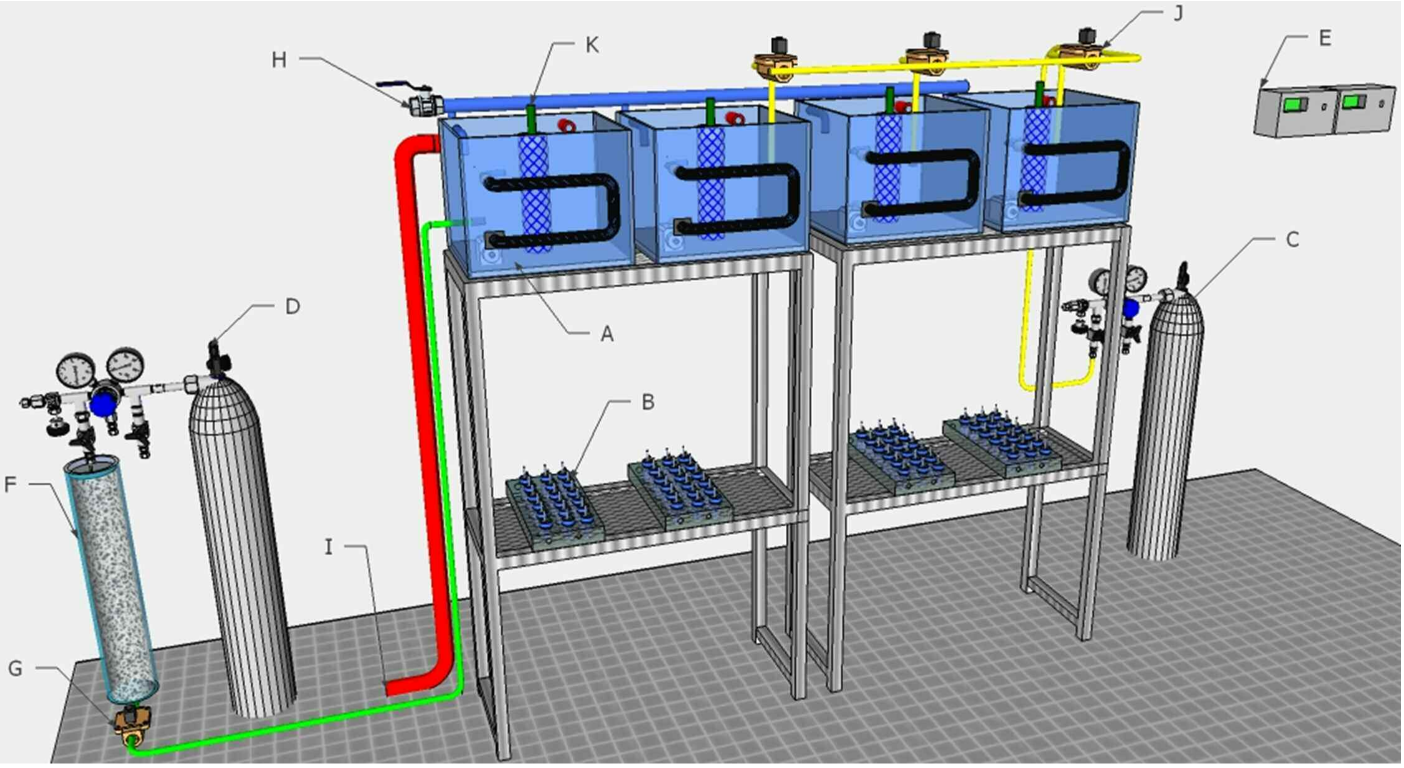


Fig. 5. Experimental setup used to control and modify seawater pH in each polyp flat. A) large 150-L tanks for seawater conditioning at pH 8.10, 7.80, 7.50, and 7.20; B) polyp flats containing 18 isolated polyps in each incubation chamber; C) 50 kg CO_2 cylinder; D) 50 kg compressed air cylinder; E) pH controller and data logger; F) soda lime filter; G) CO_2-free air solenoid valve; H) filtered seawater inlet line; I) drain outlet line; J) CO_2 solenoid valve; K) glass electrodes for pH and PT100 probes for temperature measurements. For simplicity, we have not shown all tubing connecting the conditioning tanks to each polyp flat, but note that all tubing is connected to the lower part of the U-shaped black pipeline depicted in A.

was to investigate the effects of different acidified conditions on the physiology, structure, performance, and reproduction of jellyfish polyps.

pH manipulation experiment and tests of system performance

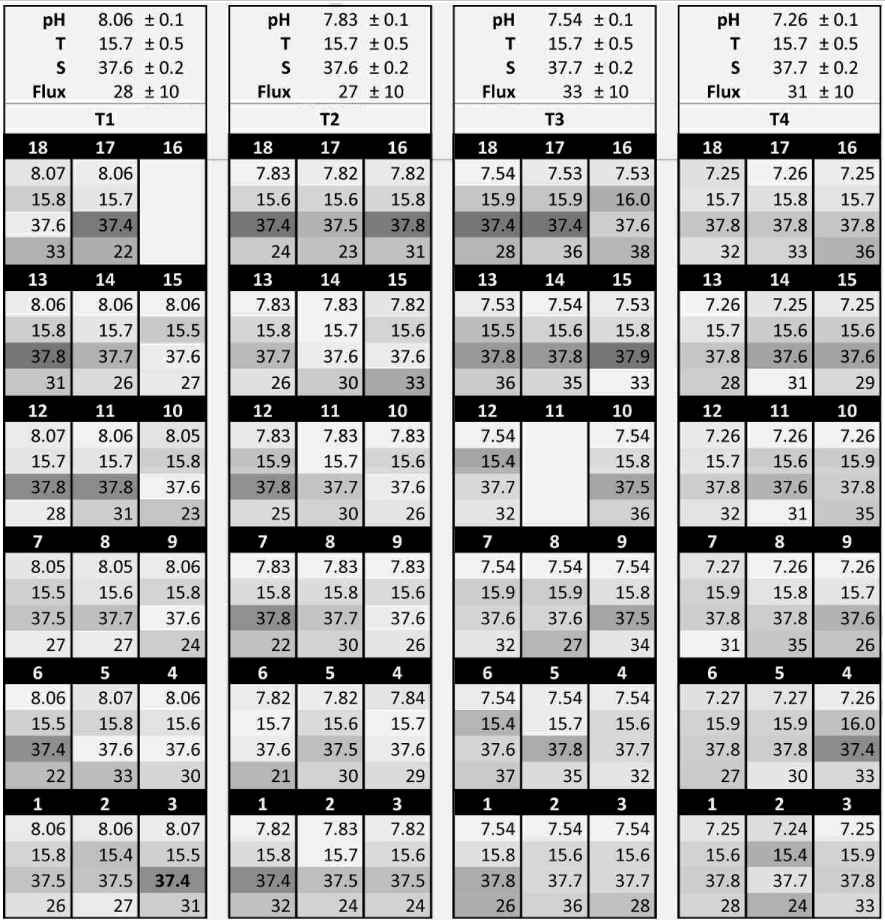
In order to test the efficiency of the system in maintaining stable conditions of seawater pH, temperature, and flow rate in all replicates of each treatment, periodic measurements were taken in each of the 72 incubation chambers after adjusting the seawater pH to the four desired levels (Tables 2-4). To conduct these measurements, small amounts of water (~25 mL) draining from each incubation chamber were collected in plastic test tubes, and pH (total scale), temperature (°C), and salinity were measured. Afterwards, the flow rate (mL/min) through the polyp flat was measured using a chronometer and a volumetric flask. The whole set of measurements (pH, temperature, salinity, and flow rate) took approximately 1 min per polyp flat, fast enough to ensure unchanged conditions in the sampled water. Sensors and equipment used in these measurements were a Metrohm 826 pH mobile with a glass electrode Aquatrode Plus from Metrohm (± 0.003pH units) calibrated with a TRIS buffer for pH (total scale), an Ebro TFX-410 Pt1000 temperature probe (± 0.1 °C) for temperature, and a YSI 30 probe (± 0.1) for salinity.

Assessment

Accuracy and precision

As outlined above, the primary objective of this continuous-flow system was to overcome the problems of maintaining

Table 2. First example of measurements of pH (total scale), temperature (T, in °C), salinity (S), and flow rate (in mL/min). Each parameter was measured in each of the 18 polyp flats (1 to 18) in the four pH treatments (T1 toT4). Data are given in separated panels for each treatment, which are divided into eighteen boxes which identify each polyp flat. Each polyp flat box contains the four measured parameters ordered as in the panels' headers. Headers for each treatment contain the average of each parameter over the 18 polyp flats ± the maximum difference from the mean that we considered acceptable for the proper performance of the system. This maximum difference is used to color code the measured values in the following way: Values marked in white are those that are closer to the average of the eighteen measurements whereas values marked in dark gray are the most distant from the average. Values outside the ± maximum difference are all in dark gray.



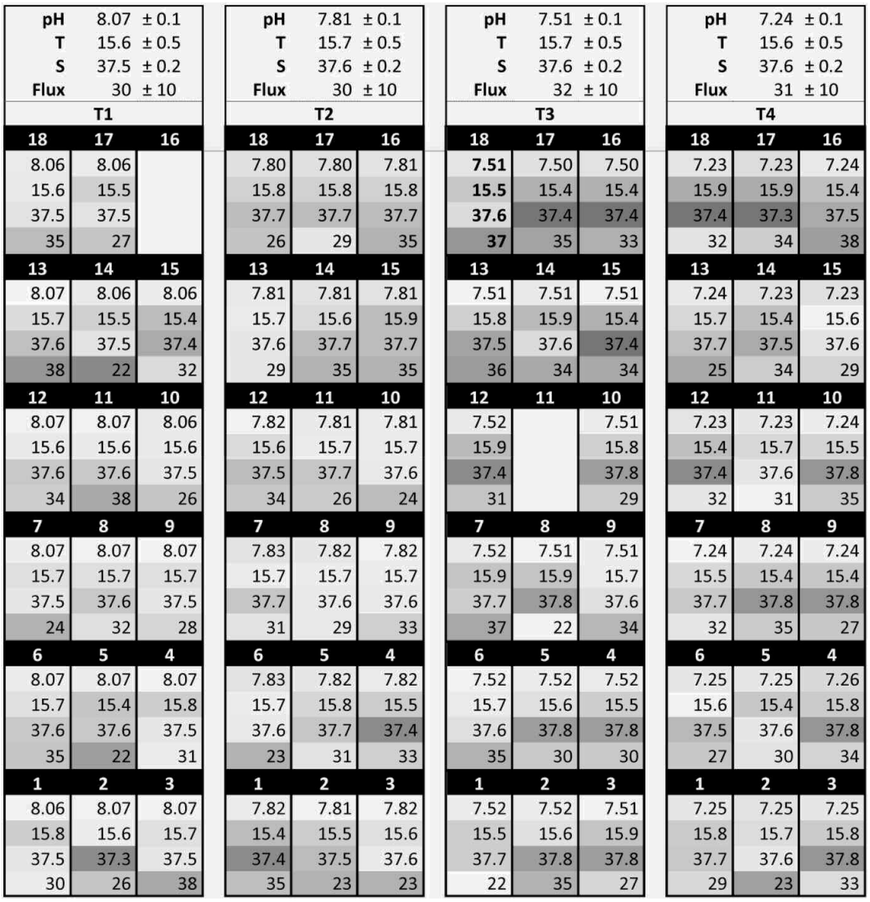
pH	8.06	± 0.1
T	15.7	± 0.5
S	37.6	± 0.2
Flux	28	± 10
T1		
18	**17**	**16**
8.07	8.06	
15.8	15.7	
37.6	37.4	
33	22	
13	**14**	**15**
8.06	8.06	8.06
15.8	15.7	15.5
37.8	37.7	37.6
31	26	27
12	**11**	**10**
8.07	8.06	8.05
15.7	15.7	15.8
37.8	37.8	37.6
28	31	23
7	**8**	**9**
8.05	8.05	8.06
15.5	15.6	15.8
37.5	37.7	37.6
27	27	24
6	**5**	**4**
8.06	8.07	8.06
15.5	15.8	15.6
37.4	37.6	37.6
22	33	30
1	**2**	**3**
8.06	8.06	8.07
15.8	15.4	15.5
37.5	37.5	**37.4**
26	27	31

pH	7.83	± 0.1
T	15.7	± 0.5
S	37.6	± 0.2
Flux	27	± 10
T2		
18	**17**	**16**
7.83	7.82	7.82
15.6	15.6	15.8
37.4	37.5	37.8
24	23	31
13	**14**	**15**
7.83	7.83	7.82
15.8	15.7	15.6
37.7	37.6	37.6
26	30	33
12	**11**	**10**
7.83	7.83	7.83
15.9	15.7	15.6
37.8	37.7	37.6
25	30	26
7	**8**	**9**
7.83	7.83	7.83
15.8	15.8	15.6
37.8	37.7	37.6
22	30	26
6	**5**	**4**
7.82	7.82	7.84
15.7	15.6	15.7
37.6	37.5	37.6
21	30	29
1	**2**	**3**
7.82	7.83	7.82
15.8	15.7	15.6
37.4	37.5	37.5
32	24	24

pH	7.54	± 0.1
T	15.7	± 0.5
S	37.7	± 0.2
Flux	33	± 10
T3		
18	**17**	**16**
7.54	7.53	7.53
15.9	15.9	16.0
37.4	37.4	37.6
28	36	38
13	**14**	**15**
7.53	7.54	7.53
15.5	15.6	15.8
37.8	37.8	37.9
36	35	33
12	**11**	**10**
7.54		7.54
15.4		15.8
37.7		37.5
32		36
7	**8**	**9**
7.54	7.54	7.54
15.9	15.9	15.8
37.6	37.6	37.5
32	27	34
6	**5**	**4**
7.54	7.54	7.54
15.4	15.7	15.6
37.6	37.8	37.7
37	35	32
1	**2**	**3**
7.54	7.54	7.54
15.8	15.6	15.6
37.8	37.7	37.7
26	36	28

pH	7.26	± 0.1
T	15.7	± 0.5
S	37.7	± 0.2
Flux	31	± 10
T4		
18	**17**	**16**
7.25	7.26	7.25
15.7	15.8	15.7
37.8	37.8	37.8
32	33	36
13	**14**	**15**
7.26	7.25	7.25
15.7	15.6	15.6
37.8	37.6	37.6
28	31	29
12	**11**	**10**
7.26	7.26	7.26
15.7	15.6	15.9
37.8	37.6	37.8
32	31	35
7	**8**	**9**
7.27	7.26	7.26
15.9	15.8	15.7
37.8	37.8	37.6
31	35	26
6	**5**	**4**
7.27	7.27	7.26
15.9	15.9	16.0
37.8	37.8	37.4
27	30	33
1	**2**	**3**
7.25	7.24	7.25
15.6	15.4	15.9
37.8	37.7	37.8
28	24	33

Table 3. Second example of measurements of pH (total scale), temperature (T, in °C), salinity (S), and flow rate (in mL/min), following the same scheme and color coding as Table 1.



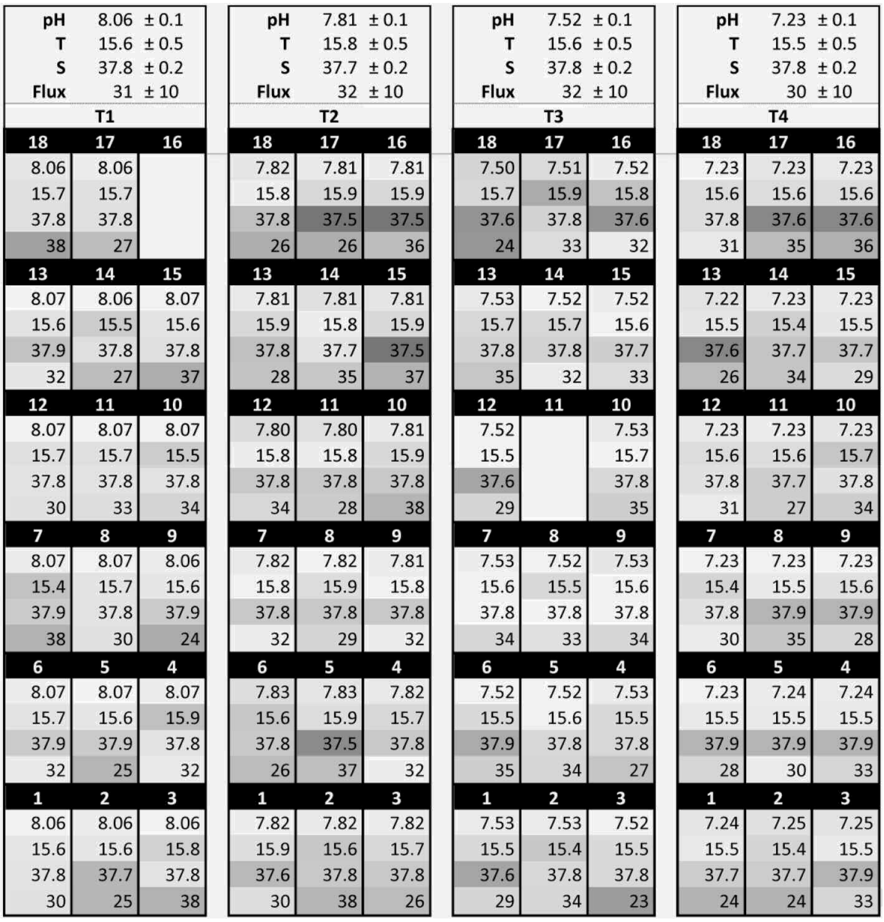
pH	8.07	± 0.1	**pH**	7.81	± 0.1	**pH**	7.51	± 0.1	**pH**	7.24	± 0.1
T	15.6	± 0.5	**T**	15.7	± 0.5	**T**	15.7	± 0.5	**T**	15.6	± 0.5
S	37.5	± 0.2	**S**	37.6	± 0.2	**S**	37.6	± 0.2	**S**	37.6	± 0.2
Flux	30	± 10	**Flux**	30	± 10	**Flux**	32	± 10	**Flux**	31	± 10
T1			**T2**			**T3**			**T4**		
18	**17**	**16**	**18**	**17**	**16**	**18**	**17**	**16**	**18**	**17**	**16**
8.06	8.06		7.80	7.80	7.81	**7.51**	7.50	7.50	7.23	7.23	7.24
15.6	15.5		15.8	15.8	15.8	**15.5**	15.4	15.4	15.9	15.9	15.4
37.5	37.5		37.7	37.7	37.7	**37.6**	37.4	37.4	37.4	37.3	37.5
35	27		26	29	35	**37**	35	33	32	34	38
13	**14**	**15**	**13**	**14**	**15**	**13**	**14**	**15**	**13**	**14**	**15**
8.07	8.06	8.06	7.81	7.81	7.81	7.51	7.51	7.51	7.24	7.23	7.23
15.7	15.5	15.4	15.7	15.6	15.9	15.8	15.9	15.4	15.7	15.4	15.6
37.6	37.5	37.4	37.6	37.7	37.7	37.5	37.6	37.4	37.7	37.5	37.6
38	22	32	29	35	35	36	34	34	25	34	29
12	**11**	**10**	**12**	**11**	**10**	**12**	**11**	**10**	**12**	**11**	**10**
8.07	8.07	8.06	7.82	7.81	7.81	7.52		7.51	7.23	7.23	7.24
15.6	15.6	15.6	15.6	15.7	15.7	15.9		15.8	15.4	15.7	15.5
37.6	37.6	37.5	37.5	37.7	37.6	37.4		37.8	37.4	37.6	37.8
34	38	26	34	26	24	31		29	32	31	35
7	**8**	**9**	**7**	**8**	**9**	**7**	**8**	**9**	**7**	**8**	**9**
8.07	8.07	8.07	7.83	7.82	7.82	7.52	7.51	7.51	7.24	7.24	7.24
15.7	15.7	15.7	15.7	15.7	15.7	15.9	15.9	15.7	15.5	15.4	15.4
37.5	37.6	37.5	37.7	37.6	37.6	37.7	37.8	37.6	37.7	37.8	37.8
24	32	28	31	29	33	37	22	34	32	35	27
6	**5**	**4**	**6**	**5**	**4**	**6**	**5**	**4**	**6**	**5**	**4**
8.07	8.07	8.07	7.83	7.82	7.82	7.52	7.52	7.52	7.25	7.25	7.26
15.7	15.4	15.8	15.7	15.8	15.5	15.7	15.6	15.5	15.6	15.4	15.8
37.6	37.6	37.5	37.6	37.7	37.4	37.6	37.8	37.8	37.5	37.6	37.8
35	22	31	23	31	33	35	30	30	27	30	34
1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
8.06	8.07	8.07	7.82	7.81	7.82	7.52	7.52	7.51	7.25	7.25	7.25
15.8	15.6	15.7	15.4	15.5	15.6	15.5	15.6	15.9	15.8	15.7	15.8
37.5	37.3	37.5	37.4	37.5	37.6	37.7	37.8	37.8	37.7	37.6	37.8
30	26	38	35	23	23	22	35	27	29	23	33

stable water conditions, in this case temperature, pH, and water flow rate, along a long-term experiment. As mentioned, the system is fed from filtered seawater whose salinity varied naturally from 37.8 to 38.6 during the experimental period. No attempt was made to adjust and/or maintain the salinity of the water constant along the experiment. Data obtained in three different measurements performed over different days to test the system (pH, temperature, and flow rate) are shown in Tables 2-4, where a grayscale color code of measured values for each polyp flat is used to illustrate the extent of deviation of each container to the averaged values.

The accuracy and precision of the polyp flat system for maintaining the measured variables constant in time but different among treatments were statistically tested using a hierarchical linear model (two-way nested ANOVA). To avoid problems with repeated measurements (longitudinal data), a specific error structure was added to the model, leaving individual incubation chamber variation in time to be nested inside each treatment (Logan 2010), allowing for comparisons of selected parameters among treatments and also among consecutive days. In order to pass normality assumptions, rank transformations were applied to the data. All analyses were performed using the free statistical platform R (R Core Team 2012).

Statistical analysis showed differences in pH levels among treatments ($F_{3,204}$ = 119.43, $P < 0.01$) but no differences were detected among experimental days ($F_{2,204}$ = 0.231, P = 0.794). These results indicate a proper reproducibility of achieved pH levels in all incubation chambers of each treatment (Fig. 6A). Regarding those variables that were set fixed among the different pH treatments and experimental days, statistical analysis showed no differences for temperature and flow rate between treatments ($F_{3,204}$ = 0.31, P = 0.82 and $F_{3,204}$ = 0.65, P = 0.59, respectively) nor between days ($F_{2,204}$ = 2.42, P = 0.091 and $F_{2,204}$ = 0.81, P = 0.45, respectively) (Fig. 6 B and C). These results give strength to the robustness of this system to maintain constant the selected conditions throughout the experiment. Regarding salinity, however, stronger deviations from the mean were measured (color code in Tables 2-4). Because salinity was the last parameter to be taken, interpretation of these data has to be made with caution, given that vessels were open several times during measurements, and different extents of evaporation could have increased the uncertainty in the salinity

Table 4. Third example of measurements of pH (total scale), temperature (T, in °C), salinity (S), and flow rate (in mL/min), following the same scheme and color coding as Table 1.



pH	8.06	±0.1	pH	7.81	±0.1	pH	7.52	±0.1	pH	7.23	±0.1
T	15.6	±0.5	T	15.8	±0.5	T	15.6	±0.5	T	15.5	±0.5
S	37.8	±0.2	S	37.7	±0.2	S	37.8	±0.2	S	37.8	±0.2
Flux	31	±10	Flux	32	±10	Flux	32	±10	Flux	30	±10
T1			T2			T3			T4		
18	**17**	**16**	**18**	**17**	**16**	**18**	**17**	**16**	**18**	**17**	**16**
8.06	8.06		7.82	7.81	7.81	7.50	7.51	7.52	7.23	7.23	7.23
15.7	15.7		15.8	15.9	15.9	15.7	15.9	15.8	15.6	15.6	15.6
37.8	37.8		37.8	37.5	37.5	37.6	37.8	37.6	37.8	37.6	37.6
38	27		26	26	36	24	33	32	31	35	36
13	**14**	**15**	**13**	**14**	**15**	**13**	**14**	**15**	**13**	**14**	**15**
8.07	8.06	8.07	7.81	7.81	7.81	7.53	7.52	7.52	7.22	7.23	7.23
15.6	15.5	15.6	15.9	15.8	15.9	15.7	15.7	15.6	15.5	15.4	15.5
37.9	37.8	37.8	37.8	37.7	37.5	37.8	37.8	37.7	37.6	37.7	37.7
32	27	37	28	35	37	35	32	33	26	34	29
12	**11**	**10**	**12**	**11**	**10**	**12**	**11**	**10**	**12**	**11**	**10**
8.07	8.07	8.07	7.80	7.80	7.81	7.52		7.53	7.23	7.23	7.23
15.7	15.7	15.5	15.8	15.8	15.9	15.5		15.7	15.6	15.6	15.7
37.8	37.8	37.8	37.8	37.8	37.8	37.6		37.8	37.8	37.7	37.8
30	33	34	34	28	38	29		35	31	27	34
7	**8**	**9**	**7**	**8**	**9**	**7**	**8**	**9**	**7**	**8**	**9**
8.07	8.07	8.06	7.82	7.82	7.81	7.53	7.52	7.53	7.23	7.23	7.23
15.4	15.7	15.6	15.8	15.9	15.8	15.6	15.5	15.6	15.4	15.5	15.6
37.9	37.8	37.9	37.8	37.8	37.8	37.8	37.8	37.8	37.8	37.9	37.9
38	30	24	32	29	32	34	33	34	30	35	28
6	**5**	**4**	**6**	**5**	**4**	**6**	**5**	**4**	**6**	**5**	**4**
8.07	8.07	8.07	7.83	7.83	7.82	7.52	7.52	7.53	7.23	7.24	7.24
15.7	15.6	15.9	15.6	15.9	15.7	15.5	15.6	15.5	15.5	15.5	15.5
37.9	37.9	37.8	37.8	37.5	37.8	37.9	37.8	37.8	37.9	37.9	37.9
32	25	32	26	37	32	35	34	27	28	30	33
1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
8.06	8.06	8.06	7.82	7.82	7.82	7.53	7.53	7.52	7.24	7.25	7.25
15.6	15.6	15.8	15.9	15.6	15.7	15.5	15.4	15.5	15.5	15.4	15.5
37.8	37.7	37.8	37.6	37.8	37.8	37.6	37.8	37.8	37.7	37.7	37.9
30	25	38	30	38	26	29	34	23	24	24	33

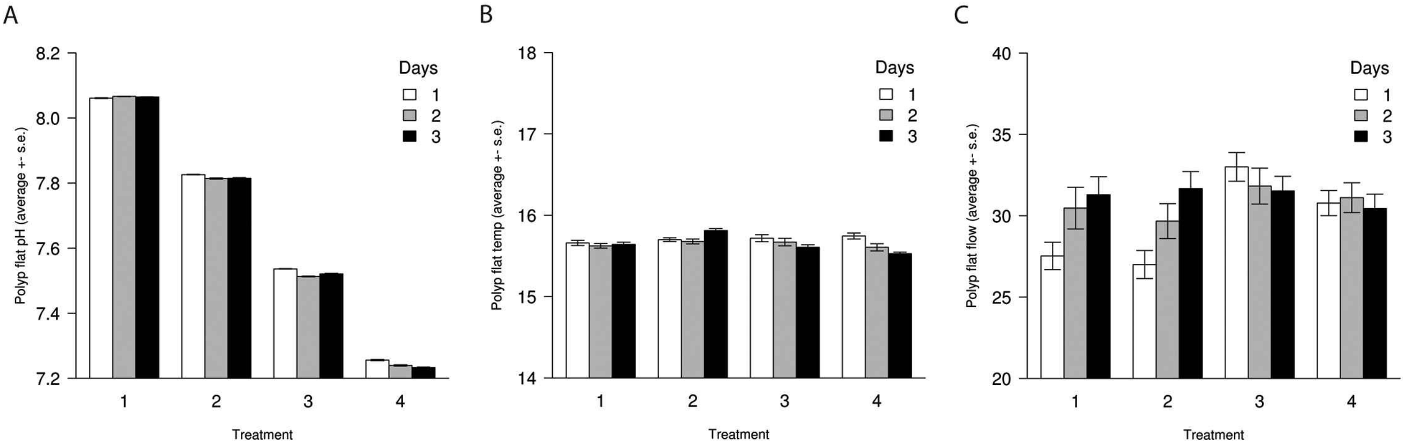


Fig. 6. Results of A) pH, B) temperature (in °C), and C) flow rate (in mL/min) averaged over all the polyp flats of each treatment measured at three different days during the experiment.

results. Therefore, it is possible that the salinity range to which these organisms were subjected within the polyp flats was lower than that measured in the open plastic containers.

Health status of the jellyfish polyps

During the experimental period, all polyps remained attached to their individual incubation chamber and developed properly, indicating that the polyp flat constituted an adequate system for the maintenance and experimentation of individual specimens. After 268 days of experiment, the total mortality was only 14% (10 out of a total of 72 polyps).

Discussion

A number of experiments to determine the effect of different environmental parameters (especially temperature and salinity) on jellyfish polyps have been conducted in the past. In all these studies (summarized in Table 1), water was renewed manually at discrete intervals of time. In most of these cases, the water was renewed when the polyps were fed, once or twice a week. It was mentioned by some of the authors that the physico-chemical conditions of the seawater changed along the experiment at different levels due to the low water renewal rate (e.g. Winans and Purcell 2010). Based on our previous experience, low water renewal posed problems for maintaining constant physicochemical conditions also due to the small volumes of the incubation chambers. As can be seen in Table 1, the jellyfish polyps (very small in size, from 1 to 2 mm high) were always placed in small containers, from 5 to 160 mL. Using small test volumes with inefficient seawater renewal might lead to unfavorable conditions for experimentation (Connor and Wilson 1972) because of accumulation of waste products, depletion of dissolved oxygen, changes in pH or because of bacterial communities composition. To solve these problems, a new design of incubation chamber was necessary in which seawater could run constantly through an open system, ensuring the necessary water renewal and maintaining constant the experimental conditions. To facilitate a broad utilization by the scientific community, the new system had to be simple and economically affordable.

Regarding the environmental stress of ocean acidification, on which research has focused recently, experiments of pH manipulation on jellyfish published so far are limited to a single study (Winans and Purcell 2010). This study focused on *Aurelia labiata*, a species typical for the west coast of North America and revealed that pH values affected the size of the statoliths, small calcium sulphate crystals (Becker et al. 2005) enclosed in the statocysts, the equilibrium organs in jellyfish. However, the pH adjustment in this study was performed by adding HCl (also affecting alkalinity), whereas in our case, we bubbled CO_2, a method that maintains the alkalinity constant and provides a more realistic approach.

At the time of writing this paper, our new system had been in use for 268 days, showing to be accurate and adequate for experimentation on jellyfish polyps. It is also easy to maintain, and therefore, suitable for long-term studies on the response of these organisms to environmental stressors such as ocean acidification. The mortality of polyps during our experiment was only 14% of the total number of polyps, which represents a very low mortality rate compared with other studies (Purcell et al. 2012). In general, mortality events in this kind of experiments occur due to the polyp manipulation and water evaporation, which increases salinity (Purcell et al. 2012). Overall, we conclude that this new system ensures a very good survival rate compared with previous studies. The performance assessment presented in this study attests to the suitability and reliability of this system to meet the current needs of environmental laboratory research on jellyfish polyps, taking advantage of the benefits of working in a continuous flow system. This prototype adds to the current pool of newly designed devices (e.g., Fangue et al. 2010; McGraw et al. 2010; Bockmon et al. 2013; Hoffmann et al. 2013) aimed at providing better tools for testing the effects of acidification and other environmental stressors in marine organisms, a discipline that has recently been identified as research front number one in Ecology and Environmental Sciences (King and Pendlebury 2013).

Comments and recommendations

In order to conduct experimental work with jellyfish polyps, several key aspects need to be considered. The polyps need some time to re-attach to the bottom of the incubation chamber. It is important to ensure that the animals are fixed before turning on the running water system. From our experience, depending on the species, the attaching process can take from a few days to one week, if polyps are in good conditions. The size of the mesh covering the water outlets of the incubation chambers has to be chosen based on the size of the polyps and the food that needs to be provided. In our experiment with *Aurelia* sp. polyps, which were fed with nauplii of *A. salina*, 60 μm represents an adequate mesh size. As future improvements to the system, peristaltic pumps could be used to facilitate the reproducible regulation of the flow rates of seawater to the incubation chambers. In addition, in order to allow the automatic and continuous measurement of selected physicochemical parameters, specific sensors could be implemented.

Overall, this study presents a relatively simple and affordable system that can greatly improve the results obtained from testing the effects of a range of environmental pressures on the eco-physiology of jellyfish polyps.

The authors have provided a multimedia Web Appendix where a multidirectional view of the full system, with details and close-up views of specific parts, will help researchers interested in reproducing it.

References

Astorga, D., J. Ruiz, and L. Prieto. 2012. Ecological aspects of early life stages of Cotylorhiza tuberculata (Cnidaria: Scyphozoa) affecting its pelagic population success. Hydrobiologia 690:141-155 [doi:10.1007/s10750-012-1036-x].

Attrill, M. J., J. Wright, and M. Edwards. 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnol. Oceanogr. 52:480-485 [doi:10.4319/lo.2007.52. 10480].

Becker, A., and others. 2005. Calcium sulfate hemihydrate is the inorganic mineral in statoliths of Scyphozoan medusae (Cnidaria). Dalton Trans. 8:1545-1550 [doi:10.1039/b416246c].

Bockmon, E. E., C. A. Frieder, M. O. Navarro, L. A. White-Kershek, and A. G. Dickson. 2013. Technical Note: Controlled experimental aquarium system for multi-stressor investigation of carbonate chemistry, oxygen saturation, and temperature. Biogeosciences 10:5967-5975 [doi:10.5194/bg-10-5967-2013].

Boero, F., J. Bouillon, C. Gravili, M. P. Miglietta, T. Parsons, and S. Piraino. 2008. Gelatinous plankton: irregularities rule the world (sometimes). Mar. Ecol. Prog. Ser. 356:299-310 [doi:10.3354/meps07368].

Brotz, L., W. Cheung, K. Kleisner, E. Pakhomov, and D. Pauly. 2012. Increasing jellyfish populations: trends in Large Marine Ecosystems. Hydrobiologia 690:3-20 [doi:10.1007/s10750-012-1039-7].

Clayton, T. D., and R. H. Byrne. 1993. Spectrophotometric seawater pH measurements: total hydrogen ion concentration scale calibration of m-cresol purple and at-sea results. Deep-Sea Res. 40:2115-2129 [doi:10.1016/0967-0637(93)90048-8].

Connor, P. M., and K. W. Wilson. 1972. A continuous-flow apparatus for assessing the toxicity of substances to marine animals. J. Exp. Mar. Biol. Ecol. 9:209-215 [doi:10.1016/0022-0981(72)90033-0].

Dickson, A. G., C. L. Sabine, and J. R. Christian. 2007. Guide to best practices for ocean CO_2 measurements. PICES special publication, 3.

Duarte, C. M., and others. 2012. Is global ocean sprawl a cause of jellyfish blooms? Front. Ecol. Environ. 11:91-97 [doi:10.1890/110246].

Fangue, N. A., M. J. O'Donnell, M. A Sewell, P. G. Matson, A. C. MacPherson, and G. E. Hofmann. 2010. A laboratory-based, experimental system for the study of ocean acidification effects on marine invertebrate larvae. Limnol. Oceanogr. Methods 8:441-452 [doi:10.4319/lom.2010.8.441].

Fuentes, V., and others. 2011. Life cycle of the jellyfish *Rhizostoma pulmo* (Scyphozoa: Rhizostomeae) and its distribution, seasonality and inter-annual variability along the Catalan coast and the Mar Menor (Spain, NW Mediterranean). Mar. Biol. 158:2247-2266 [doi:10.1007/s00227-011-1730-7].

Han, C. -H., and S. -I. Uye. 2010. Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita*. Plankton Benthos Res. 5:98-105 [doi:10.3800/pbr. 598].

Hoffmann, L. J., E. Breitbarth, C. M. McGraw, C. S. Law, K. I. Currie, and K .A. Hunter. 2013. A trace-metal clean, pH-controlled incubator system for ocean acidification incubation studies. Limnol. Oceanogr. Methods 11:53-61 [doi:10.4319/lom.2013.11.53].

Holst, S. 2012. Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. Hydrobiologia 690:127-140 [doi:10.1007/s10750-012-1043-y].

———, and G. Jarms. 2007. Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea. Mar. Biol. 151:863-871 [doi:10.1007/s00227-006-0530-y].

Ishii, H., T. Ohba, and T. Kobayashi. 2008. Effects of low dissolved oxygen on planula settlement, polyp growth and asexual reproduction of *Aurelia aurita*. Plankton Benthos Res. 3 (Suppl.):107-113 [doi:10.3800/pbr. 3107].

Kamiyama, T. 2011. Planktonic ciliates as a food source for the scyphozoan *Aurelia aurita* (s.l.): Feeding activity and assimilation of the polyp stage. J. Exp. Mar. Biol. Ecol. 407:207–215 [doi:10.1016/ jjembe.2011.06.016].

King, C., and D. A. Pendlebury. 2013. Research Fronts 2013: 100 top-ranked specialities in the sciences and social sciences. Thomson Reuters.

Liu, W.-C., W.-T. Lo, J. E. Purcell, and H.-H. Chang. 2009. Effects of temperature and light intensity on asexual reproduction of the Scyphozoan, *Aurelia aurita* (L.) in Taiwan. Hydrobiologia 616:247-258 [doi:10.1007/s10750-008-9597-4].

Logan, M. 2010. Biostatistical design and analysis using R. Wiley-Blackwell.

McGraw, C. M., and others. 2010. An automated pH-controlled culture system for laboratory-based ocean acidification experiments. Limnol. Oceanogr. Methods 8:686-694 [doi:10.4319/lom.2010. 8686].

Pelejero, C., E. Calvo, and O. Hoegh-Guldberg. 2010. Paleo-perspectives on ocean acidification. Trends Ecol. Evol. 25:332-344 [doi:10.1016/ jtree.2010.02.002].

Pérez, F. F., and F. Fraga. 1987. A precise and rapid analytical procedure for alkalinity determination. Mar. Chem. 21:169-182 [doi:10.1016/0304-4203(87)90037-5].

———, A. F. Ríos, T. Rellán, and M. Alvarez. 2000. Improvements in a fast potentiometric seawater alkalinity determination. Cienc. Mar. 26:463-478.

Prieto, L., D. Astorga, G. Navarro, and J. Ruiz. 2010. Environmental control of phase transition and polyp survival of a massive-outbreaker jellyfish. PLoS ONE 5(11):e13793 [doi:10.1371/journal.pone.0013793].

Purcell, J. E. 2007. Environmental effects on asexual reproduction rates of the Scyphozoan, *Aurelia labiata*. Mar. Ecol. Prog. Ser. 348:183-196 [doi:10.3354/meps07056].

———. 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Ann. Rev. Mar. Sci. 4:209-235 [doi:10.1146/annurev-marine-120709-142751].

———, S. Uye, and W. T. Lo. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350:153-174 [doi:10.3354/meps07093].

———, D. Atienza, V. Fuentes, A. Olariaga, U. Tilves., C. Colahan, and J.-M. Gili. 2012. Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. Hydrobiologia 690:169-180 [doi:10.1007/s10750-012-1047-7].

Richardson, A. J., and M. J. Gibbons. 2008. Are jellyfish increasing in response to ocean acidification? Limnol. Oceanogr. 53:2040-2045 [doi:10.4319/lo.2008.53. 52040].

———, A. Bakun, G. C. Hays, and M. J. Gibbons. 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol. Evol. 24:312-322 [doi:10.1016/j.tree.2009.01.010].

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing. <http://www.R-project.org/>.

Thein, H., H. Ikeda, and S-I Uye. 2012. The potential role of podocysts in perpetuation of the common jellyfish *Aurelia aurita* s.l. (Cnidaria: Scyphozoa) in anthropogenically perturbed coastal waters. Hydrobiologia 690:157-167 [doi:10.1007/s10750-012-1045-9].

Willcox, S., N. A. Moltschaniwskyj, and C. Crawford. 2007. Asexual reproduction in scyphistomae of *Aurelia* sp.: Effects of temperature and salinity in an experimental study. J. Exp. Mar. Biol. Ecol. 353:107-114 [doi:10.1016/j.jembe.2007.09.006].

Winans, A. K., and J. E. Purcell. 2010. Effects of pH on asexual reproduction and statolith formation of the scyphozoan, *Aurelia labiata*. Hydrobiologia 645:39-52 [doi:10.1007/s10750-010-0224-9].

Submitted 15 October 2013
Revised 11 February 2014
Accepted 13 March 2014

Environmental factors that influence the distribution of *Carybdea marsupialis* (Lineo, 1978, Cubozoa), in south-western Mediterranean coasts

© Eduardo OBIS

Environmental factors that influence the distribution of *Carybdea marsupialis (*Lineo, 1978, Cubozoa), in south-western Mediterranean coasts

Antonio Canepa[1*], Verónica Fuentes[1], Mar B. Belmar [2,3], Melissa Acevedo[1], Kilian Toledo-Guedes[4], Antonio Ortiz[2], Elia Durá[2], César Bordehore[2], Josep-Maria Gili[1].

[1] Institut de Ciències del Mar – Consejo Superior de Investigaciones Científicas, Passeig Marítim de la Barceloneta, 37-49, 08003 Barcelona, Spain.

[2] Departamento de Ecología e Instituto Multidisciplinar para el Estudio del Medio "Ramon Margalef" IMEM, Universidad de Alicante, Ap. 99 E-03080, Alicante, Spain.

[3] Department of Biological and Environmental Sciences and Technologies (DiSTeBA), University of Salento, Lecce 73100, Italy.

[4] Departamento de Ciencias del Mar y Biología Aplicada. Universidad de Alicante, E- 03690, Alicante, Spain.

***CORRESPONDING AUTHOR: canepa@icm.csic.es**

Running page head: Environmental restriction of *Carybdea marsupialis*

ABSTRACT: Jellyfish blooms cause important ecologic and socio-economic problems. Among jellyfish, cubozoans are infamous for their painful sometimes deadly stings and are a major public concern in tropical to subtropical areas; however, there is little information about the possible causes of their outbreaks. After a bloom of the cubomedusae *Carybdea marsupialis* (Carybdeidae) along the coast of Denia (SW Mediterranean, Spain) in 2008 with negative consequences for local tourism, the necessity to understand the ecological restrictions on medusae abundance and distribution was evident. Here we use different models (GAM and zero-inflated models) to understand the environmental restrictions that affect the abundance of *C. marsupialis* along the coast of Denia and the factors that lead to zero-inflated data in order to propose guidelines to conduct monitoring programs. Selected variables differed among medusa size classes, showing different environmental restriction associated to the developmental stages of the species. Variables implicated with dispersion (e.g. wind and current speed and direction) affected mostly small and medium size classes. Sea surface temperature, salinity and proxies of primary production (chlorophyll-a, phosphates, nitrates) were related to the abundances of small and large size classes, highlighting the roles of springtime salinity changes and increased primary production that may promote and maintain high densities of this species. The increased primary (and secondary) production due to anthropogenic impact is implicated as the factor enabling high numbers of *C. marsupialis* to thrive. Recommendations for monitoring blooms of this species along the study area and applicable to Mediterranean Sea include focus effort in coastal waters enriched by anthropogenic activities.

KEY WORDS: box-jellyfish; generalized additive models; zero-inflated models; primary production; physical factors; monitoring programs.

INTRODUCTION

The anthropogenic forcing in coastal areas associated with jellyfish blooms is increasing worldwide, thus negative ecological and socio-economic impacts of these blooms are expected to increase (Purcell 2012, IPCC 2013). Among jellyfish, the Class Cubozoa is infamous for its powerful and even deadly members, which generate major public concern in tropical to subtropical areas (Rottini et al. 1995, Tibballs 2006). The most infamous species are the sea wasp (*Chironex fleckeri*) and from the family Carukiidae, which are responsible for the dangerous and increasing Irukandji syndrome (Gershwin et al. 2013). In addition cubozoans have received much scientific attention because of their complex visual physiology and ecology (Coates 2003, Nilsson et al. 2005), swimming and orientation capabilities (Gordon & Seymour 2009, Garm et al. 2012) and mating behaviours (Lewis & Long 2005). On the other hand, the ecology of cubozoans is still poorly understood (Kingsford et al. 2012) with few papers dealing with quantitative spatial distribution (reviewed in Kingsford & Mooney 2014).

The Mediterranean Sea has been affected historically with blooms of six conspicuous jellyfish species (Gili & Pagès 2005, Canepa et al. 2014, De Donno et al. 2014). Recently, increases in the abundances and frequency of blooms have been shown (Kogovšek et al. 2010, Brotz et al. 2012, Condon et al. 2013). In the Mediterranean Sea, *Carybdea marsupialis* is the only representative of the Class Cubozoa. This medusa was first reported from the Adriatic Sea by Claus in 1878 (Di Camillo et al. 2006), occasionally appearing in high densities, as reported mostly anecdotally in the Adriatic region (Acevedo et al. 2013). *C. marsupialis* is important because of its painful sting and has been the second most important stinging jellyfish on the south coast of Italy, leading to important economical impacts (De Donno et al. 2014). Along the coast of Denia (south-west Mediterranean coast) where Bordehore et al. (2011) showed an unusually high density during the summer of 2008, *C. marsupialis* stung as many as 185 people d^{-1} and caused major public concern.

In order to establish monitoring programs to further develop risk assessment of jellyfish-human interactions, scientific effort to understand the physical and environmental restriction on the abundance and distribution of stinging cubozoans are greatly needed (Kingsford & Mooney 2014). Research dealing with the environmental conditions affecting abundance and spatial patterns of jellyfish species and particularly with Class Cubozoa is under development (Decker et al. 2007, Bentlage et al. 2009). Most members of this Class are coastal and the most influential variables are changes in salinity associated with the presence and dynamics of riverine runoff, temperature and currents (Hartwick 1991, Bentlage et al. 2009, Bordehore et al. 2011), changes in primary production associated with inter-annual climatic fluctuations (Chiaverano et al. 2013) and the presence of sandy bottom and/or seagrass (algae) coverage (Matsumoto 1995, Gordon et al. 2004, Tahera & Kazmi 2008, Bordehore et al. 2011). For a synthetic analysis see Kingsford & Mooney (2014).

As for many other planktonic species, jellyfish show highly patchy distributions (Omori & Hamner 1982), resulting in high numbers of zeroes in the data collected (Martin et al. 2005). The consequences of many zeroes is the tendency to over dispersion and incorrect interpretation of the results if no adjustment is made to the analysis, e.g. use of the proper family distribution, like Poisson or Negative Binomial, or use of specific models like zero-inflated models (Barry & Welsh 2002, Liu et al. 2011). Use of zero-inflated models allows for the identification and effects assessment of two kinds (true and false) of zeroes. True zeroes result from real ecological effects like demographic processes, competition, or poor habitat quality (e.g. absence of proper substrate), or by the patchy distribution of the species in a three dimensional environment. By contrast, false zeroes are caused by failing to detect (or record) the species even when the site was suitable. For this case, avoiding mechanisms of the species (e.g. fast response swimming to net detection) and/or low quality sampling protocol (e.g. small area sampled) can be the responsible for false zeroes (Martin et al. 2005).

The objectives of the present study were to evaluate the role of environmental variables on the abundance and spatio-temporal distribution of a coastal cubozoan species, *Carybdea marsupialis*, which has negative interactions with humans, and to provide recommendations for the establishment of monitoring programs.

MATERIALS AND METHODS

Study site

The study area was located at the south of Valencia Gulf along the coast of Denia (Western Mediterranean Sea). The geographic extension of the study site ranged between 38º 52’ 01.28’’ and 38º 50’ 03.12’’ latitude N, covering ~ 12 kilometres. At this area six sites were selected, from North to South: Almadrava ‘**AL**’, Molins ‘**MO**’, Blay beach ‘**BB**’, Rasset ‘**RA**’, Marineta Cassiana ‘**MC**’ and Les Rotes ‘**RO**’ (Fig. 1). Beach morphology ranged from sandy beaches with high slopes (**AL**), sandy beaches with very low profiles and meadows of the algae (*Caulerpa fructifera*) (**MC**), sandy beaches with rocky reefs and seagrass (*Posidonia oceanica*) meadows (**MO** and **BB**) to hard bottom substrate covered mostly by the “photophillic” algae community (**RO**) (Ballesteros, 1993). For a full site description see (Bordehore et al. 2011).

Carybdea marsupialis medusae sampling

Cubomedusan surveys were conducted from the beginning of July 2010 to the end of July 2011 covering an annual cycle. The abundance of *C. marsupialis* medusae was measured weekly at three coastal transects of 20 meters length at each of the six sites. Three kinds of nets were used on each transect: 200 µm, 500 µm and 4 mm mesh sizes to include the whole size range of the species. The sampling area covered a band approximately 10 m wide and a bottom depth between 0.50 to 1.60 m. The captured cubomedusae were anaesthetized with menthol crystals (Pope 2007) for 20 to 40 minutes and then preserved in buffered sea water-formaldehyde solution (4%). To estimate the volume of water filtered by each net, a G.O.ENVIROMENTAL (MODEL 2030H) flow meter was secured in the mouth of each net.

Medusae caught were counted and measured. The Diagonal Bell Width (DBW), the distance between the bases of two opposite pedalia, which bear the tentacles, was measured with a calibrated stereoscopic microscope (Leica S8APO) for medusae ≤10 mm wide and with Vernier callipers (precision ± 0.05 mm) for larger medusae. Afterwards, medusae were grouped in three categories representing different developmental stages (Acevedo et al. 2013) based on the DBW: small (≤ 5 mm), medium (between 5 and 15 mm) and large (≥ 15 mm).

Environmental variables sampling

Sea surface temperature (SST) and salinity profiles were taken in three points at each of the six beaches sampled, coinciding with the location and time of the medusa abundance transects. Data were recorded using a CTD (Compact-CTD Lite, model ACTD-CMP). The instrument was previously programmed for continuous registration at intervals of 1 second.

Surface currents were obtained by deploying a drift buoy at each beach and recording time and its geographical position at the beginning and at the end of the tree transects, using a GPS Garmin (MODEL GPS 72H). Data were analysed and the surface current direction and speed were obtained.

Chlorophyll-a (Chl a), phosphate and nitrate data were obtained from 15 coastal stations. These stations form part of a larger monitoring program along the coast of Denia covering more than 20 kilometres from Z1 (northern station) to Z15 (southern station) (Fig. 1). From each spatially coincident stations (marked in bold and with an asterisk in Fig. 1), 5 litres of surface water were taken and two replicates from 500 to 1500 ml (depending on turbidity of the water) were filtered. For the Chl a analysis water was filtered through a 47 mm diameter GF/F glass fibre filter. For Chl a quantification, 24 hours extraction with 90 % acetone solution was run in dark and constant temperature (4 ºC) conditions. The extract (90% acetone was used as a solvent) was transferred into the measuring cuvette of a TURNER fluorometer. Chl a measurements were always done against a blank (reference) cuvette. The fluorometer used a wide excitation band around 450 nm and measured at 670 nm. Then, the extract was acidified and measured again after chlorhydric was added, although correction for phaeopigment was not applied in our analysis. Total Chl a µg l^{-1} was then calculated following Wasmund et al. (2006). The average Chl a content of each sampling station was used in our analysis.

For the Suspended Particulate Matter (SPM) analysis, surface seawater was filtered through a (pre-weighed) 25 mm diameter GF/F glass fibre filter and preserved at -20ºC. SPM filters were placed in the stove at 60ºC for 24 hours and after this period were weighted using a micro-balance (Mettler Toledo MX5, precision 1 µg). Total SPM (both organic and inorganic) content in the water was calculated as the difference between pre-weighed and dried filter weight, divided by the volume of water filtered for each sample. The average SPM content (µg l^{-1}) of each sampling station was used in our analysis.

For the nitrate and phosphate analysis, two 10-ml samples of sea water were frozen at -20ºC. Nutrient analysis of the samples was performed by the Nutrient Analysis Service at the Marine Science Institute (ICM-CSIC) with an AA3 (Bran + Luebbe) system (formerly known as Technicon), and the mean quantity of nitrate and phosphate (µmol l^{-1}) of each sampling station were used.

Wind speed (m s^{-1}) and direction (grades) were obtained from a coastal meteorological station at Dènia (http://www.xuss.es).

Statistical Analysis

The abundance (response variable) of the three developmental stages (small, medium and large) were analysed independently and in total. For the modelling process, a subset of the environmental (explanatory) variables was selected in order to avoid collinearity. A Pearson product-moment correlation test was used to elucidate any significant relationship among environmental variables (Zuur et al. 2009). If the Pearson's correlation coefficient between each pair of the environmental variables tested was higher than 0.5, the least important variable (in terms of its biological-ecological theoretical relationship) was dropped from the model.

Different models were used to describe and characterize the relationship among cubozoan abundance (counts) and the explanatory (environmental) variables selected. The models used were: Generalized Additive Models using a Poisson (GAM-P) and a Negative Binomial (GAM-NB) error distribution family and Zero-inflated Models using a Poisson (ZI-P) and a Negative Binomial (ZI-NB) error distribution family. All the models had a logistic-link function. The error family distribution selected allowed for heterogeneous, discrete (integers) and always non-negative data. Because the abundance (count) of *Carybdea marsupialis* depends on the sample size, all the models used the filtered volume as an offset (Penston et al. 2008, Zuur et al. 2009).

Generalized additive models are extensions of linear models that allow the response variable to be distributed other than normally and the linear predictor is a sum of smooth function of the covariates involved in the model (Hastie & Tibshirani 1986, Wood 2006). Thus a general model for a GAM is:

$$Y_i = \alpha + f\left(X_{ij}\right) + \varepsilon_i$$

where Y_i is the response variable (medusa count), X_i is a covariate, f the smoothing function and ε_i are the residuals of the model. The response variable (*C. marsupialis* counts) was modelled with both a Poisson and a Negative Binomial distribution. The amount of smoothing was predefined as a maximum of k=4 (equivalent to a third order polynomial model) for all the environmental variables selected. A cubic spline (a curve made up of sections of cubic polynomial regressions) was used as a smoothing function for the linear predictor and with a maximum of 15 iterations in order to reach mathematical convergence (Wood 2006).

Zero-inflated models (also called mixture models) deal with the extra zeroes by dividing the zero counts as coming from two different processes, the count data, which may produce zeroes (true zeroes), and also values larger than zero (abundance data) and the binomial process contains only zeroes (false zeroes) and values larger than zero (abundance data)(Barry & Welsh 2002). Count data was modelled with a Poisson (ZI-P) or negative binomial (ZI-NB) GLM. The probability of measuring a false zero versus all other types of data (counts and true zeros) was modelled with a binomial GLM (Zuur et al. 2009).

The probability distribution for the ZI-P model for both the binary part of the data (false zeros versus all other types of data) and for the Poisson distribution (the count data) is:

$$P(y_i = 0) = \Pi_i + (1 - \Pi_i) \times \mathrm{e}^{-\mu_i}$$

$$P(Y_i = y_i \mid y_i > 0) = (1 - \Pi_i) \times \frac{\mu^{y_i} \times \mathrm{e}^{-\mu_i}}{y_i!}$$

where $P(y_i)$ is the probability that at site $_i$ we count a cubomedusa, Π_i is the probability to count a false zero, Y_i is the response variable for observation $_i$, y_i is a possible outcome of Y_i, μ_i is the mean and $P(Yi = y_i \mid y_i > 0)$ is the probability that y_i is a non-zero count.

Similarly, the probability distribution for the ZI-NB model for both the binary part of the data (false zeroes versus all other types of data) and for the negative binomial distribution (the count data) which allows for over-dispersion from the non-zero counts is:

$$P(y_i = 0) = \Pi_i + (1 - \Pi_i) \times \left(\frac{\kappa}{\mu_i + \kappa} \right)^{\kappa}$$

$$P(Y_i = y_i \mid y_i > 0) = (1 - \Pi_i) \times fNB(y)$$

where κ is the dispersion parameter (the smaller the κ, the larger the over-dispersion) and $fNB(y)$ is the density function for a Negative Binomial distribution, see Zuur et al. (2009) for details.

In order to incorporate the role of explanatory variables into the count data (values larger than zero) the sample mean μ_i was modelled following:

$$\mu_i = e^{\alpha + \beta_1 \times X_1 + \ldots + \beta_q \times X_q}$$

where α represents the intercept of the multiple regression and β and X are the slope and the environmental variable term, respectively. Similarly, the role of explanatory variables to generate false zeroes Π_i was modelled following:

$$\Pi_i = \frac{e^{\upsilon+\gamma_1 \times Z_{i1}+...+\gamma_q \times Z_{iq}}}{1+e^{\upsilon+\gamma_1 \times Z_{i1}+...+\gamma_q \times Z_{iq}}}$$

where υ is the intercept of the logistic regression of environmental variables and zero non-zero data, γs are the regression coefficients and Zs are the explanatory variables (that may be different to the variables that influence the positive counts). The general mathematical formulations for the mean, variance, models structure and error distribution used are summarized in Table S1.

The optimal model was determined through a backwards selection based on the significance of the each explanatory variable and using the Akaike's Information Criterion (AIC) (Akaike 1974). This method negatively penalizes excess parameters; it prevents the over-parameterization and allows evaluation of which model has the best fit (i.e. the lower the AIC value, the better the model (Zuur et al. 2009)). Nested models were compared using the likelihood ratio test with the function lrtest from the *lmtest* R package (Zeileis & Hothorn 2002).

Finally all the optimal models (GAM-P, GAM-NB, ZI-P and ZI-NB) were visually validated and compared using AIC, log likelihood and degrees of freedom (Df). To assess the degree of concordance between the observed and fitted values, the Pearson correlation coefficient (r) and the Spearman rank correlation (p) were obtained. Additionally, the intercept (α) and slope (b) from a linear regression between the observed versus fitted values were obtained in order to test the hypothetical perfect fit, where the intercept (α) equals 0 and the slope (b) equals 1, as suggested by (Zuur et al. 2009).

All the figures and statistical analyses were made using the free statistical platform R, version

3.0.2 (R Core Team 2013). For the GAM models the *mgcv* package (Wood 2011) and for the zero-inflated models the *pscl* package (Zeileis et al. 2008) were used.

RESULTS

Spatio-temporal distribution of *Carybdea marsupialis*

Total *Carybdea marsupialis* medusae captured were 2002, 413 and 285 small, medium and large medusae, respectively (Table S2). The weekly numbers of medusae collected had high variability among sites (Table S2, Fig. 2). All sites, except AL had weeks during which no medusae were collected, while peak abundance varied dramatically. Small individuals (DBW ≤ 5 mm) had similar abundances at all beaches except MC and RO, which had the fewest accumulated number of medusae (89 and 7 individuals, respectively). Site AL had high accumulated captures of all medusa sizes small (452), medium (147) and 10-times the number of large medusae than at other sites (Fig. 3, Table S2).

The temporal sampling showed a succession in size (growth) of medusae through the sampling period (Fig. 4). The small medusae (DBW = 1.8 ± 1.1 mm, both years) were the first to be caught during spring and until the end of the summer (Fig. 4, upper panel) and the large medusae (DBW = 19.8 ± 4.6 mm) were caught from the summer until mid- Autumn season (Fig. 4).

Spatio-temporal variability of environmental variables

SST (ºC) was highest at the beginning and at the end of the study period (mean values ~ 27 ºC), corresponding to the spring of 2010 and summer season of 2011. The lowest values were during the winter (mean values ~ 13 ºC). The general pattern followed a typical annual seasonal cycle that was similar among the different sites (Table S3, Fig. 5).

Salinity showed less variation through the sampling period. Higher values were recorded in the summer season when mean salinity values were near 37.5. Lower values occurred during the autumn (mean of 36.8) and early spring (mean of 36.9), with records as low as 33 and the maximum intra-seasonal variability. Spatial distribution of salinity also was consistent among sites, but MC and RO were most variable and RA showed the lowest value recorded, 32.98 (Table S3, Fig. 6).

Chl a concentration was highest during the summer months (average 2.03 µg l^{-1}) (Table S3), especially during 2010. The lowest values were recorded during winter- early spring months (average ~ 0.04 µg l^{-1}), reflecting the low biological production during these months. Additionally, Chl a concentration showed a high between-site variability where AL, MO and BB (from north to south) showed a common pattern with highest concentration during the summer months of 2010 (> 1.5 µg l^{-1}), decreasing over the rest of the sampling period and with a small peak during spring months of 2011. By contrast, RA, MC and RO (from north to south) showed low values (< 1.0 µg l^{-1}) during the whole study period (Fig. 7).

Nitrate showed a seasonal cycle with the highest concentrations (average ~ 12 µmol l^{-1}) found during autumn to winter and the lowest values during the summer period. One site (MO) showed a remarkable peak (23.71 µmol l^{-1}) during autumn (Fig. 8, Table S3).

Phosphate concentration showed high variability throughout the study period. An increase from winter to summer was not common to all sites (Fig. 9). Particularly, AL showed a clear peak in summer 2010 (0.11 µmol l^{-1}) followed by a decrease in concentration to a minimum in autumn-winter (0.03 µmol l^{-1}), but RA had an opposite pattern with highest phosphate concentrations (0.22 µmol l^{-1}) in the autumn. The other sites had low phosphate concentrations through the sampling period with a slow increase at the end of the spring and summer 2011 (Fig. 9).

Suspended particulate matter (SPM) showed high between-site variability with a general increase throughout the sampling period, except at sites MC and RO (Fig. 10). The increase pattern was evident for the soft bottom sites with low or few seagrass/algae coverage and was associated to coastal dynamics.

Currents showed a general southward direction with high between-site variability, reflecting the effect of beach orientation and coastal morphology (Fig. 11). In general, a positive onshore transport was evident for AL, RA and MC, where SW and W were the main current directions, with flow parallel to the coast at BB and MO, and transport offshore at RO. Sites MO and RO showed the highest current speeds for most of the sampling period (Table S3).

Wind speed and direction reflected the overall values for the coast of Denia. The main wind direction was N, NE with low speed (category 1 = 0 - 2 m s^{-1}), followed by S, SSW winds at medium speed (category 2 = 2 - 4 m s^{-1}) and finally by E, SE winds with the highest velocities (categories 1-3, < 6 m s^{-1}) (Fig. 12). Wind speed ranged from 0.75 (m s^{-1}) during autumn to 5.40 (m s^{-1}) during the summer months with the lowest variability values recorded during the winter months (Table S3).

Statistical analysis

Variable Selection. The Pearson's correlation coefficient was lower than 0.5, except for the correlation between SPM and nitrate ($r = 0.52$, p-value <0.01). In this case, SPM was dropped from the model (Fig. S1).

Model results. Visual inspection of the relationships between the standardized residuals and the fitted values, residuals versus explanatory variables and from the histogram of the residuals revealed that models with negative binomial error distribution (GAM-NB and ZI-NB) had residuals with less structure and heterogeneity and thus were closer to a normal distribution than those based on Poisson error distribution family (not shown). Similarly, models with a negative binomial error distribution family performed better (in terms of AIC score) than those with Poisson error distribution family (Table S4). Thus, interpretation of the results was based on GAM-NB and ZI-NB. Data for all optimal models and statistics used for their comparison are summarized in Table S4. The significance of the selected environmental variables varied among models and size classes of the *Carybdea marsupialis* medusae. GAM-NB models selected more terms to explain the variability in medusa abundance, resulting in higher degrees of freedom and higher values (except for "Large" medusae) of AIC than the ZI-NB models (Table S4). Results from the optimal models (GAM-NB and ZI-NB) are shown in Tables 4-7 for small, medium, large and total *C. marsupialis* medusae. Because the distribution of medium medusae was not zero-inflated, the ZI-NB was not calculated. The partial effect of common significant explanatory variables for both models was based on the GAM-NB because they had generally higher coefficients (Pearson correlation coefficient (*r*) and Spearman rank correlation (*p*)) for the correlation between observed versus fitted values than did the ZI-NB models (Table S4).

For small medusae, ZI-NB and GAM-NB models had and AIC of 1566.9 and 1663.6 with 10 and 23 degrees of freedom, respectively (Table 1). The GAM-NB model explained a total of 60.0 % of the deviance. Partial effects of common significant explanatory variables for both models (SST, nitrate and phosphate) on the abundance of *C. marsupialis* are shown in Fig. 13. SST had a positive effect on the abundance of small medusae with a maximum at ~23 ºC where a further increase in temperature did not affect their abundance (Fig. 13A). The effect of nitrate and phosphate can be seen as optimum responses, in that increasing values of these response variables generated a positive effect on *C. marsupialis* abundance, but after optima (~ 7 µmol $l^{-1}$and 0.09 µmol l^{-1} for nitrate and phosphate, respectively), the general effect was reduction in abundance (Fig. 13B, C). The GAM-NB model also showed that salinity, Chl a, wind speed and direction, and current direction were significantly associated with the abundance of small *C. marsupialis* medusae (Table 4). The zero-inflated model coefficients revealed that SST, wind speed, the sine of wind direction and the concentration of Chl a, were responsible for the high numbers of zeroes in the data (*i.e.* the zero inflation) (Table 1).

For medium medusae, the ZI-NB model was not performed because the distribution was not zero-inflated. The GAM-NB model had an AIC value of 473.6 with 9 degrees of freedom (Table 2) and was able to explain 51.1% of the deviance. This model revealed that SST, wind speed, current speed and the sine of wind direction explained the variability of the medium medusae. The partial effects of these variables, over the abundance of medium medusae are shown in Fig. 14. SST had a significant "optimum" effect on the abundance of medium medusae, as for the small medusae, with an optimum value ~ 26 ºC. The negative effect over ~ 27 ºC showed higher uncertainty (Fig. 14A). The wind speed effect on abundance showed a similar “optimum” curve, in which increasing wind speed had a positive effect on abundance until ~ 3.5 m s^{-1} after which abundance was reduced (Fig. 14B). The significant effect of the sine of the wind direction revealed that higher values in the zonal (east-west) component of the wind (westerly winds), resulted in higher medusa abundance (Fig. 14C). Finally medium medusae were generally negatively affected by the current speed (2.91 degrees of freedom in the GAM-NB models) (Fig. 14D, Table 2).

For large medusae, ZI-NB and GAM-NB models had AIC values of 487.6 and 474.9 with 9 and 20 degrees of freedom, respectively (Table 3). The explained deviance for the GAM-NB was 72.4 %. Partial effects of common significant explanatory variables for both models (SST, current speed and the cosine of current direction) on the abundance of *C. marsupialis* are shown in Fig. 15. The effect of SST showed a positive pattern on the abundance of large medusae with a maximum effect at ~ 23 ºC (Fig. 15A). Current speed had a negative effect, but velocities higher than 0.8 m s^{-1}resulted in a positive effect, although few observations and wide confidence interval made this prediction questionable (Fig. 15B). The cosine of the current direction, which is the north-south component, showed that predominant currents towards the south tended to diminish the abundance of large medusae (Fig. 14C), but its effect was site specific (Fig. 11) due to the geographical orientation of the sampling area (Fig. 1). The GAM-NB model also showed that Chl a, phosphate and wind speed and direction were significantly associated with the abundance of large medusae (Table 3). ZI-NB models showed that SST and Chl a concentration were the variables that explained the Zero-Inflated data (Table 3).

For the total captures, the ZI-NB and GAM-NB models had AIC values of 2507.8 and 3743.4 with 8 and 26 degrees of freedom, respectively (Table 4). The GAM-NB model explained 47.8% of the deviance. Common variables from GAM-NB and ZI-NB that explained the distribution of *C. marsupialis* medusae were SST, phosphate and wind direction (sine). The partial effect of SST showed a positive relationship with medusa abundance until a maximum of ~ 25 ºC, after where further increase in temperature had a negative effect (Fig. 16A). Phosphate showed a similar positive relationship until a maximum at ~ 0.07 µmol l^{-1} and a negative effect at higher phosphate concentrations (Fig. 16B). Wind direction also had an important effect on the abundance of *C. marsupialis* medusae (Fig 16C). Easterly winds (negative values of the sine of wind direction) had a negative effect and westerly winds (positive values) had a positive effect on medusa abundances. Zero-inflated data were explained by SST and wind speed (Table 4). The GAM-NB model also highlighted physical variables like wind and current speed, current direction and chemical variables like salinity, nitrate and Chl a as explanatory variables that were significantly related with the abundances of *C. marsupialis* medusae (Table 4).

DISCUSSION

Associations of environmental variables with *Carybdea marsupialis* medusae

The effects of environmental variables on the local (~ tens of kilometres) abundance of the cubomedusan *Carybdea marsupialis* showed that SST was the main driver along the SW Mediterranean coast. SST variation was consistent among sites and the high values reported (~ 30 ºC) showed the effect of the coastal morphology and low beach dynamics in the study area. Temporal variation of SST reflected the common seasonality found along the Mediterranean Sea (Duarte et al. 1999). A sudden increase in SST was correlated with the appearance of small medusae in the study area reflecting the role of SST in the life cycle of metagenetic species (reviewed in Lucas et al. 2012, Purcell et al. 2012).

The effect of ontogenetic development led to many zero data for small medusae. The between-site variability in the temperature effect was evident at RA and MC sites, where medusae appeared at the same time and larger than at the other sites; the proportion of medium medusae also occurred earlier at this site than the others (Acevedo unpublished data). One characteristic of these sites is their low profile (slope < 5º) and very shallow depth (0 to 1.5 m) that generate local conditions of high SST in spring, which could have enhanced the growth of small medusae into medium size, resulting in a numerous zeroes for small medusae compared to others sites (Table S3).

Medium size medusae were the most numerous with few zero captures (Table S2). Their “optimum” response to temperature possibly reflected the fact that at the beginning of the summer, warmer temperatures were related to their growth (environmental conditions support their physiological requirements) and, later, the apparent negative effect of temperature may be due to their transformation into the large size class (ontogenetic growth associated with the investment in reproduction) (Fig. 4).

Salinity showed low between-site variability (Fig. 6). Seasonal variability showed the effects of high rain and river discharge during the spring months where the minimum salinity values were recorded. The reduction in salinity was related to the proximity of the “Girona” River in the northern part of the study area (AL) and to groundwater discharges in the southern area (MC, RA and RO). Maximum values were recorded in summer and winter associated with dry conditions in the study area (Gadea et al. 2013).

Most small medusae collected were recently detached medusae, possibly suggesting when and where the medusae were produced from the benthic phase (cubopolyps) and the stimuli for metamorphosis. Nevertheless, metamorphosis of *C. marsupialis* polyps into medusae along the coast of Denia seemed not to be one synchronized event, because small medusae were sampled from mid-spring to late summer months (Fig. 4). Temperature and salinity showed sudden changes (increases and decreases, respectively) during the spring period (week 47, Fig. 5 and 6). Concurrently, small medusae were captured in samples in spring 2011 (week 45) (Fig. 4), suggesting a relationship between changing environmental variables and the metamorphosis of *C. marsupialis* cubopolyps. Canepa et al. (2013) showed that salinity reduction accelerated the metamorphosis of its congener *Carybdea* sp. from Puerto Rico. There, salinity reduction was associated to high rain conditions resulting in an increase in primary and secondary production (Yoshioka et al. 1985, Gilbes et al. 1996). Similarly, association of juvenile medusae with estuarine habitats was proposed for the cubozoan *Chironex fleckeri* (Brown 1973, cited in Kingsford & Mooney 2014, Hartwick 1991), but see (Mooney & Kingsford 2012).

In addition to the effects of river and ground water discharges on salinity, Chl a, phosphate and nitrate were also affected. In addition, the abundance of small *C. marsupialis* medusae was significantly correlated with Chl a, nitrate and phosphate (Table 1) along the coast of Denia. There, fresh water runoff is high but restricted to spring (González Hidalgo et al. 2003) and the surrounding sea is characterized by oligotrophic waters (Duarte et al. 1999, Siokou-Frangou et al. 2010). Thus, reduction of salinity with associated increases in nutrients and coastal production increased the production of *C. marsupialis* medusae.

Chl a was highest in the three northern sites (AL, MO, BB, from north to south) and lowest values in the three southern sites (RA, MC, RO) (Fig. 7). The range of Chl a values recorded (0.04 – 2.03 µg l^{-1}) are in accord with those reported for the Catalan Sea (Olivos et al. 2002). Chl a average concentrations were highest in summer (0.76 ± 0.59 µg l^{-1}) and lowest in spring (0.17 ± 0.11 µg l^{-1}). The effects of river discharges on the primary production explain the high Chl a concentration recorded in this study at the northern sites, as proposed by Gadea et al (2013) who found maximum values (11.71 µg l^{-1}) associated with large discharge of nutrient-rich waters in an enclosed estuarine area. Even though the northern sites can be influenced by the Girona River, the temporarily high values of Chl a recorded at the beginning of the study period (Fig. 7) seem to be an unusual situation. Synergistic effects of fresh water discharge and processes relative to beach nourishment (Sardá et al. 2000) and locally nutrient rich water discharges seemed to occur, but we cannot directly address this issue. We speculate that the local industry adds high nitrate loads in freshwater as commonly found in Spain where there is traditional farming and agricultural industry (Sebastiá et al. 2012). Along the coast of Denia, fertilizers are overused in intensive agricultural activities and the excess seeps into ground water, rivers, and streams, letting nitrogen reach the coastal areas in high concentrations (Gadea et al. 2013). High values of phosphate in coastal areas also are associated with agricultural activities, as well as with the discharge of waste waters from the coastal sewage plants in Denia (Sebastiá et al. 2012, Gadea et al. 2013). In this way, increased primary production is associated with high levels of phosphates along the coast of Denia and related to the rainy season in spring when terrestrial runoff and river discharges are enhanced, and also during summer when local tourism increases discharge from the coastal sewage plants (Fig. 1, Sebastiá et al. 2012, Gadea et al. 2013). Small and large *C. marsupialis* medusae were associated with variables related to fresh water discharge (salinity reduction) and/or to local increases in productivity, as indicated by nitrate, phosphate and Chl a (Olivos et al. 2002, Ludwig et al. 2009).

The wind speeds (0.75 to 5.40 m s^{-1}) and seasonal patterns we determined (Table S3) were in agreement with those characterized for the coast of Alicante (Cabello & Orza 2010), with the main direction (E, SE) characteristic of the sea breeze in this area (Azorin-Molina et al. 2011). During our study, no high values of wind were detected, in part because the sampling was restricted to low to moderate wind speeds (< Beaufort Scale “3” equivalent). Sea surface currents highlighted the predominantly southward current (Siokou-Frangou et al. 2010) in the NW Mediterranean Sea and also the potential effect of coast morphology, especially the effect of breakwaters on currents that may increase the retention of near shore waters (Bordehore et al. 2011).

Dispersion related variables (i.e. wind and current speed and direction) affected mainly the small and medium size classes defined in this study in agreement with their role as the dispersive phase of this species. This reflects their characteristics as passive drifters and may explain the lack of differences in abundance among the sampling sites (Fig. 3, upper and middle panels). Variables associated with the zero-inflated data (Table 1) reflect the fact that at high wind stress (rough conditions caused by high wind speeds associated with the effects of beach orientation), the captures of small medusae were zero even when the other variables where considered “good” by the model. The medusa behaviour of avoidance of rough conditions and off-shore transport of small medusae due to wind-driven surface currents may be responsible for the increased number of “false” zeroes. Thus, future sampling for this small and medium size classes should avoid rough sea surface conditions to avoid zero-inflated data.

Large cubomedusae (≥15 mm DBW) are the size when gonadal tissue becomes visible. Large medusae are important from a management perspective because their stings are painful and have become problematic for local tourism (C. Bordehore personal observations). The distribution of large *C. marsupialis* medusae was restricted mainly to one site (AL) where 234 medusae (of 285 total) were captured during the study. This site is a sandy beach with *Posidonia oceanica* meadows, high slope and strong coastal dynamics and closely to a river discharge (Girona River) (Bordehore et al. 2011). This site had the highest values of Chl a and phosphate, mostly at the beginning of the study period, reflecting the association of large medusae with these variables (Table 3). Field observations revealed that high turbidity in the surf zone was related to captures of the largest medusae. One explanation could be their avoidance of high levels of solar irradiance. Photosensitive behaviour and obstacle avoidance is common in cubozoan species (Kingsford & Mooney 2014). Also, these areas of low visibility and high dynamics could make more of their large prey available and also allow large medusae to remain undetected by their large epibenthic invertebrate prey (Acevedo unpublished data), thereby generating advantageous feeding conditions for these large non-visual entangling predators (Carrette et al. 2002). Cubozoans are strong swimmers that can cover distances up to kilometres d^{-1} (Gordon & Seymour 2009) with complex visual systems (Coates 2003) that have the ability to select areas with optimum conditions. Thus the high numbers of large medusae associated with soft bottom and patchy meadows of seagrass, as previously reported by Bordehore et al. (2011), can be explained by the abundance of their prey typically found in those ecosystems (Bazairi et al. 2010).

When all captures of *C. marsupialis* were analysed together, medusae were mainly associated with temperature, phosphate and wind direction (sine) (Table 4). Nevertheless, other significant variables in the GAM-NB model showed that generally, low salinity and high productivity (Chl a) were associated with the high abundance of *C. marsupialis* medusae when physical conditions (wind current speed and direction) lead to medusae being recorded at the coastal area sampled. A similar positive association with Chl a was established from a long-term study in Hawaii, where the cubozoan *Alantina moseri* also was positively associated with zooplankton biomass (Chiaverano et al. 2013).

The high numbers of zeroes for the total data were explained by just two variables, temperature and wind speed (Table 4). Those variables represent the conditions where the species 'should' be present but was not captured. In the case of wind speed the response is more or less clear, as the behavioural avoidance responses of this species can explain the fact that many transects resulted in zero captures. Along the coast of Denia, one hypothesis is that medusae are able to select the depth and closeness to the shoreline, as previously demonstrated for large *Chironex fleckeri* medusae, which swam to the calm leeward side of Magnetic Island (North Queensland, Australia) when conditions were choppy on the windward side (Brown 1973). Due to the limitations of our sampling methods (shoreline sampling), we cannot discuss the distribution of *C. marsupialis* further from the coast or vertically through the water column. Temperature, on the other hand, had a confounding effect because the most captures were of small medusae, which due to growth appeared negatively related to high temperatures (inflating the number of zeroes) as they became medium and large size class.

In a study conducted during 2008 and 2009 in the same area, Bordehore et al. (2011) using a hand net of 5-mm mesh (comparable to large and medium medusae abundance in our study) did not capture *C. marsupialis* medusae south of the RA site (Fig. 1). Two sampling sites further south in both studies were MC, a sandy beach with high cover (> 80%) of the green algae *Caulerpa prolifera* and located just south of the port of Denia, and RO a rocky-bottom beach fully covered with a benthic photophilic algae community. In our study, the highest mean medusa density was found in MC (2.4 indiv. m^{-3}) containing all sizes (Fig. 3). Establishment of local populations will depend ultimately on the ecosystem characteristics of the new area, where for *C. marsupialis* the need for sandy bottom with seagrass/algae meadows (absent in RO site) seems evident, as has been demonstrated for other cubozoan species, such as *Carybdea rastonii*, *Chiropsella bronzie* and *Chiropsoides buitendijki* (Matsumoto 1995, Gordon et al. 2004, Tahera & Kazmi 2008, reviewed in Kingsford & Mooney 2014).

Medusae densities in the two studies were more or less comparable at the other sites, with the second highest mean density at AL (1.1 indiv. m^{-3}). Nevertheless, the maximum density at AL in our study was more than four times greater than reported by Bordehore et al. (2011) for the same site (53 vs. 18 indiv. m^{-3}). Similarly, at all but one of the sites (MO), the maximum densities recorded during our study period were greater than in the previous study. In total, for the coast of Denia the mean density of *C. marsupialis* medusae in 2010-2011 was twice that in 2008-2009 (0.8 vs. 0.4 indiv. m^{-3}) with the average maximum densities been three times greater (16.2 vs. 5.6 indiv. m^{-3}).

The distribution of *C. marsupialis* medusae seems to reflect the dispersion of the small and medium size classes by the onshore transport due to surface currents and high levels of primary and secondary production associated with the bottom type (sandy bottom and algae/seagrass meadows). Those factors allow *C. marsupialis* medusae to thrive where high densities were also recorded previously (Bordehore et al. 2011). *Carybdea marsupialis* have been recorded several places in the Mediterranean Sea, but rarely generating blooms (sensu Pitt & Lucas 2014, reviewed in Acevedo et al. 2013). Along the coast of Denia, high abundances of *C. marsupialis* were associated with variables indicating high local productivity (Table 4). In those areas, coastal production is based on the discharge of rivers that deliver not only fresh water and terrestrial sediment to the coast, but also large amounts of nitrate and other crop fertilizers (Bordehore et al. 2011, Gadea et al. 2013), enhancing the coastal productivity in this area (Sebastiá et al. 2012). Particularly in AL, in addition to the combination of high levels of Chl a and phosphate, Bordehore et al. (2011) suggested the role of stone breakwaters as new substrata that enhanced the settlement of the benthic stage of this species. Similarly, along the Italian Adriatic shore stinging reports of *C. marsupialis* have increased in recent years (De Donno et al. 2014), as well as installations of several stone breakwaters parallel to the coast (F. Boero, personal communication). Thus, the blooming of *C. marsupialis* medusae associated with coastal areas can be a warning of coastal eutrophication and general environmental degradation.

Statistical Modeling

In general, the models based on the negative binomial error distribution performed better than those with the Poisson based error distribution. For small medusae, the correlation between the observed and the fitted values was higher with GAM-NB model (*r* and *p* value = 0.44 and 0.68, respectively), which also had the second lowest AIC (1818.62), followed by ZI-NB (AIC= 1646.90, Table 3). For the medium size medusae, although GAM-P had a better Pearson correlation (*r* = 0.60) between the observed and fitted values, the GAM-NB had a much lower AIC value, which indicates a better model. Finally for large medusae, GAM-NB models performed better in all the statistics evaluated, with high Pearson (*r*) and Spearman rank (*p*) correlations and with an intercept close to zero (0.1) and slope close to 1 (0.8), which are indicative of a perfect fit (Zuur et al. 2009). This can be attributed to the fact that large medusae were more restricted in space and time, with less variability in the environmental variables; therefore, the models could explain in greater detail (> 70% of the deviance explained) and predict their abundances more accurately.

The poor performance of Poisson error distribution models reflect the fact that count data coming from patchily distributed organisms like gelatinous zooplankton tend to show over dispersion (Liu et al. 2011) and use of negative binomial error distribution family or zero-inflated models is necessary to account for this characteristic (Martin et al. 2005, Liu et al. 2011). In our study, GAM-NB models had higher correlations between observed versus fitted values, making their predictions of the effects of the environmental variables on the abundance of *C. marsupialis* believable. The reason to include the ZI models is based on the fact that these models allowed for ecological interpretation of the underlying processes producing the false zeroes in the medusae counts, resulting in improvement of the ecological analyses (Martin et al. 2005, Zeileis et al. 2008). In the case of *C. marsupialis*, which can congregate at high densities (reviewed in Acevedo et al. 2013) and its sting causes public concern and important economic costs (De Donno et al. 2014), it is important to accurately assess the risk and to develop monitoring programs. Tools that promote understanding which variables explain its distribution, and also conditions that will maximize the efficiency of the survey effort are of high value (Kingsford & Mooney 2014). Thus, our work presents important and highly needed information about seasonality, spatial patterns and the influence of environmental factors on the abundance of a coastal box jellyfish and also recommendations for the establishment of monitoring programs.

Recommendations for monitoring and mitigation

In order to address some recommendations, results from the present study suggests two steps. First, in order to detect the presence and estimate the abundance of *C. marsupialis*, coastal sampling should start in mid-spring and use ~ 500 µm mesh size to collect the small medusae. Sampling during rough sea conditions should be avoided to minimize underestimation and false negative records. Once the population is established and the presence of medium size is confirmed, the large medusae should be sampled with greater mesh size (~ 4 mm) to collect the most, large stinging individuals. In this case, sampling should be restricted to popular beaches with sandy bottom associated with three dimensional structures like seagrass/algae meadows, new breakwaters or other artificial substrata. Similarly, for beaches with low wave dynamics and higher temperature due to shallow profiles, sampling for large individuals should start earlier in those sites. Second, crop fertilizers and sewage discharges should be reduced in highly populated or industrialized areas. Most importantly, high amounts of nutrients reaching the coast (by rivers or ground water discharges) should be prevented, especially in early spring. In order to decrease the amount of sewage water, solutions are related with the improvement in technology adding the tertiary biological treatment to the sewage plants and by relocating the submarine pipeline farther away to the coast, in places where the currents will spread the effluents. The idea behind this recommendation is to diminish the secondary production mostly in those places where habitat is good for *C. marsupialis*, soft bottom, sandy to gravel-sandy beaches and seagrasses meadows.

Acknowledgements. The authors thank Isidro Rico for field and laboratory assistance. This work was funded by the LIFE Programme of the European Commission, the Ministry of the Environment of Spain and the Conselleria de Medi Ambient from the Generalitat Valenciana CUBOMED project (LIFE08 NAT ES64). A.C. was supported by a doctoral fellowship from the Chilean National Commission for Scientific and Technological Research (CONICYT – PFCHA/ Doctorado al Extranjero 4ª Convocatoria, 72120016). We especially thank Jennifer Purcell for her guidance and contributions to the manuscript.

REFERENCES

Acevedo MJ, Fuentes VL, Olariaga A, Canepa A, Belmar MB, Bordehore C, Calbet A (2013) Maintenance, feeding and growth of *Carybdea marsupialis* (Cnidaria: Cubozoa) in the laboratory. J Exp Mar Bio Ecol 439:84–91

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Automat Contr AC-19:716–723

Azorin-Molina C, Chen D, Tijm S, Baldi M (2011) A multi-year study of sea breezes in a Mediterranean coastal site: Alicante (Spain). Int J Climatol 31:468–486

Ballesteros E (1993) Species composition and structure of a photophilic algal community dominated by *Halopteris scoparia* (L.) Sauvageau from the North-Western Mediterranean. Collectanea Botanica 22: 5-24

Barry SC, Welsh AH (2002) Generalized additive modelling and zero inflated count data. Ecol Model 157:179–188

Bazairi H, S Ben Haj, F Boero, D Cebrian, S De Juan, A Limam, J Lleonart, G Torchia, and C Rais (2010) The Mediterranean Sea Biodiversity: state of the ecosystems, pressures, impacts and future priorities. UNEP-MAP RAC/SPA, Tunis

Bentlage B, Peterson AT, Cartwright P (2009) Inferring distributions of chirodropid box-jellyfishes (Cnidaria: Cubozoa) in geographic and ecological space using ecological niche modeling. Mar Ecol Prog Ser 384:121–133

Bordehore C, Fuentes VL, Atienza D, Barberá C, Fernandez-Jover D, Roig M, Acevedo-Dudley MJ, Canepa AJ, Gili JM (2011) Detection of an unusual presence of the cubozoan *Carybdea marsupialis* at shallow beaches located near Denia, Spain (south-western Mediterranean). Mar Biodivers Rec 4:1–6

Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. Hydrobiologia 690:3–20

Brown TW (1973) *Chironex fleckeri* – distribution and movements around Magnetic Island, North Queensland, 13th August 1973 edn. James Cook University Press, Townsville

Cabello M, Orza JAG (2010) Wind speed analysis in the province of Alicante, Spain. Potential for small-scale wind turbines. Renew Sustain Energy Rev 14:3185–3191

Canepa A, Fuentes V, Sabatés A, Piraino S, Boero F, Gili J-M (2014) *Pelagia noctiluca* in the Mediterranean Sea. In: Pitt KA, Lucas CH (eds) Jellyfish Blooms. Springer, Netherlands, p 237–266

Canepa A, Purcell JE, Belmar MB, Acevedo M, Gentile M, Fuentes V (2013) Salinity effects on asexual reproduction of *Carybdea* sp. (Cnidaria: Cubozoa). J Plankton Res 36:585-590

Carrette T, Alderslade P, Seymour J (2002) Nematocyst ratio and prey in two Australian cubomedusans, *Chironex fleckeri* and *Chiropsalmus* sp. Toxicon 40:1547–1551

Chiaverano LM, Holland BS, Crow GL, Blair L, Yanagihara AA (2013) Long-term fluctuations in circalunar beach aggregations of the box jellyfish *Alatina moseri* in Hawaii, with links to environmental variability. PLoS One 8:e77039

Coates MM (2003) Visual ecology and functional morphology of Cubozoa (Cnidaria). Integr Comp Biol 43:542–8

Condon RH, Duarte CM, Pitt KA, Robinson KL, Lucas CH, Sutherland KR, Mianzan HW, Bogeberg M, Purcell JE, Decker MB, Uye S, Madin LP, Brodeur RD, Haddock SHD, Malej A, Parry GD, Eriksen E, Quiñones J, Acha M, Harvey M, Arthur JM, Graham WM (2013) Recurrent jellyfish blooms are a consequence of global oscillations. Proc Natl Acad Sci USA 110:1000–1005

Decker MB, Brown CW, Hood RR, Purcell JE, Gross TF, Matanoski JC, Bannon RO, Setzler-Hamilton EM (2007) Predicting the distribution of the scyphomedusa *Chrysaora quinquecirrha* in Chesapeake Bay. Mar Ecol Prog Ser 329:99–113

Di Camillo C, Bo M, Puce S, Tazioli S, Bavestrello G (2006) The cnidome of *Carybdea marsupialis* (Cnidaria: Cubomedusae) from the Adriatic Sea. J Mar Biol Assoc UK 86:705-709

Donno A De, Idolo A, Bagordo F, Grassi T, Leomanni A, Serio F, Guido M, Canitano M, Zampardi S, Boero F, Piraino S (2014) Impact of Stinging Jellyfish Proliferations along South Italian Coasts: Human Health Hazards, Treatment and Social Costs. Int J Environ Res Public Health 11:2488–2503

Duarte CM, Agustí S, Kennedy H, Vaqué D (1999) The Mediterranean climate as a template for Mediterranean marine ecosystems : the example of the northeast Spanish littoral. Prog Oceanogr 44:245–270

Gadea I, Rodilla M, Sospedra J, Falco S, Morata T (2013) Seasonal dynamics of the phytoplankton community in the Gandia coastal area , southern Gulf of Valencia. Thalassas 29:35–58

Garm A, Bielecki J, Petie R, Nilsson D-E (2012) Opposite patterns of diurnal activity in the box jellyfish *Tripedalia cystophora* and *Copula sivickisi*. Biol Bull 222:35–45

Garm A, O’Connor M, Parkefelt L, Nilsson D-E (2007) Visually guided obstacle avoidance in the box jellyfish *Tripedalia cystophora* and *Chiropsella bronzie*. J Exp Biol 210:3616–3623

Gershwin L-A, Richardson AJ, Winkel KD, Fenner PJ, Lippmann J, Hore R, Avila-Soria G, Brewer D, Kloser RJ, Steven A, Condie S (2013) Biology and ecology of Irukandji jellyfish (Cnidaria: Cubozoa). Adv Mar Biol 66:1–85

Gilbes F, López JM, Yoshioka PM (1996) Spatial and temporal variations of phytoplankton chlorophyll a and suspended particulate matter in Mayagüez Bay, Puerto Rico. J Plankton Res 18:29–43

Gili J-M, Pagès F (2005) Les proliferacions de meduses. Bolletí la Soc d'Historia Nat les Balear 48:9–22

González Hidalgo JC, Luís M De, Raventós J, Sánchez JR (2003) Daily rainfall trend in the Valencia Region of Spain. Theor Appl Climatol 75:117–130

Gordon M, Hatcher C, Seymour J (2004) Growth and age determination of the tropical Australian cubozoan *Chiropsalmus* sp. Hydrobiologia 530-531:339–345

Gordon MR, Seymour JE (2009) Quantifying movement of the tropical Australian cubozoan *Chironex fleckeri* using acoustic telemetry. Hydrobiologia 616:87–97

Hartwick RF (1991) Distributional ecology and behaviour of the early life stages of the box-jellyfish *Chironex fleckeri*. Hydrobiologia 216-217:181–188

Hastie T, Tibshirani R (1986) Generalized Additive Models. Stat Sci 1:297–318

IPCC (2013) Climate Change 2013: The Physical Science Basis. In: Stocker, TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V and Midgley PM (eds) Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, NY

Kingsford MJ, Mooney CJ (2014) The ecology of box jellyfishes (Cubozoa). In: Pitt KA, Lucas CH (eds) Jellyfish Blooms. Springer, Dordrecht, pp 267–302

Kingsford MJ, Seymour JE, O'Callaghan MD (2012) Abundance patterns of cubozoans on and near the Great Barrier Reef. Hydrobiologia 690:257–268

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

Lewis C, Long TAF (2005) Courtship and reproduction in *Carybdea sivickisi* (Cnidaria: Cubozoa). Mar Biol 147:477–483

Liu H, Ciannelli L, Decker MB, Ladd C, Chan K-S (2011) Nonparametric threshold model of zero-inflated spatio-temporal data with application to shifts in jellyfish distribution. J Agric Biol Environ Stat 16:185–201

Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. In: Lesser MP (ed) Advances in Marine Biology, 1st edn. Elsevier Ltd., Amsterdam, p 133–196

Ludwig W, Dumont E, Meybeck M, Heussner S (2009) River discharges of water and nutrients to the Mediterranean and Black Sea: Major drivers for ecosystem changes during past and future decades? Prog Oceanogr 80:199–217

Martin TG, Wintle BA, Rhodes JR, Kuhnert PM, Field SA Low-Choy SJ, Tyre AJ, Possingham HP (2005) Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecol Lett 8:1235–46

Matsumoto GI (1995) Observations on the anatomy and behaviour of the cubozoan *Carybdea rastonii* Haacke. Mar Freshw Behav Physiol 262:139–148

Mooney CJ, Kingsford MJ (2012) Sources and movements of *Chironex fleckeri* medusae using statolith elemental chemistry. Hydrobiologia 690:269–277

Nilsson D-E, Gislén L, Coates MM, Skogh C, Garm A (2005) Advanced optics in a jellyfish eye. Nature 435:201–205

Olivos A, Masó M, Camp J (2002) Aportes continentales de nutrientes y su posible influencia sobre las relaciones estequiométricas (DIN:P:Si) en las aguas del noreste del Mediterráneo español (Mar Catalán). Ciencias Mar 28:393–406

Omori M, Hamner WM (1982) Patchy distribution of zooplankton: Behavior, population assessment and sampling problems. Mar Biol 72:193–200

Penston MJ, Millar CP, Zuur A, Davies IM (2008) Spatial and temporal distribution of *Lepeophtheirus salmonis* (Krøyer) larvae in a sea loch containing Atlantic salmon, *Salmo salar* L., farms on the north-west coast of Scotland. J Fish Dis 31:361–71

Pitt KA, Lucas CH (2014) Jellyfish blooms. Springer, Dordrecht

Pope LG (2007) Sexual dimorphism and symmetry variation in the freshwater jellyfish, *Craspedacusta sowerbii* (Lankester). MSc dissertation, University of Southern Illinois, Carbondale, IL

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Ann Rev Mar Sci 4:209–235

Purcell JE, Atienza D, Olariaga A, Tilves U, Colahan C (2012) Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. Hydrobiologia 690:169-180

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/ (accessed 07 March 2014)

Rottini G, Gusmani L, Parovel E, Avian M, Patriarca P (1995) Purification and properties of a cytolytic toxin in venom of the jellyfish *Carybdea marsupialis*. Toxicon 33:315–326

Sardá R, Pinedo S, Gremare A, Taboada S (2000) Changes in the dynamics of shallow sandy-bottom assemblages due to sand extraction in the Catalan Western Mediterranean Sea. ICES J Mar Sci 57:1446-1453

Sebastiá MT, Estornell J, Rodilla M, Martí J, Falco S (2012) Estimation of chlorophyll « A » on the Mediterranean coast using a QuickBird image. Rev Teledetección 37:23–33

Siokou-Frangou I, Christaki U, Mazzocchi MG, Montresor M, Ribera d'Alcá M, Vaqué D, Zingone A (2010) Plankton in the open Mediterranean Sea : a review. Biogeosciences 7:1543–1586

Tahera Q, Kazmi QB (2008) New records of two jellyfish medusae (Cnidaria: Scyphozoa: Catostylidae: Cubozoa: Chirodropidae) from Pakistani waters. Mar Biodivers Rec 1:1–4

Tibballs J (2006) Australian venomous jellyfish, envenomation syndromes, toxins and therapy. Toxicon 48:830–859

Ueno S, Mitsumori S, Noda M, Ikeda I (2000) Effect of comparative lightness of obstacles on swimming behaviour of *Carybdea rastonii* (Cnidaria; Cubozoa). J Natl Fish Univ 48(3): 255–258

Wasmund N, Topp I, Schories D (2006) Optimising the storage and extraction of chlorophyll samples. Oceanologia 48:125–144

Wood SN (2006) Generalized Additive Models. An introduction with R. Chapman and Hall/CRC

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc Ser B (Statistical Methodol) 73:3–36

Yoshioka PM, Owen GP, Pesante D (1985) Spatial and temporal variations in Caribbean zooplankton near Puerto Rico. J Plankton Res 7:733–751

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2:7–10

Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. J Stat Softw 27:1–25

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, NY

LEGENDS TO TABLES AND FIGURES

TABLES

Table S2. Descriptive statistics for the number and density (indiv. m^{-3}) in parentheses of *Carybdea marsupialis* medusae captured by site (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’) on the coast of Denia, Spain. Minimum 'Min', maximum 'Max', sum 'Sum', mean 'Mean' and standard deviation 'SD' values are showed for each class size and for the total medusae captured.

Table S3. Descriptive statistics for the selected environmental variables through the sampling period for all sites surveyed (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’) on the coast of Denia, Spain. Values are shown by season

Table S4. Model comparison for the generalized additive models with a Poisson family distribution (GAM-P), generalized additive models with a negative binomial family distribution (GAM-NB), zero-inflated Poisson (ZI-P) and zero-inflated negative binomial (ZI-NB) models. The Pearson correlation coefficient (r), Spearman rank correlation (p), intercept (α) and slope (b) of a linear regression between the observed versus fitted values, Akaike Information Criterion (AIC), log likelihood (Log lik) and degrees of freedom (Df) are showed for each size class of *Carybdea marsupialis* medusae on the coast of Denia, Spain. NA = Not Available

Table 1. Model results for small *Carybdea marsupialis* medusae on the coast of Denia, Spain. The selected environmental variables and values for Akaike Information Criterion (AIC), Log likelihood (Log lik) and degrees of freedom (Df) of the models are shown

Table 2. Model results for medium size *Carybdea marsupialis* medusae on the coast of Denia, Spain. The selected environmental variables and values for Akaike's information Criterion (AIC), Log likelihood (Log lik) and degrees of freedom of the models are showed. NA = not available (the distribution was not zero-inflated)

Table 3. Model results for large *Carybdea marsupialis* medusae on the coast of Denia, Spain. The selected environmental variables and values for Akaike's information Criterion (AIC), Log likelihood (Log lik) and degrees of freedom (Df) of the models are shown

Table 4. Model results for total *Carybdea marsupialis* medusae on the coast of Denia, Spain. The selected environmental variables and values for Akaike's information Criterion (AIC), Log likelihood (Log lik) and degrees of freedom (Df) of the models are shown

Table S1. Mathematical model formulation for the generalized additive models with Poisson family distribution (GAM-P), generalized additive models with negative binomial family distribution (GAM-NB), zero-inflated Poisson (ZI-P) and zero-inflated negative binomial (ZI-NB) models

FIGURES

Figure 1. Study area for *Carybdea marsupialis* medusae along the coast of Denia, Spain (Western Mediterranean Sea).). Medusae, environmental data and nutrient samples were collected from stations labeled in bold with an asterisk and labeled (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’). The stations marked in gray were not sampled for medusae and are not considered further. The general current flow, the Girona River and the sewage outfall are also indicated

Figure 2. Spatio-temporal variability of captured *Carybdea marsupialis* medusae along the coast of Denia, Spain. Data are presented as a whisker-boxplot, where the horizontal line represents the median, the boxes represent the interquartile range and the whiskers represent the range of observations (when visible). Different panels refer to sampling sites (see text). Note different y-axis ranges

Figure 3. Spatial variability of total captured *Carybdea marsupialis* medusae at sites (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’) along the coast of Denia, Spain. Upper, middle and lower panels show the total small, medium and large medusae, respectively. Abundances represent the total numbers collected from the beginning of July 2010 to the end of July 2011; note that the legend categories differ among panels

Figure 4. Temporal variability of captured *Carybdea marsupialis* medusae from the beginning of July 2010 to the end of July 2011 at sites (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’) along the coast of Denia, Spain. Upper, medium and lower panels show the total small, medium and large medusae, respectively. Shaded areas represent the seasons corresponding to the weeks sampled

Figure 5. Temporal variability of sea surface temperature SST (ºC) from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplots, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the ranges of observations (when visible). Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’)

Figure 6. Temporal variability of salinity from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplots, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the ranges of observations (when visible). Dots show values twice the standard deviation. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’)

Figure 7. Temporal variability of Chl a (µg l^{-1}) from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplots, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the ranges of observations (when visible). A loess smoothing line was added to help visualize temporal patterns. Dots show values twice the

standard deviation. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’)

Figure 8. Temporal variability of nitrate (µmol l^{-1}) from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplot, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the ranges of observations (when visible). A loess smoothing line was added to help visualize temporal patterns. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’)

Figure 9. Temporal variability of phosphate (µmol l^{-1}) from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplots, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the range of observations (when visible). A loess smoothing line was added to help visualize temporal patterns. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’)

Figure 10. Temporal variability of suspended sarticulate matter (SPM in µg l^{-1}) from the beginning of July 2010 to the end of July 2011. Data are presented as a whisker-boxplot, where the horizontal line represents the median, the boxes represent the interquartile range and the whiskers represent the range of observations (when visible). A loess smoothing line was added to help visualize temporal patterns. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins

‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’)

Figure 11. Current direction (degrees) and current speed (four categories, m s^{-1}) from the beginning of July 2010 to the end of July 2011. Number of observations represents the amount of current records, in some particular angle and velocity combination. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’)

Figure 12. Wind direction (degrees) and wind speed (three categories, m s^{-1}) from the beginning of July 2010 to the end of July 2011 at sites along the coast of Denia, Spain. The lengths of the bars represent the numbers of wind recorded by direction and velocity combination

Figure 13. Partial effects of A) temperature, B) nitrate and C) phosphate on the abundance of small *Carybdea marsupialis* medusae. Central (bold) lines show the best fits and the shaded areas show the confidence intervals of the GAM-NB model. Bottom vertical lines represent observations

Figure 14. Partial effects of A) temperature, B) wind speed, C) wind direction (sine) and D) current speed on the abundance of medium size *Carybdea marsupialis* medusae. Central (bold) lines show the best fits and the shaded areas show the confidence intervals of the GAM-NB model. Bottom vertical lines represent observations

Figure 15. Partial effects of A) temperature, B) current speed and C) current direction (cosine) on the abundance of large *Carybdea marsupialis* medusae. Central (bold) lines show the best fit and the shaded areas show the confidence intervals of the GAM-NB model. Bottom vertical lines represent observations

Figure 16. Partial effects of A) temperature, B) phosphate and C) wind direction (sine) on the abundance of total *Carybdea marsupialis* medusae. Central (bold) lines show the best fit and the shaded areas show the confidence intervals of the GAM-NB model. Bottom vertical lines represent observations

Figure S1. Collinearity analysis for all environmental variables. Lower-left panels show scatter plots with a loess smoothing line (in red) to help visualize patterns. Central (Diagonal) panels show histograms of the environmental variables and upper-right panels show the values of the Pearson's correlation coefficients for each pair of variables, with text size proportional to its value

Table 1. Model results for small *Carybdea marsupialis* medusae on the coast of Denia, Spain. The selected environmental variables and values for Akaike Information Criterion (AIC), Log likelihood (Log lik) and degrees of freedom (Df) of the models are shown

Model	Parameter	Slope	z-value	p-value	AIC	Log lik	Df
ZI-NB (Count model coefficients)	Temperature	-0.22	-4.2	< 0.001			
	Nitrate	-0.14	-3.7	< 0.001			
	Phosphate	23.3	3.6	< 0.001			
ZI-NB (ZI model coefficients)	Temperature	-0.4	-2.8	< 0.001			
	Wind speed	-3.6	-3.9	< 0.001			
	Sine (wind direction)	-2.5	-3.9	< 0.001			
	Chl a	-5.3	-3.3	< 0.001	1566.9	-773.4	10
GAM-NB	Temperature	1.95	26.63	< 0.001			
	Salinity	2.96	36.21	< 0.001			
	Wind speed	2.00	70.90	< 0.001			
	Sine (wind direction)	3.00	89.62	< 0.001			
	Cos (wind direction)	2.95	52.92	< 0.001			
	Sine (current direction)	2.99	31.96	< 0.001			
	Cos (current direction)	2.91	21.38	< 0.001			
	Chl a	2.96	66.55	< 0.001			
	Nitrate	2.15	26.85	< 0.001			
	Phosphate	2.00	67.47	< 0.001	1663.6	-808.5	23

Table 2. Model results for medium size *Carybdea marsupialis* medusae on the coast of Denia, Spain. The selected environmental variables and values for Akaike's information Criterion (AIC), Log likelihood (Log lik) and degrees of freedom of the models are showed. The ZI-NB models were not appropriate because the distribution was not zero-inflated.

Model	Parameter	Slope	Chi-squared	p-value	AIC	Log lik	Df
GAM-NB	Temperature	1.89	17.20	< 0.001			
	Wind speed	1.98	38.84	< 0.001			
	Sine (wind direction)	1.00	11.59	< 0.001			
	Current speed	2.91	24.47	< 0.001	473.6	-228	9

Table 3. Model results for large size individuals of *Carybdea marsupialis*. The selected environmental variables and values for AIC, Log likelihood and degrees of freedom of the models are showed.

Model	Parameter	Slope	z-value	p-value	AIC	Log lik	Df
ZI-NB (Count model coefficients)	Temperature	-0.49	-3.8	< 0.001			
	Current speed	-25.27	-4.37	< 0.01			
	Cos (Current direction)	-1.54	-4.52	< 0.001			
	Nitrate	-0.3	-2.33	< 0.05			
ZI-NB (ZI model coefficients)	Temperature	-1.5	-3.72	< 0.001			
	Chl a	-39.81	-3.26	< 0.001	487.6	-234.8	9
GAM-NB	Temperature	1.92	12.81	< 0.01			
	Wind speed	1.82	24.69	< 0.001			
	Sine (wind direction)	2.19	8.22	< 0.05			
	Cos (wind direction)	2.99	9.68	< 0.05			
	Current speed	2.70	77.93	< 0.001			
	Cos (current direction)	2.34	20.19	< 0.001			
	Chl a	2.95	54.54	< 0.001			
	Phosphate	2.00	27.61	< 0.001	474.9	-217.6	20

Table 4. . Model results for total *Carybdea marsupialis* medusae on the coast of Denia, Spain. The selected environmental variables and values for Akaike's information Criterion (AIC), Log likelihood (Log lik) and degrees of freedom (Df) of the models are shown.

Model	Parameter	Slope	z-value	p-value	AIC	Log lik	Df
ZI-NB (Count model coefficients)	Temperature	-0.13	-2.5	< 0.05			
	Phosphate	23.52	3.24	< 0.001			
	Sine (wind direction)	0.98	3.62	< 0.001	2507.8	-1246	8
ZI-NB (ZI model coefficients)	Temperature	-0.68	-4.63	< 0.001			
	Wind speed	-2.42	-3.13	< 0.05	2507.8	-1246	8
GAM-NB	Temperature	1.98	69.1	< 0.001			
	Salinity	2.96	29.63	< 0.001			
	Wind speed	1.99	180.35	< 0.001			
	Sine (wind direction)	1.68	74.65	< 0.001			
	Cos (wind direction)	2.92	166.5	< 0.001			
	Current speed	2.85	15.37	< 0.01			
	Sine (current direction)	2.91	40.38	< 0.001			
	Chl a	2.92	47.23	< 0.001			
	Nitrate	2.94	46.94	< 0.001			
	Phosphate	1.97	79.82	< 0.001	3743.4	-1845.6	26

Table S1. Mathematical model formulation for the generalized additive models with Poisson family distribution (GAM-P), generalized additive models with negative binomial family distribution (GAM-NB), zero-inflated Poisson (ZI-P) and zero-inflated negative binomial (ZI-NB) models.

MODEL	Mean	Variance	Model	Error Distribution
GAM-P	$E(Y_i) = \mu_i$	$var(Y_i) = \mu_i$	$Y_i = \alpha + f(X_{ij}) + \varepsilon_i$	$\varepsilon_i \sim N(0, \sigma^2)$
GAM-NB	$E(Y_i) = \mu_i$	$var(Y_i) = \mu_i + \frac{\mu_i^2}{k}$	$Y_i = \alpha + f(X_{ij}) + \varepsilon_i$	$\varepsilon_i \sim N(0, \sigma^2)$
ZI-P	$\mu_i = e^{\alpha+\beta_1 \times X_1 + \ldots + \beta_q \times X_q}$ $E(Y_i) = \mu_i \times (1 - \Pi_i)$	$var(Y_i) = (1 - \Pi_i) \times (\mu_i + \Pi_i \times \mu_i^2)$	$P(Y_i = 0) = \Pi_i + (1 \quad \Pi_i) \times \mathrm{e}^{\ \mu_i}$ $P(Y_i = y_i \mid y_i > 0) = (1 \quad \Pi_i) \times \frac{\mu^{y_i} \times \mathrm{e}^{\ \mu_i}}{y_i!}$	$\varepsilon_i = \frac{Y_i - (1 - \Pi_i) \times \mu_i}{\sqrt{var(Y_i)}}$
ZI-NB	$\mu_i = e^{\alpha+\beta_1 \times X_1 + \ldots + \beta_q \times X_q}$ $E(Y_i) = \mu_i \times (1 - \Pi_i)$	$var(Y_i) = (1 - \Pi_i) \times \left(\mu_i + \frac{\mu_i^2}{k}\right) + \mu_i^2 \times (\Pi_i{}^2 + \Pi_i)$	$P(Y_i = 0) = \Pi_i + (1 \quad \Pi_i) \times \left(\frac{\kappa}{\mu_i + \kappa}\right)^{\kappa}$ $P(Y_i = y_i \mid y_i > 0) = (1 \quad \Pi_i) \times fNB(y)$	$\varepsilon_i = \frac{Y_i - (1 - \Pi_i) \times \mu_i}{\sqrt{var(Y_i)}}$

Table S2. Descriptive statistics for the number and density (in parentheses; indiv. m^{-3}) of three sizes (Small, Medium, Large) of *Carybdea marsupialis* medusae captured by site (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’) on the coast of Denia, Spain. Minimum 'Min', maximum 'Max', sum 'Sum', mean 'Mean' and standard deviation 'SD' values are showed for each class size and for the total medusae captured.

Site	Small					Medium					Large				
	Min	Max	Sum	Mean	SD	Min	Max	Sum	Mean	SD	Min	Max	Sum	Mean	SD
AL	0.0	117	452	4.5	14.2	1	39	147	4.0	6.5	0.0	53	234	2.2	7.1
	(0.0)	(91.6)	(269.7)	(2.7)	(10.6)	(0.1)	(6.6)	(34.1)	(0.9)	(1.6)	(0.0)	(5.2)	(18.6)	(0.2)	(0.6)
MO	0.0	324	426	4.7	34.2	1	2	6	1.2	0.5	0.0	4	11	0.1	0.5
	(0.0)	(62.3)	(111.2)	(1.2)	(6.7)	(0.1)	(0.3)	(0.9)	(0.2)	(0.1)	(0.0)	(0.8)	(1.5)	(0.01)	(0.1)
BB	0.0	80	569	5.4	12.7	1	18	75	3.0	3.8	0.0	5	13	0.1	0.6
	(0.0)	(68.5)	(418.3)	(4.0)	(9.6)	(0.04)	(1.9)	(10.3)	(0.4)	(0.5)	(0.0)	(0.5)	(1.3)	(0.01)	(0.1)
RA	0.0	119	459	5.2	16.8	1	16	51	2.7	4.2	0.0	4	11	0.1	0.5
	(0.0)	(40.2)	(184.8)	(2.1)	(5.8)	(0.04)	(1.6)	(7.9)	(0.4)	(0.4)	(0.0)	(0.4)	(1.2)	(0.01)	(0.1)
MC	0.0	61	89	1.2	7.2	1	121	134	16.8	42.2	0.0	4	16	0.2	0.6
	(0.0)	(11.5)	(24.7)	(0.3)	(1.5)	(0.1)	(16.6)	(19.1)	(2.4)	(5.6)	(0.0)	(0.5)	(2.0)	(0.02)	(0.1)
RO	0.0	2	7	0.1	0.3	1	0	0	0.0	0.0	0.0	0	0	0.0	0.0
	(0.0)	(0.9)	(3.4)	(0.1)	(0.2)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
All Sites	0.0	117	2002	3.8	18.0	1	121	413	4.4	13.1	0.0	53	285	0.5	3.1
	(0.0)	(91.6)	(1012.2)	(1.9)	(7.4)	(0.0)	(16.6)	(72.3)	(0.8)	(2.0)	(0.0)	(5.2)	(24.6)	(0.04)	(0.3)

Table S3. Descriptive statistics for the selected environmental variables from the beginning of July 2010 to the end of July 2011for all sites surveyed (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’) on the coast of Denia, Spain. Values are shown by season

Variable	Site	Spring				Summer				Autumn				Winter			
		Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
SST (ºC)	AL	20.27	25.41	22.46	1.80	21.50	28.10	25.32	1.69	18.04	24.54	21.23	2.37	13.41	13.70	13.58	0.10
	MO	20.15	25.16	22.24	1.62	20.71	27.14	25.20	1.57	18.17	24.10	20.69	2.33	13.21	13.37	13.29	0.06
	BB	20.41	24.82	22.28	1.67	22.80	27.3	25.33	1.44	17.98	24.68	21.10	2.41	13.09	13.22	13.15	0.05
	RA	21.19	27.1	23.45	2.23	23.28	29.54	25.97	1.88	18.23	24.49	21.17	2.31	13.20	13.36	13.27	0.06
	MC	21.25	22.33	21.74	0.36	22.45	28.06	25.82	1.45	16.50	25.16	21.00	2.68	12.61	13.63	13.38	0.38
	RO	19.56	23.79	21.56	1.63	22.28	27.86	25.27	1.57	14.87	24.37	20.64	3.19	11.42	13.88	13.51	0.79
	All Sites	19.56	27.1	22.31	1.79	20.71	29.54	25.48	1.63	14.87	25.16	20.97	2.55	12.82	13.88	13.36	0.37
Salinity	AL	35.08	37.04	36.43	0.58	36.70	37.72	37.25	0.23	35.47	37.21	36.88	0.29	37.18	37.44	37.31	0.08
	MO	35.70	37.07	36.93	0.53	36.03	37.76	37.28	0.27	36.19	37.33	36.92	0.19	36.40	37.40	37.19	0.33
	BB	34.67	37.30	36.84	0.51	36.92	37.84	37.49	0.2	36.92	37.36	37.02	0.21	37.51	37.56	37.54	0.02
	RA	32.98	37.39	36.91	0.87	36.02	37.83	37.48	0.25	36.38	37.41	37.01	0.29	35.63	37.64	37.22	0.77
	MC	36.37	37.09	36.93	0.2	33.29	37.68	37.06	0.69	36.03	37.23	36.70	0.29	37.12	37.63	37.48	0.18
	RO	35.63	37.22	36.82	0.33	36.72	37.76	37.40	0.21	35.78	37.62	37.02	0.37	37.07	37.57	37.47	0.15
	All Sites	32.98	37.39	36.74	0.58	33.29	37.84	37.33	0.38	35.47	37.62	36.92	0.29	35.63	37.64	37.36	0.37
Chl a (µg L^{-1})	AL	0.18	0.30	0.26	0.06	0.55	2.03	1.18	0.62	0.64	0.96	0.77	0.13	0.50	0.50	0.50	0.00
	MO	0.13	0.34	0.28	0.10	0.41	1.92	1.23	0.58	0.85	1.01	0.93	0.07	0.40	0.40	0.40	0.00
	BB	0.10	0.15	0.14	0.03	0.36	2.00	0.98	0.63	0.52	1.03	0.68	0.23	0.25	0.25	0.25	0.00
	RA	0.07	0.11	0.10	0.02	0.35	0.57	0.49	0.08	0.48	0.91	0.66	0.19	0.42	0.42	0.42	0.00
	MC	0.11	0.11	0.11	0.00	0.17	0.40	0.28	0.08	0.17	0.34	0.24	0.07	0.16	0.16	0.16	0.00
	RO	0.04	0.34	0.13	0.14	0.25	0.57	0.36	0.13	0.31	0.38	0.34	0.03	0.12	0.12	0.12	0.00
	All Sites	0.04	0.34	0.17	0.11	0.17	2.03	0.76	0.59	0.17	1.03	0.60	0.28	0.12	0.50	0.32	0.00
Nitrate (µmol L^{-1})	AL	1.53	2.14	1.74	0.30	1.09	2.79	1.99	0.74	2.63	6.24	4.51	1.57	2.75	2.75	2.75	0.00
	MO	2.64	18.15	13.38	7.30	1.00	5.33	2.62	1.73	2.64	23.71	10.28	8.92	12.42	12.42	12.42	0.00

Variable	Site	Spring				Summer				Autumn				Winter			
		Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
	BB	0.73	3.13	2.39	1.13	0.55	6.89	2.91	2.58	2.61	7.97	5.09	2.19	6.63	6.63	6.63	0.00
	RA	0.22	0.22	0.22	0.00	0.22	0.93	0.47	0.28	0.93	3.07	2.17	0.94	6.41	6.41	6.41	0.00
	MC	0.89	0.89	0.89	0.00	0.18	0.6	0.31	0.17	0.27	8.71	3.85	3.63	2.73	2.73	2.73	0.00
	RO	0.44	4.92	3.54	2.11	0.21	2.95	1.12	1.10	0.93	1.70	1.35	0.34	0.83	0.84	0.84	0.00
	All Sites	0.22	18.15	4.03	5.64	0.18	6.89	1.58	1.71	0.27	23.71	4.61	5.04	0.83	12.42	5.45	3.89
Phosphate (µmol L^{-1})	AL	0.06	0.07	0.06	0.00	0.03	0.11	0.06	0.03	0.03	0.05	0.03	0.01	0.03	0.03	0.03	0.00
	MO	0.04	0.07	0.05	0.01	0.03	0.06	0.05	0.02	0.03	0.07	0.06	0.02	0.02	0.02	0.02	0.00
	BB	0.03	0.06	0.04	0.01	0.04	0.06	0.05	0.01	0.02	0.05	0.04	0.01	0.04	0.04	0.04	0.00
	RA	0.03	0.06	0.04	0.01	0.02	0.05	0.03	0.01	0.03	0.22	0.11	0.08	0.05	0.05	0.05	0.00
	MC	0.05	0.05	0.05	0.00	0.01	0.05	0.02	0.02	0.00	0.04	0.02	0.02	0.02	0.02	002	0.00
	RO	0.02	0.07	0.03	0.02	0.02	0.06	0.04	0.02	0.00	0.06	0.04	0.02	0.08	0.08	0.08	0.00
	All Sites	0.02	0.07	0.05	0.01	0.02	0.11	0.04	0.02	0.00	0.22	0.05	0.05	0.02	0.08	0.04	0.02
SPM (mg L^{-1})	AL	16.12	24.92	21.87	4.27	10.64	24.71	16.69	5.20	10.64	26.32	18.27	6.45	12.83	12.83	12.83	0.00
	MO	17.39	28.69	25.21	5.32	10.83	17.74	14.95	2.92	13.38	33.94	23.00	8.32	11.52	11.53	11.53	0.00
	BB	16.25	25.03	22.32	4.13	11.87	24.22	15.79	4.94	12.45	22.45	16.95	4.10	16.59	16.59	16.59	0.00
	RA	10.59	19.86	16.64	4.52	12.36	27.92	17.39	6.17	13.86	22.85	17.99	3.82	18.79	18.80	18.80	0.00
	MC	12.09	12.09	12.09	0.00	8.11	14.70	14.24	2.36	10.98	16.00	14.24	2.27	17.30	17.30	17.30	0.00
	RO	13.00	16.51	14.08	1.65	7.65	15.02	11.59	2.80	9.50	13.08	11.20	1.56	11.44	11.44	11.44	0.00
	All Sites	10.59	28.69	19.36	5.98	7.65	27.92	14.67	4.89	9.50	33.94	17.00	6.16	11.44	18.80	14.60	2.97
Current speed (m s^{-1})	AL	0.02	0.03	0.03	0.00	0.01	0.08	0.05	0.02	0.01	0.06	0.03	0.02	0.01	0.01	0.01	0.00
	MO	0.03	0.15	0.08	0.05	0.03	0.15	0.08	0.03	0.01	0.07	0.03	0.02	0.05	0.05	0.05	0.00
	BB	0.03	0.04	0.04	0.00	0.03	0.09	0.06	0.02	0.01	0.07	0.03	0.02	0.04	0.04	0.04	0.00
	RA	0.02	0.04	0.03	0.01	0.01	0.09	0.04	0.02	0.02	0.05	0.04	0.01	0.04	0.04	0.04	0.00
	MC	0.01	0.02	0.01	0.01	0.01	0.14	0.03	0.03	0.00	0.03	0.02	0.01	0.02	0.02	0.02	0.00
	RO	0.01	0.06	0.03	0.02	0.00	0.12	0.05	0.03	0.01	0.06	0.04	0.02	0.07	0.07	0.07	0.00

Variable	Site	Spring				Summer				Autumn				Winter			
		Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
	All Sites	0.01	0.15	0.04	0.03	0.00	0.15	0.05	0.03	0.00	0.07	0.03	0.02	0.01	0.07	0.04	0.00
Wind speed (m s^{-1})	All Sites	2.00	4.60	3.32	1.04	1.28	5.40	2.67	1.39	0.75	2.00	1.39	0.42	1.03	1.03	1.03	0.00

Table S4. Model comparison for the generalized additive models with a Poisson family distribution (GAM-P), generalized additive models with a negative binomial family distribution (GAM-NB), zero-inflated Poisson (ZI-P) and zero-inflated negative binomial (ZI-NB) models. The Pearson correlation coefficient (r), Spearman rank correlation (p), intercept (α) and slope (b) of a linear regression between the observed versus fitted values, Akaike Information Criterion (AIC), log likelihood (Log lik) and degrees of freedom (Df) are showed for each size class of *Carybdea marsupialis* medusae on the coast of Denia, Spain. NA = Not Available.

	Small							Medium							Large						
Model	r	p	α	b	AIC	Log lik	Df	r	p	α	b	AIC	Log lik	Df	r	p	α	b	AIC	Log lik	Df
GAM-P	0.51	0.64	2.85	0.28	4371.57	-2155.90	30	0.60	0.31	2.90	0.30	765.06	-356.80	26	0.89	0.41	0.09	0.80	522.20	-235.90	25
GAM-NB	0.44	0.68	3.04	0.23	1818.62	-883.20	26	0.47	0.31	3.50	0.16	478.89	-220.20	19	0.84	0.43	0.10	0.80	462.70	-205.40	26
ZI-P	0.14	0.24	4.60	0.05	5475.66	-2714.00	24	NA	NA	NA	NA	NA	NA	NA	0.12	0.10	0.90	0.10	632.30	-292.20	24
ZI-NB	0.06	0.50	6.50	0.07	1646.90	-798.50	25	NA	NA	NA	NA	NA	NA	NA	0.40	0.40	0.40	0.30	490.40	-220.20	25

FIGURES

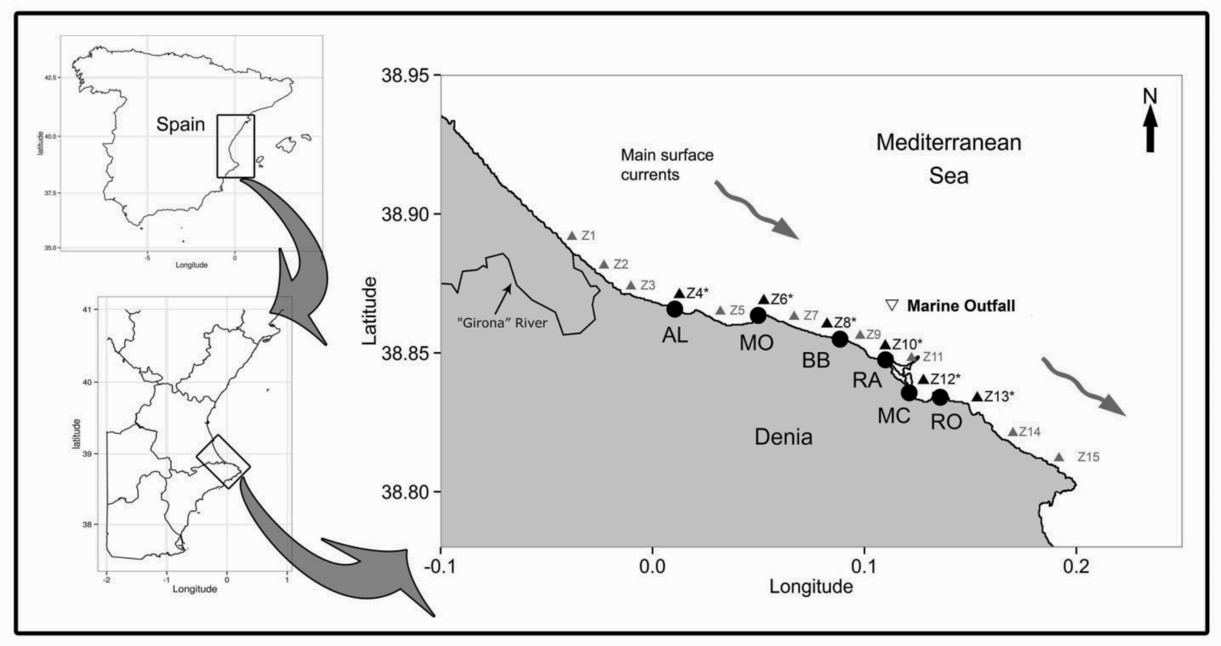


Figure 1. Study area for collection of *Carybdea marsupialis* medusae along the coast of Denia, Spain (Western Mediterranean Sea). Medusae, environmental data and nutrient samples were collected from stations labeled in bold with an asterisk and labeled (Almadrava 'AL', Molins 'MO', Blay beach 'BB', Rasset 'RA', Marineta Cassiana 'MC' and Les Rotes 'RO'). The stations marked in gray were not sampled for medusae and are not considered further. The general current flow, the Girona River and the sewage marine outfall are also indicated

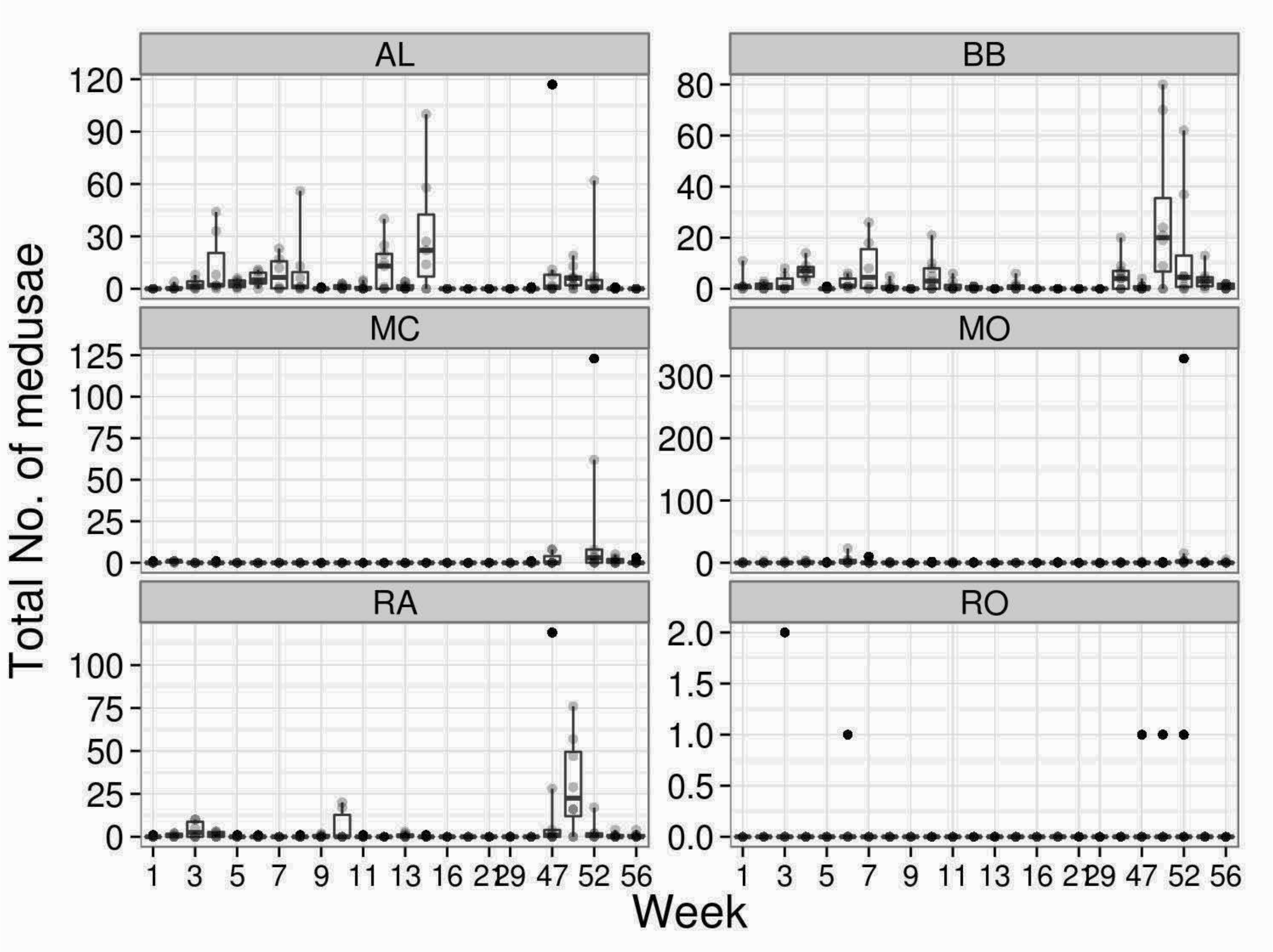


Figure 2. Spatio-temporal variability of captured *Carybdea marsupialis* medusae along the coast of Denia, Spain. Data are presented as a whisker-boxplot, where the horizontal line represents the median, the boxes represent the interquartile range and the whiskers represent the range of observations (when visible). Different panels refer to sampling sites (see text). Note different y-axis ranges.

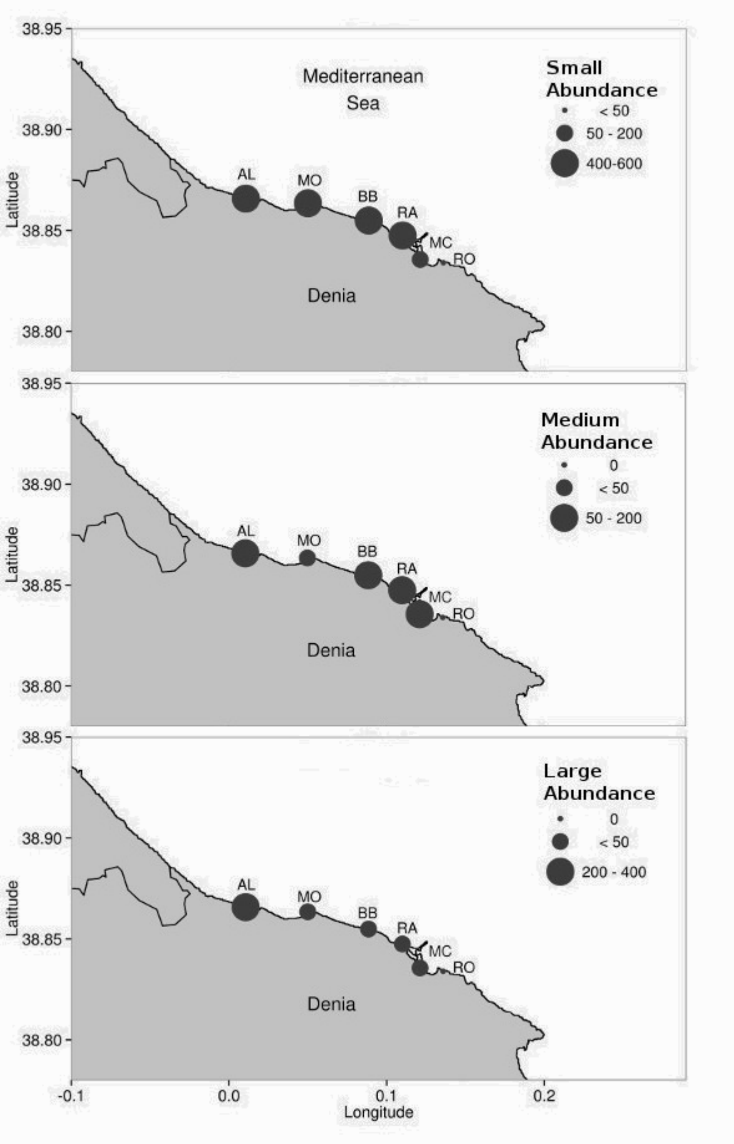


Figure 3. Spatial variability of total captured *Carybdea marsupialis* medusae at sites (Almadrava 'AL', Molins 'MO', Blay beach 'BB', Rasset 'RA', Marineta Cassiana 'MC' and Les Rotes 'RO') along the coast of Denia, Spain. Upper, middle and lower panels show the total small, medium and large medusae, respectively. Abundances represent the total numbers collected from the beginning of July 2010 to the end of July 2011; note that the legend categories differ among panels.

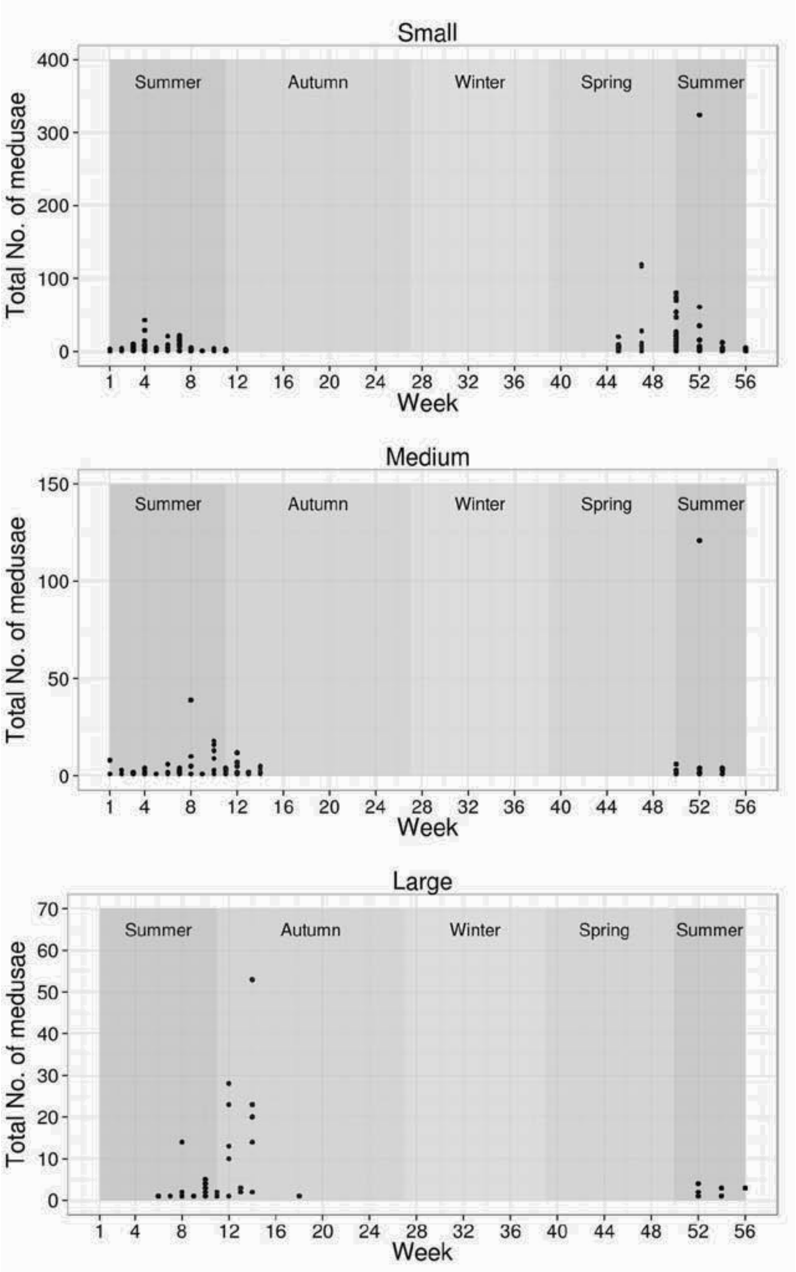


Figure 4. Temporal variability of captured *Carybdea marsupialis* medusae from the beginning of July 2010 to the end of July 2011 at sites (Almadrava 'AL', Molins 'MO', Blay beach 'BB', Rasset 'RA', Marineta Cassiana 'MC' and Les Rotes 'RO') along the coast of Denia, Spain. Upper, medium and lower panels show the total small, medium and large medusae, respectively. Shaded areas represent the seasons corresponding to the weeks sampled.

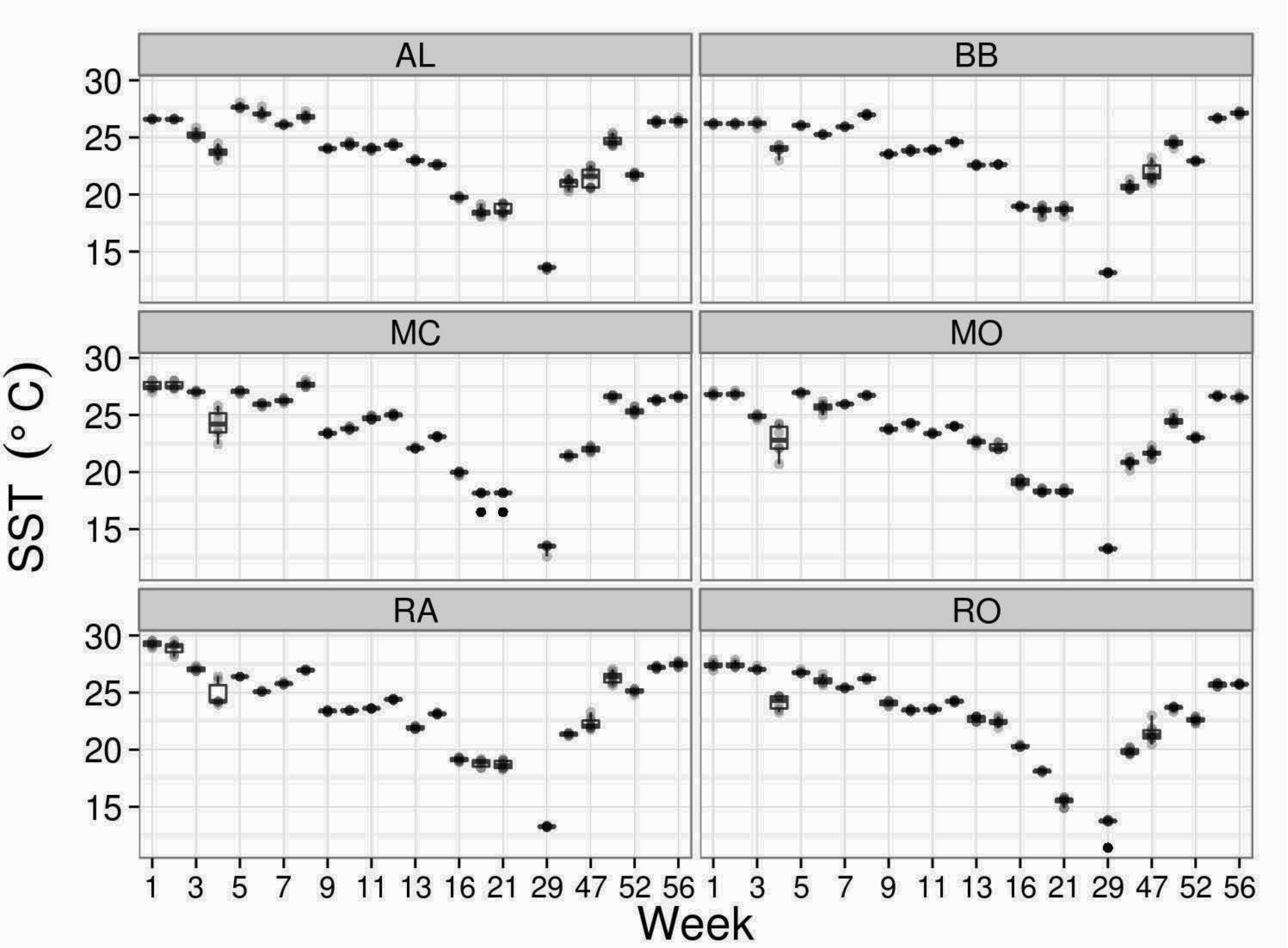


Figure 5. Temporal variability of sea surface temperature SST (ºC) from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplots, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the ranges of observations (when visible). Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’).

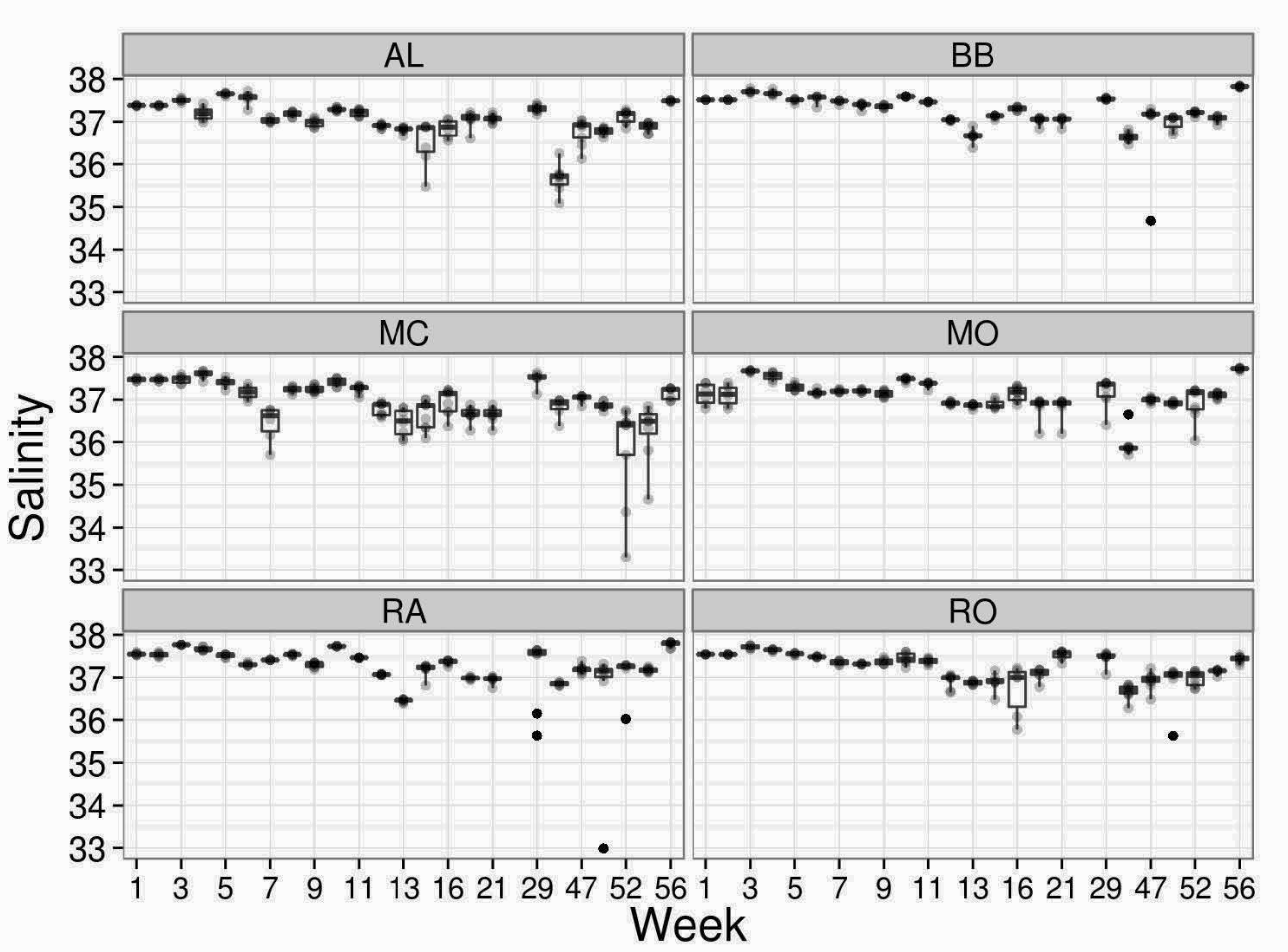


Figure 6. Temporal variability of salinity from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplots, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the ranges of observations (when visible). Dots show values twice the standard deviation. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’)..

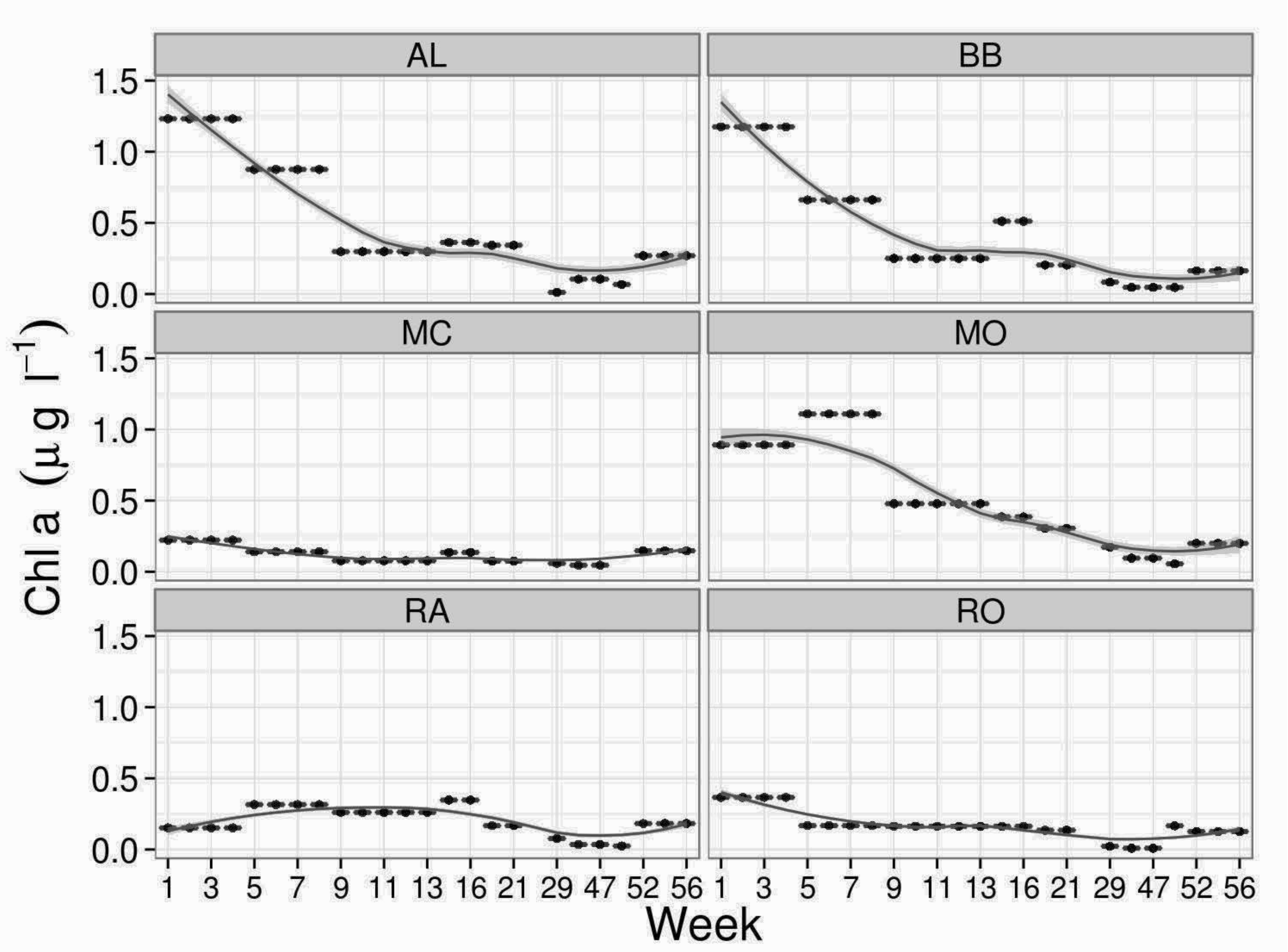


Figure 7. Temporal variability of Chl a (µg l^{-1}) from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplots, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the ranges of observations (when visible). A loess smoothing line was added to help visualize temporal patterns. Dots show values twice the standard deviation. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’).

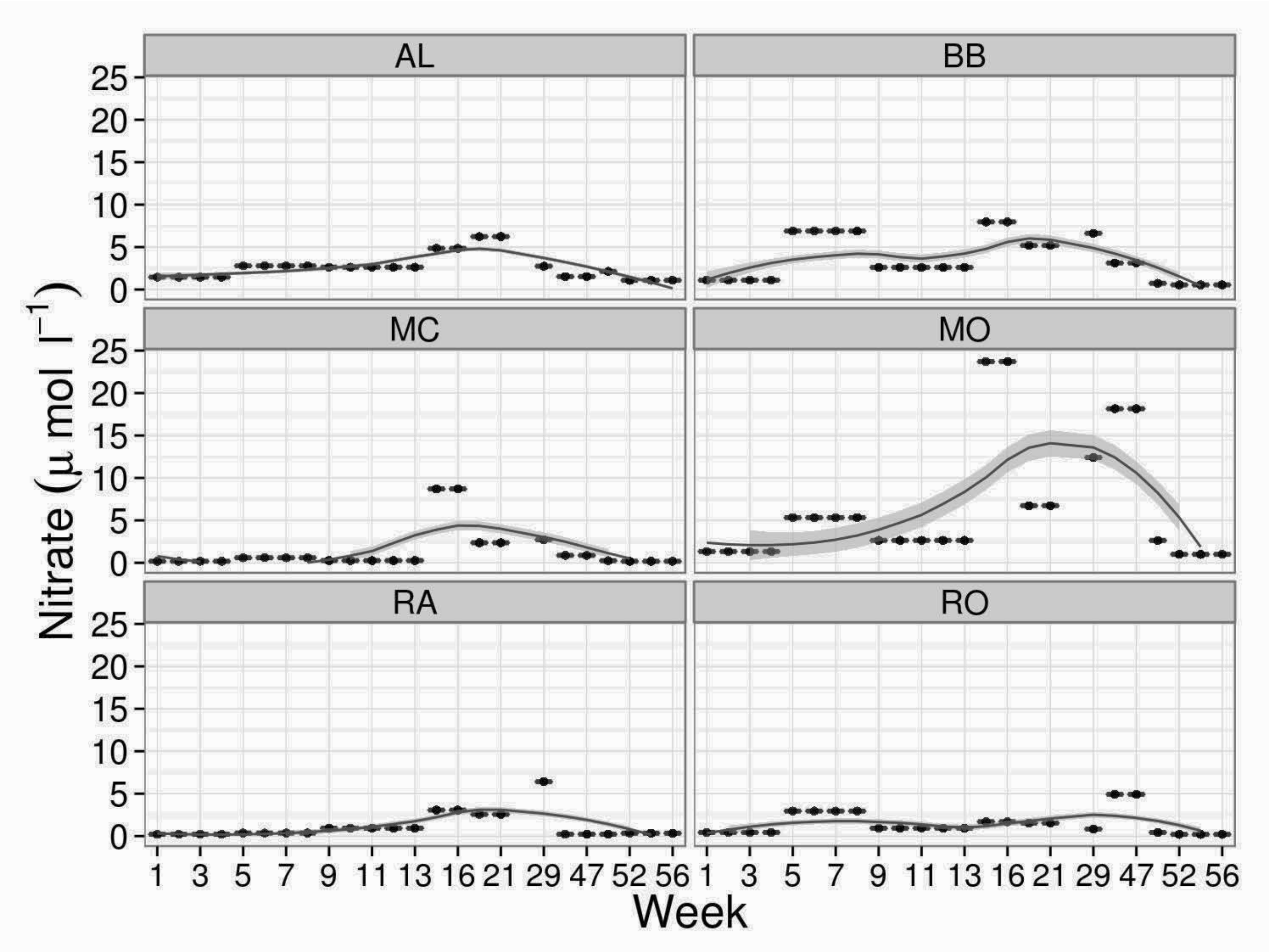


Figure 8. Temporal variability of nitrate (μmol l^{-1}) from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplot, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the ranges of observations (when visible). A loess smoothing line was added to help visualize temporal patterns. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’).

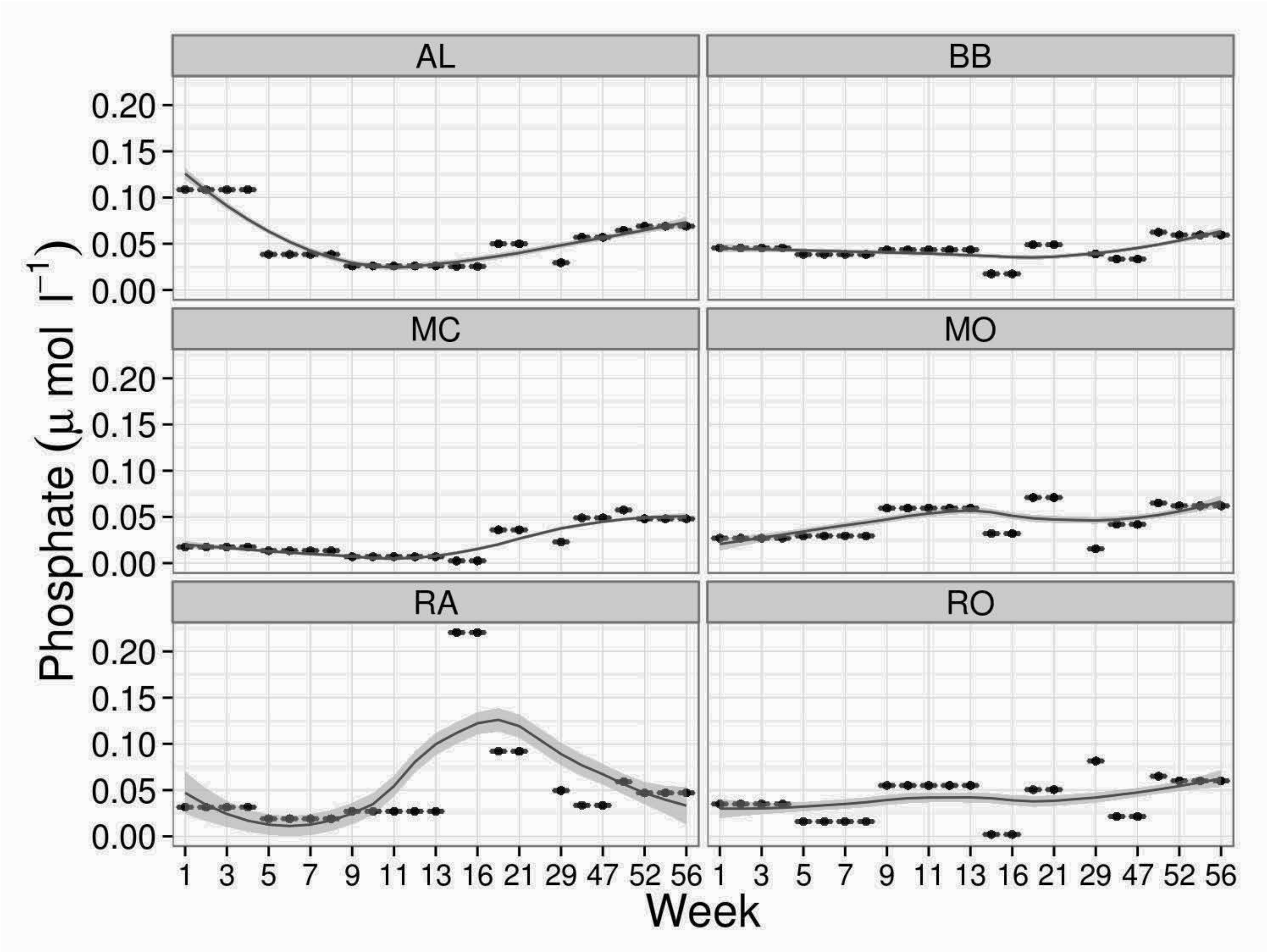


Figure 9. Temporal variability of phosphate (µmol l^{-1}) from the beginning of July 2010 to the end of July 2011. Data are presented as whisker-boxplots, where the horizontal lines represent the medians, the boxes represent the interquartile ranges and the whiskers show the range of observations (when visible). A loess smoothing line was added to help visualize temporal patterns. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava 'AL', Molins 'MO', Blay beach 'BB', Rasset 'RA', Marineta Cassiana 'MC' and Les Rotes 'RO').

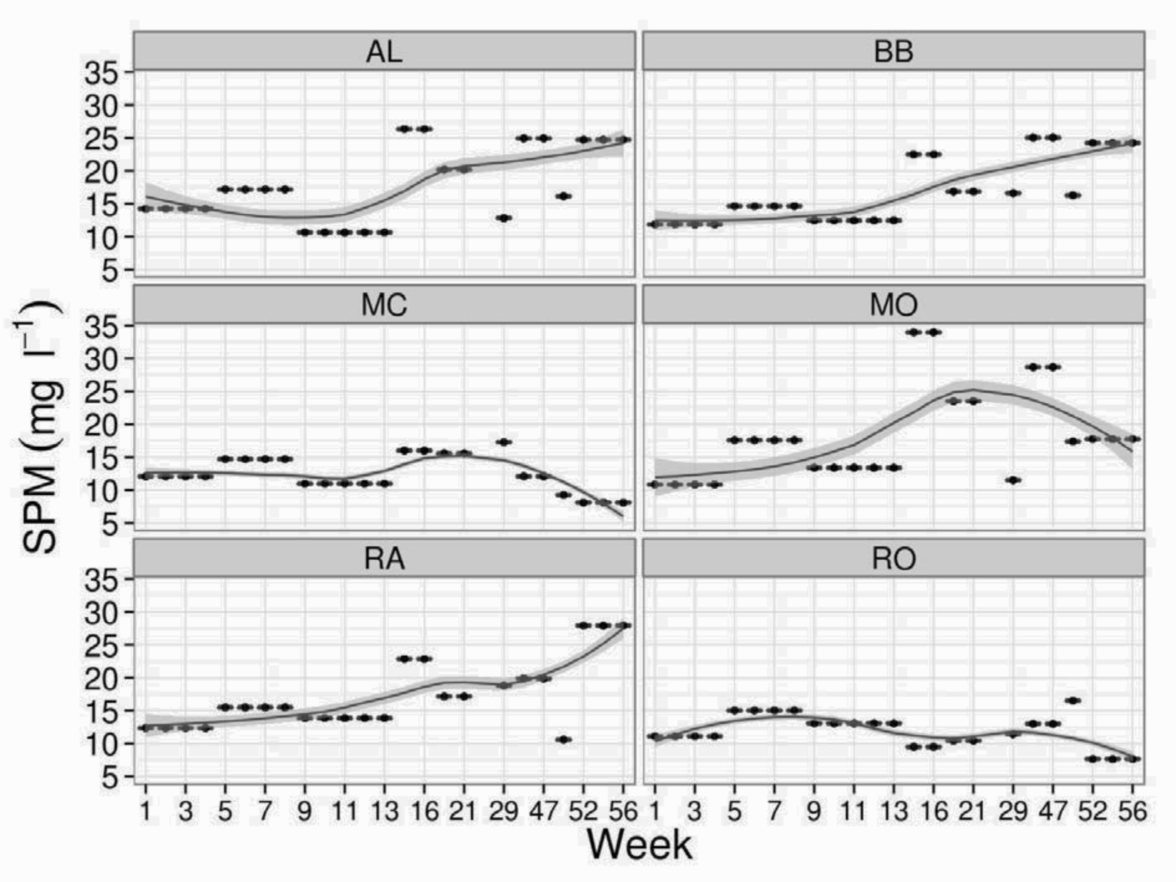


Figure 10. Temporal variability of suspended particulate matter (SPM in µg l^{-1}) from the beginning of July 2010 to the end of July 2011. Data are presented as a whisker-boxplot, where the horizontal line represents the median, the boxes represent the interquartile range and the whiskers represent the range of observations (when visible). A loess smoothing line was added to help visualize temporal patterns. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’).

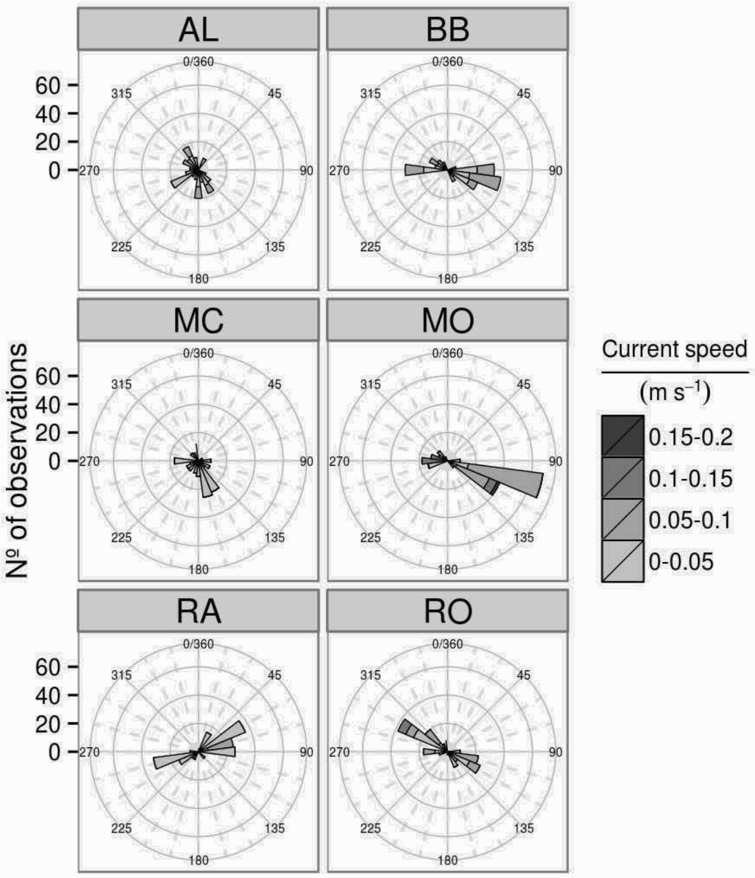


Figure 11. Current direction (degrees) and current speed (four categories, m s^{-1}) from the beginning of July 2010 to the end of July 2011. Number of observations represents the amount of current records, in some particular angle and velocity combination. Different panels refer to sampling sites along the coast of Denia, Spain (Almadrava ‘AL’, Molins ‘MO’, Blay beach ‘BB’, Rasset ‘RA’, Marineta Cassiana ‘MC’ and Les Rotes ‘RO’).

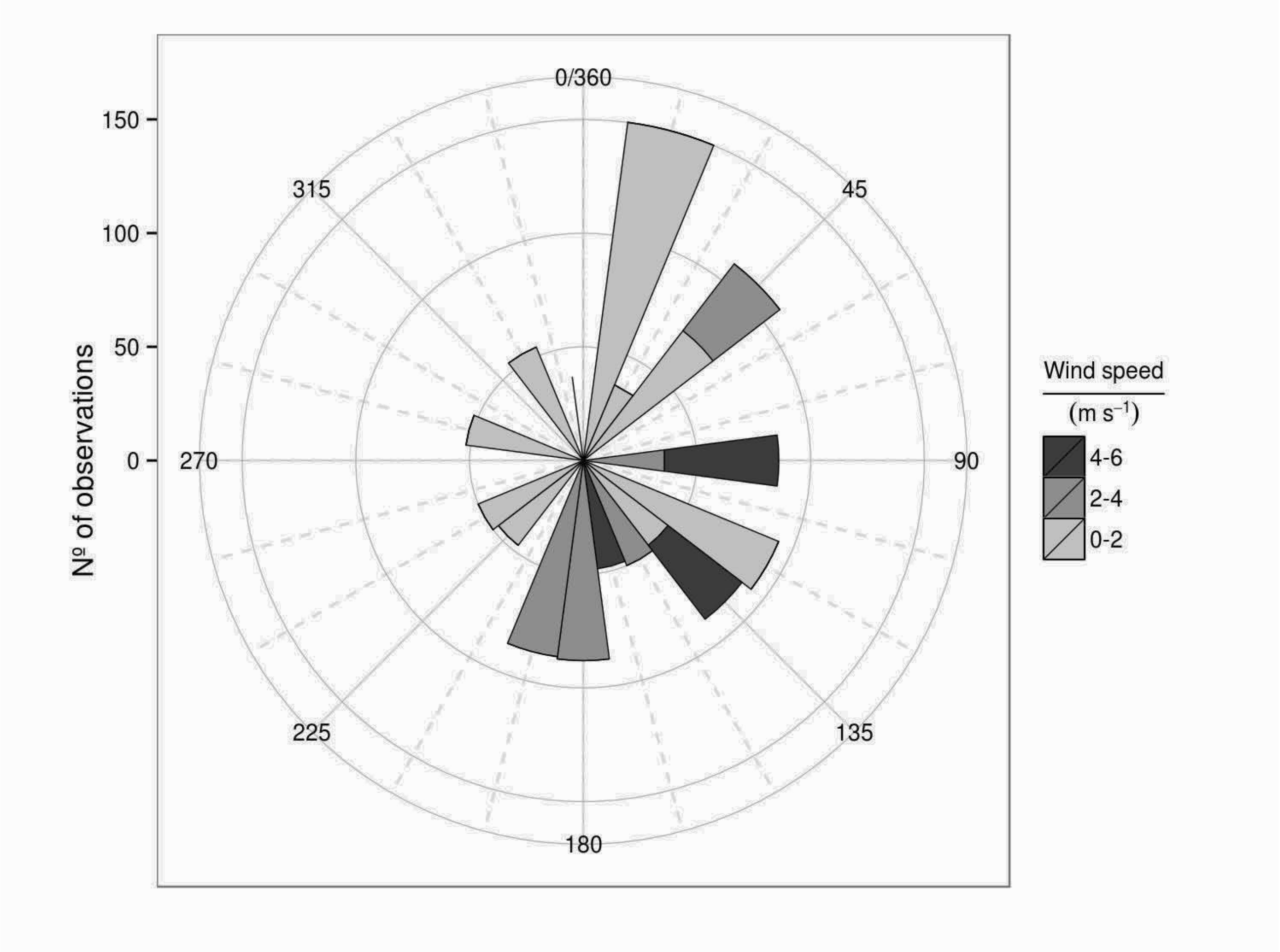


Figure 12. Wind direction (degrees) and wind speed (three categories, m s^{-1}) from the beginning of July 2010 to the end of July 2011 at sites along the coast of Denia, Spain. The lengths of the bars represent the numbers of wind recorded by direction and velocity combination.

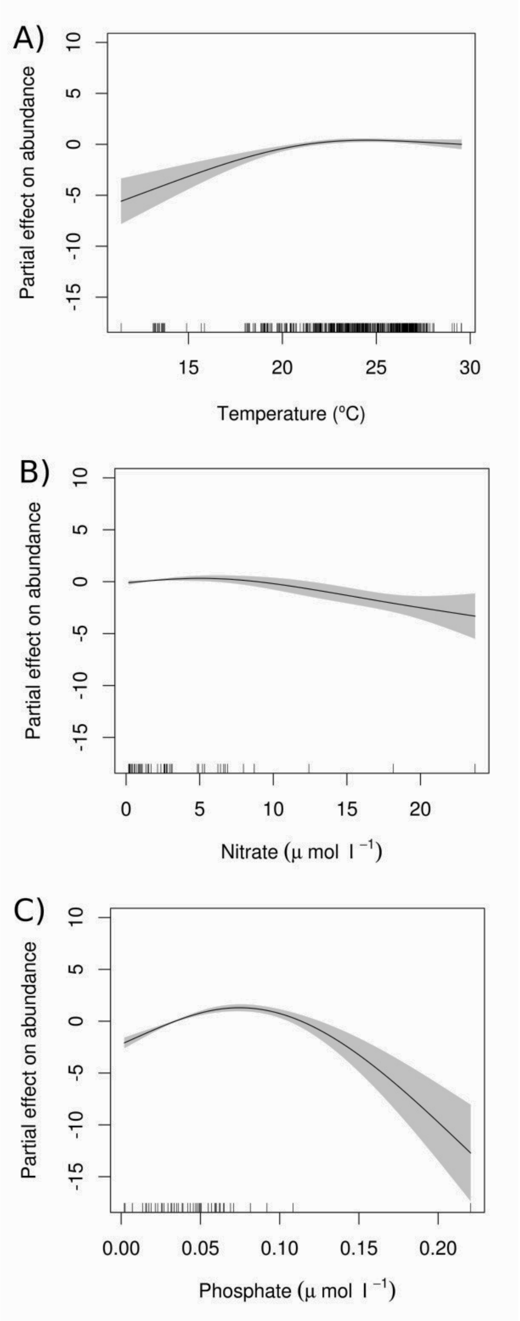


Figure 13. Partial effects of A) temperature, B) nitrate and C) phosphate on the abundance of small *Carybdea marsupialis* medusae. Central (bold) lines show the best fits and the shaded areas show the confidence intervals of the GAM-NB model. Bottom vertical lines represent observations

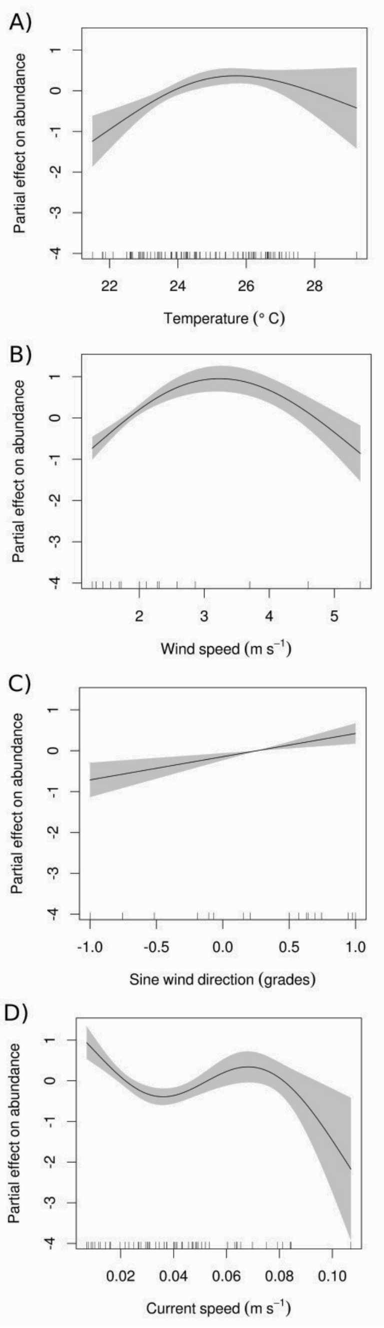


Figure 14. Partial effects of A) temperature, B) wind speed, C) wind direction (sine) and D) current speed on the abundance of medium size *Carybdea marsupialis* medusae. Central (bold) lines show the best fits and the shaded areas show the confidence intervals of the GAM-NB model. Bottom vertical lines represent observations

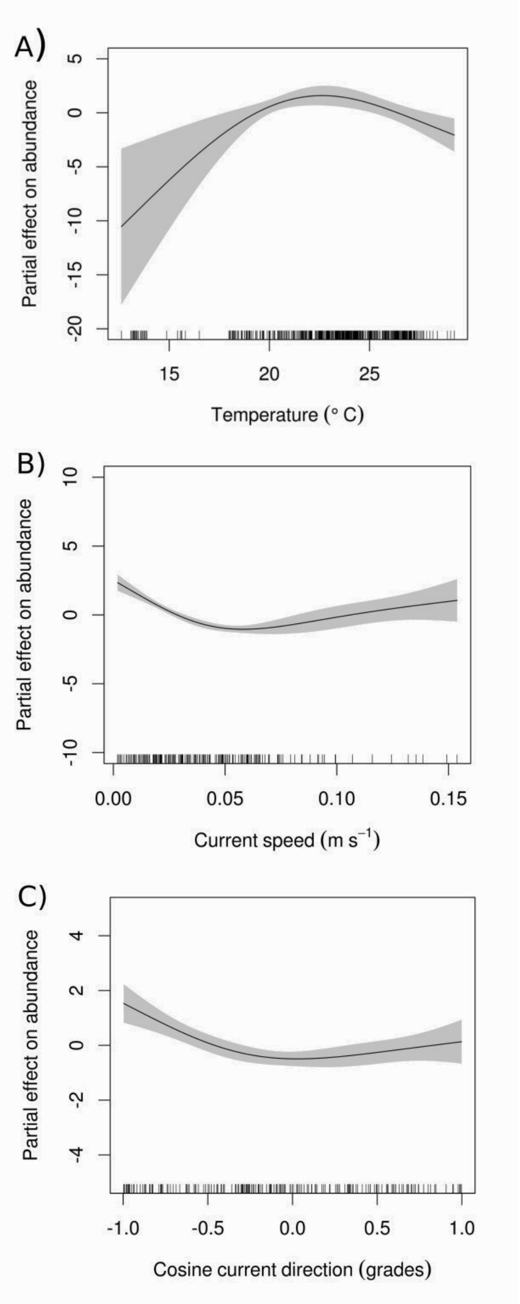


Figure 15. Partial effects of A) temperature, B) current speed and C) current direction (cosine) on the abundance of large *Carybdea marsupialis* medusae. Central (bold) lines show the best fit and the shaded areas show the confidence intervals of the GAM-NB model. Bottom vertical lines represent observations

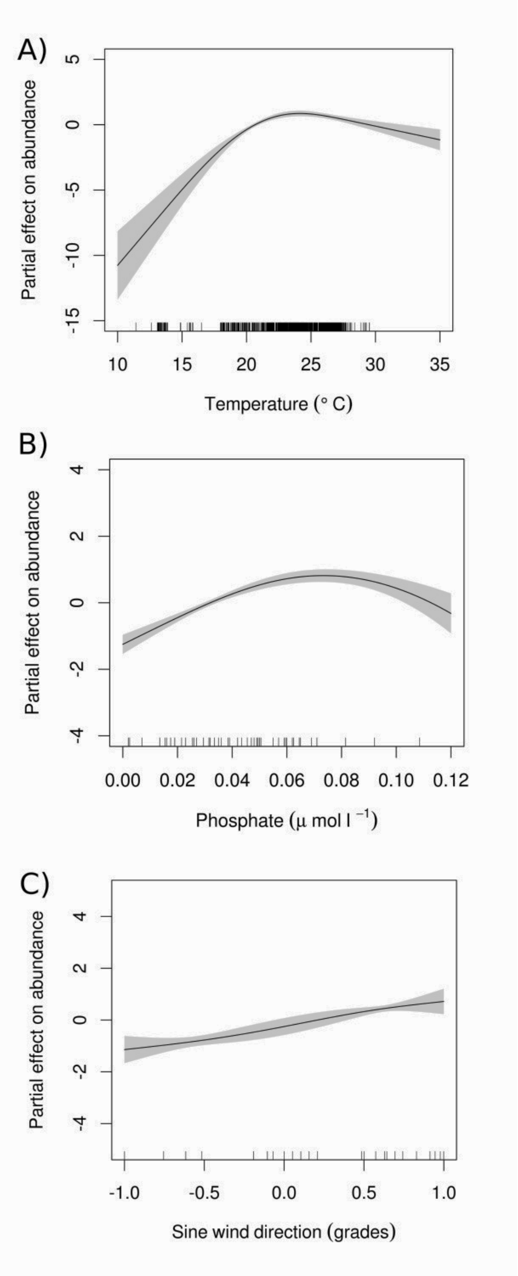


Figure 16. Partial effects of A) temperature, B) phosphate and C) wind direction (sine) on the abundance of total *Carybdea marsupialis* medusae. Central (bold) lines show the best fit and the shaded areas show the confidence intervals of the GAM-NB model. Bottom vertical lines represent observations

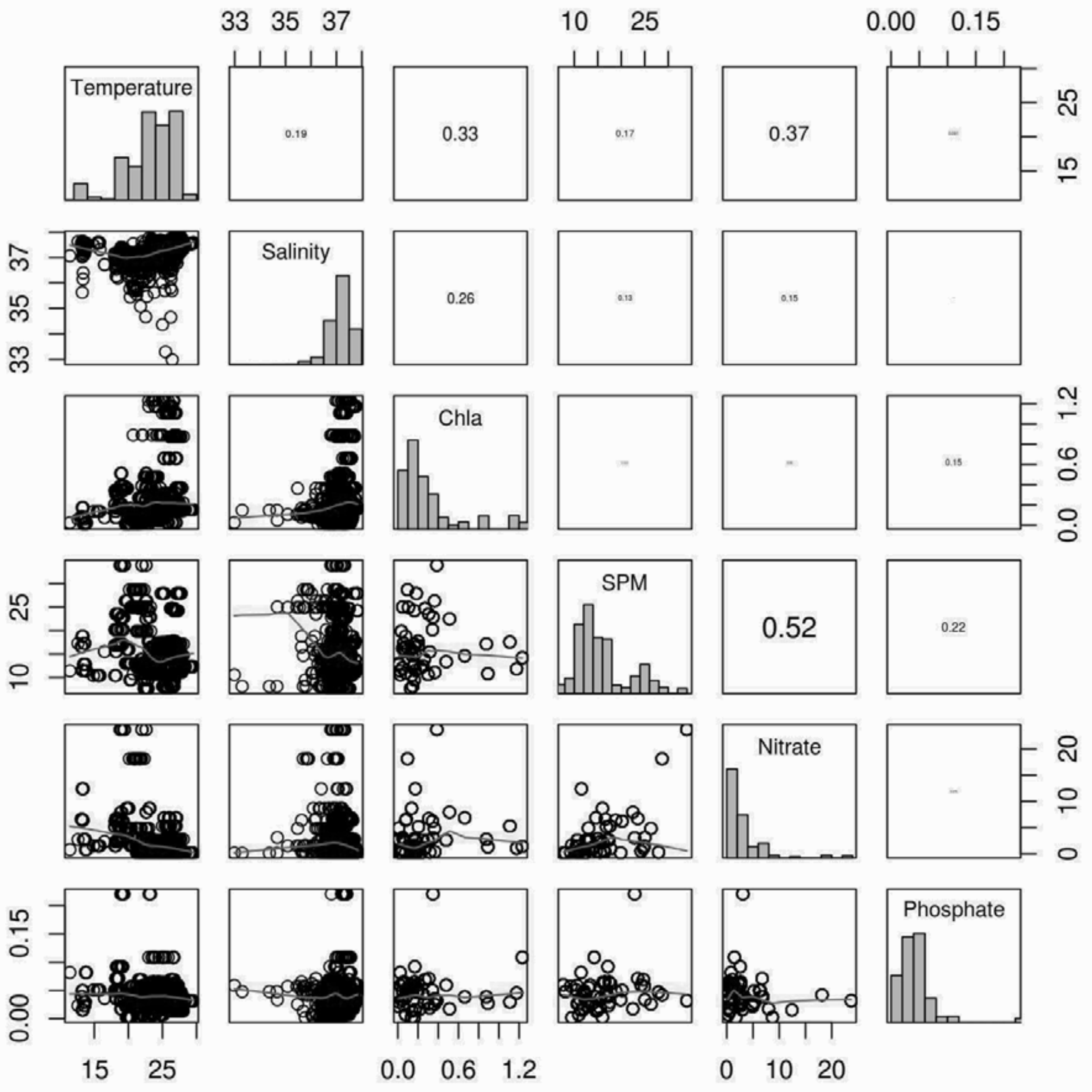


Figure S1. Collinearity analysis for all environmental variables. Lower-left panels show scatter plots with a loess smoothing line (in red) to help visualize patterns. Central (Diagonal) panels show histograms of the environmental variables and upper-right panels show the values of the Pearson's correlation coefficients for each pair of variables, with text size proportional to its value.

Pelagia noctiluca in the Mediterranean Sea

luardo OBIS

Kylie A. Pitt · Cathy H. Lucas
Editors

Jellyfish Blooms

Kylie A. Pitt • Cathy H. Lucas
Editors

Jellyfish Blooms

Springer

Editors
Kylie A. Pitt
Australian Rivers Institute and Griffith School of Environment
Griffith University
Griffith, QLD, Australia

Cathy H. Lucas
National Oceanography Centre Southampton
University of Southampton
Southampton, UK

ISBN 978-94-007-7014-0 ISBN 978-94-007-7015-7 (eBook)
DOI 10.1007/978-94-007-7015-7
Springer Dordrecht Heidelberg New York London

Library of Congress Control Number: 2013952984

© Springer Science+Business Media Dordrecht 2014
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed. Exempted from this legal reservation are brief excerpts in connection with reviews or scholarly analysis or material supplied specifically for the purpose of being entered and executed on a computer system, for exclusive use by the purchaser of the work. Duplication of this publication or parts thereof is permitted only under the provisions of the Copyright Law of the Publisher's location, in its current version, and permission for use must always be obtained from Springer. Permissions for use may be obtained through RightsLink at the Copyright Clearance Center. Violations are liable to prosecution under the respective Copyright Law.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
While the advice and information in this book are believed to be true and accurate at the date of publication, neither the authors nor the editors nor the publisher can accept any legal responsibility for any errors or omissions that may be made. The publisher makes no warranty, express or implied, with respect to the material contained herein.

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Acknowledgements

The idea for this book was conceived at the 2011 ASLO meeting in Puerto Rico when Martine van Bezooijen, a handling editor from Springer, approached us with the idea of producing a book about jellyfish blooms. Her idea followed from the great success of the four special volumes of Hydrobiologia resulting from the first three International Jellyfish Blooms symposia held in Alabama, USA (2000), Gold Coast, Australia (2007), and Mar del Plata, Argentina (2010) and the ASLO 2009 meeting in Nice. Martine was heavily involved in the production of several of these special volumes and was very keen to see a new book on the subject. A successful proposal was submitted to Springer and work on the book started in May 2011. Tragically, Martine passed away unexpectedly in early 2012 as a result of an accident. She was always very supportive of the jellyfish community and was regularly seen at the Springer stand at ASLO meetings. We would like to acknowledge her support and encouragement, as well as that of Judith Terpos who took over as handling editor of the book in mid-2012.

We would like to thank all the contributing authors for their commitment in producing excellent chapters. Without you, we would not have a book! We would also like to thank the many anonymous reviewers for their time and for providing invaluable comments that have enhanced the quality of the chapters.

Many of us have just returned from the 4th International Jellyfish Blooms Symposium held in Hiroshima, Japan, which was attended by 120 delegates from 28 countries. This represents a significant increase from the 60 or so delegates who attended the first two symposia. It was heartening to see so many Ph.D. students and early career researchers studying the science of jellyfish blooms. Recognition of both the scientific and socioeconomic importance of jellyfish blooms is clearly growing.

Finally, we would both like to acknowledge the support and encouragement provided by our families as we oversaw the production of the book.

Kylie A. Pitt
Cathy H. Lucas

Contents

Part I Ecology of Jellyfish Blooms

Part II Case Studies

Contributors

E. Marcelo Acha Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), e IIMyC (CONICET-Universidad Nacional de Mar del Plata), Mar del Plata, Argentina

Keith M. Bayha Dauphin Island Sea Lab, Dauphin Island, AL, USA

Department of Coastal Sciences, University of Southern Mississippi, Ocean Springs, MS, USA

Ferdinando Boero Università del Salento, CoNISMa, CNR-ISMAR, via Monteroni, Lecce, Italy

Richard D. Brodeur NOAA Fisheries, Northwest Fisheries Science Center, Newport, OR, USA

Joanna G. Browne Australian Rivers Institute and Griffith School of Environment, Griffith University, Gold Coast, QLD, Australia

Ariella Chelsky Budarf Australian Rivers Institute and Griffith School of Environment, Griffith University, Gold Coast, QLD, Australia

Antonio Canepa Institut de Ciencies del Mar, Consejo Superior de Investigaciones Científicas, ICM-CSIC, Barcelona, Spain

Kristin Cieciel NOAA Fisheries, Auke Bay Laboratories, Alaska Fisheries Science Center, Juneau, AK, USA

Robert H. Condon Dauphin Island Sea Lab, Dauphin Island, AL, USA

Department of Marine Science, University of South Alabama, Mobile, AL, USA

Kenneth O. Coyle Institute of Marine Science, University of Alaska, Fairbanks, AK, USA

Michael N. Dawson School of Natural Sciences, University of California, Merced, CA, USA

Mary Beth Decker Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA

Zhijun Dong Key Laboratory of Coastal Zone Environmental Processes and Ecological Remediation, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai, People's Republic of China

Thomas K. Doyle Coastal and Marine Research Centre, ERI, University College Cork, Cork, Republic of Ireland

Carlos M. Duarte The UWA Oceans Institute, The University of Western Australia, Crawley, WA, Australia

Department of Global Change Research, Instituto Mediterráneo de Estudios Avanzados, IMEDEA (UIB-CSIC), Esporles, Spain

Faculty of Marine Sciences, King Abdulaziz University, Jeddah, Saudi Arabia

Verónica Fuentes Institut de Ciencies del Mar, Consejo Superior de Investigaciones Científicas, ICM-CSIC, Barcelona, Spain

Stefan Gelcich Laboratorio Internacional en Cabio Global (CSIC-PUC) and Centro de Conservacion Marina, Departamento de Ecologia, Pontificia Universidad Católica de Chile, Cassilla, Chile

Josep-María Gili Institut de Ciencies del Mar, Consejo Superior de Investigaciones Científicas, ICM-CSIC, Barcelona, Spain

William M. Graham University of Southern Mississippi, Stennis Space Center, MS, USA

Graeme C. Hays Department of Biosciences, Swansea University, Swansea, UK

Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Warrnambool, VIC, Australia

Chris Harrod Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta, Antofagasta, Chile

School of Biological and Chemical Sciences, Queen Mary University of London, London, Uk

Jonathan D.R. Houghton School of Biological Sciences, Queen's University Belfast, Belfast, UK

John K. Keesing CSIRO Wealth from Oceans National Research Flagship, Marine and Atmospheric Research, Wembley, WA, Australia

Michael J. Kingsford ARC Centre of Excellence for Coral Reef Studies and the School of Marine and Tropical Biology, James Cook University, Townsville, QLD, Australia

Robert Lauth NOAA Fisheries, Alaska Fisheries Science Center, Seattle, WA, USA

Dongyan Liu Key Laboratory of Coastal Zone Environmental Processes and Ecological Remediation, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai, People's Republic of China

Cathy H. Lucas National Oceanography Centre Southampton, University of Southampton, Southampton, UK

Hermes Mianzan Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), e IIMyC (CONICET-Universidad Nacional de Mar del Plata), Mar del Plata, Argentina

Christopher J. Mooney ARC Centre of Excellence for Coral Reef Studies and the School of Marine and Tropical Biology, James Cook University, Townsville, QLD, Australia

Sergio Palma Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile

Stefano Piraino Università del Salento, CoNISMa, via Monteroni, Lecce, Italy

Kylie A. Pitt Australian Rivers Institute and Griffith School of Environment, Griffith University, Gold Coast, QLD, Australia

Javier Quiñones Laboratorio Costero de Pisco, Instituto del Mar del Perú (IMARPE), Ica, Peru

Kelly L. Robinson University of Southern Mississippi, Stennis Space Center, MS, USA

Ana Sabatès Institut de Ciencies del Mar, Consejo Superior de Investigaciones Científicas, ICM-CSIC, Barcelona, Spain

Agustin Schiariti Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), e IIMyC (CONICET-Universidad Nacional de Mar del Plata), Mar del Plata, Argentina

Shin-Ichi Uye Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan

Alexander Zavolokin Laboratory of Applied Biocenology, Pacific Research Fisheries Center (TINRO-Center), Vladivostok, Russia

Chapter 11
Pelagia noctiluca in the Mediterranean Sea

Antonio Canepa, Verónica Fuentes, Ana Sabatés, Stefano Piraino, Ferdinando Boero, and Josep-María Gili

Abstract Over recent decades, man's expanding influence on the oceans has begun to cause change in some regions, including in the Mediterranean Sea. New proliferations of jellyfish may be occurring in the Mediterranean Sea, possibly in response to the cumulative effects of some of these anthropogenic impacts. In the Mediterranean Sea, many of these "proliferation events" are due to *Pelagia noctiluca*, an oceanic scyphozoan that has become very abundant along the coasts. *Pelagia noctiluca* is usually considered to be the most important jellyfish species in the Mediterranean Sea due to its widespread distribution, abundance, and ecological role and also because of its negative interaction with humans. Climatic conditions that favor enhanced reproduction by *P. noctiluca* and probably also determine optimal conditions for the formation of blooms are characterized by mild winters, low rainfall, high temperature, and high-atmospheric pressure. The Medusa Project in Catalonia aims to understand the spatiotemporal dynamics of the jellyfish populations in the NW Mediterranean Sea by undertaking daily sampling during summer (May to September) of 243 beaches, covering more than 500 km of coast. Data on beach strandings along the Spanish Catalan coast revealed that jellyfish occur in greatest concentrations along the northern Catalan coast and on beaches located close to marine canyons. The arrival of *P. noctiluca* to the coast depends firstly on the offshore production of jellyfish. Oceanographic structures like fronts, which

---

A. Canepa (✉) • V. Fuentes • A. Sabatés • J.-M. Gili
Institut de Ciencies del Mar, Consejo Superior de Investigaciones Científicas,
ICM-CSIC, Passeig Marítim de la Barceloneta, 37-49, Barcelona 08003, Spain
e-mail: canepa@icm.csic.es; vfuentes@icm.csic.es; anas@icm.csic.es; gili@icm.csic.es

S. Piraino
Università del Salento, CoNISMa, via Monteroni, Lecce, LE 73100, Italy
e-mail: stefano.piraino@unisalento.it

F. Boero
Università del Salento, CoNISMa, CNR-ISMAR, via Monteroni, Lecce, LE 73100, Italy
e-mail: boero@unisalento.it

K.A. Pitt and C.H. Lucas (eds.), *Jellyfish Blooms*, DOI 10.1007/978-94-007-7015-7_11,
© Springer Science+Business Media Dordrecht 2014

enhance and maintain high levels of biological production and provide ideal conditions for feeding, growth, and reproduction of the jellyfish are present in the NW Mediterranean. The weakening of the front results in large numbers of *P. noctiluca* being driven into the coast by southeast winds. In the NW Mediterranean Sea *P. noctiluca* exert top-down control over a variety of prey including fish eggs and possibly the invasive ctenophore *Mnemiopsis leidyi*. *P. noctiluca* is also responsible for the majority of the stings incurred by bathers along the Catalan coast. Finally, we recommend that similar sampling programs should be done elsewhere to better understand changes in the distribution, abundance, and blooming patterns of dangerous jellyfish species.

Keywords Jellyfish blooms • *Pelagia noctiluca* • NW Mediterranean Sea • Catalan coast • Tourism • Long-term monitoring • Oceanography • Climate variability • Physicochemical variables • Socioeconomic impacts • Jellyfish-fish interactions

11.1 Introduction

Jellyfish are a common component of Mediterranean marine communities (Boero et al. 2008). Their spatiotemporal dynamics are highly variable, and blooms occur irregularly and are difficult to predict (Boero et al. 2008; Brotz and Pauly 2012). In Mediterranean waters, approximately 12 species of scyphomedusae form dense blooms (Axiak et al. 1991; Gili and Pagès 2005). While a possible long-term increase of jellyfish in Mediterranean waters has been noticed in recent years (Brotz et al. 2012; Condon et al. 2012), this general increase seems to be evident for only some jellyfish species (Brotz et al. 2012; Condon et al. 2013), reflecting the large variability of jellyfish dynamics (Brotz and Pauly 2012). Recently, Brotz et al. (2012) used a combination of quantitative and anecdotal data to analyze trends in gelatinous zooplankton (Cnidaria, Ctenophora, and pelagic tunicates) in 66 large marine ecosystems (LMEs). They discovered that the abundances of jellyfish and the frequency of blooms in the Mediterranean LME had increased. This general increase was subsequently corroborated for the Mediterranean Sea by Condon et al. (2013) using only quantitative data.

11.1.1 Ecology of Pelagia noctiluca

The most common and conspicuous jellyfish species in Mediterranean waters is the mauve stinger, *Pelagia noctiluca* (Forsskål 1775). This scyphozoan is a holoplanktonic species (i.e., it lacks a benthic phase in its life history) (Fig. 11.1). This characteristic allows *P. noctiluca* populations to inhabit oceanic as well as coastal ecosystems and may explain its biogeography. *P. noctiluca* is widely distributed from the warm subtropical waters of the Gulf of Mexico and the

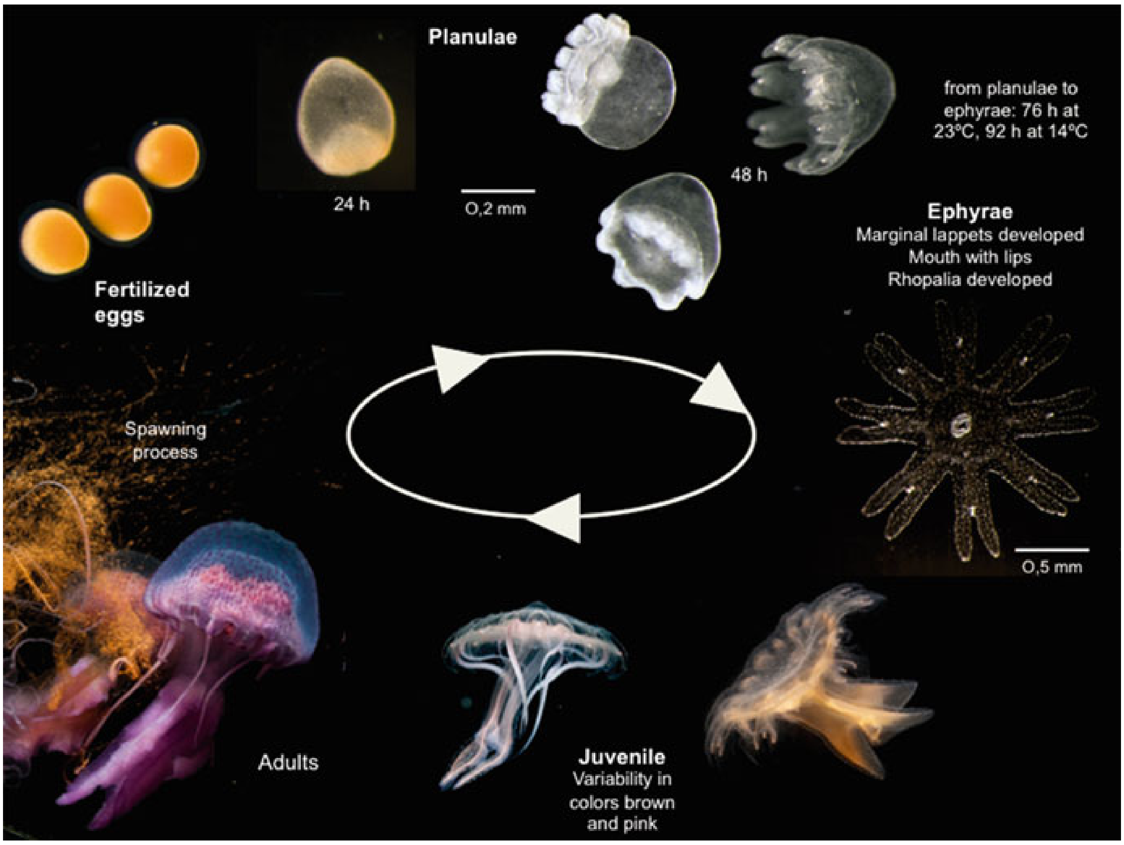


Fig. 11.1 Holoplanktonic life cycle of *Pelagia noctiluca* photographed at the ZAE (Experimental Aquaria Zone at ICM-CSIC in Barcelona) with indications on the sizes and times of developments (Photos Eduardo Obis Alberola)

Mediterranean Sea to the temperate waters of the North Sea (Russell 1970; Graham et al. 2003; Purcell 2005; Licandro et al. 2010) and up to 4° of latitude (Doyle et al. 2008; Bastian et al. 2011).

In pelagic ecosystems *P. noctiluca* has been recorded at a maximum depth of 1,400 m (Franqueville 1971, cited in Mariottini et al. 2008), but it is especially abundant on shelf slopes where concentrations of plankton occur (Sabatés et al. 1989). There, *P. noctiluca* occurs near the surface between 10 and 30 m with the maximum occurrence at 12 m, coinciding with the upper halocline/pycnocline and the layer of maximum current shear, especially at night (Graham et al. 2003; Mariottini et al. 2008). This vertical distribution pattern coincides with the nocturnal migration of zooplankton, their main prey (Malej 1989; Sandrini and Avian 1989; Sabatés et al. 2010).

Pelagia noctiluca is an important nonselective planktonic predator (Larson 1987; Morand et al. 1987; Sandrini and Avian 1989; Giorgi et al. 1991; Daly Yahia et al. 2010; Rosa et al. 2013), feeding on almost all types of zooplankton and ichthyoplankton (Giorgi et al. 1991; Zavodnik 1991; Malej et al. 1993; Sabatés et al. 2010), and may exert top-down control on marine food webs. Gut contents of *P. noctiluca* have shown a great variety of items consumed; Cladocera, Appendicularia, Copepoda, Hydromedusae, Siphonophora, and fish eggs were the most common

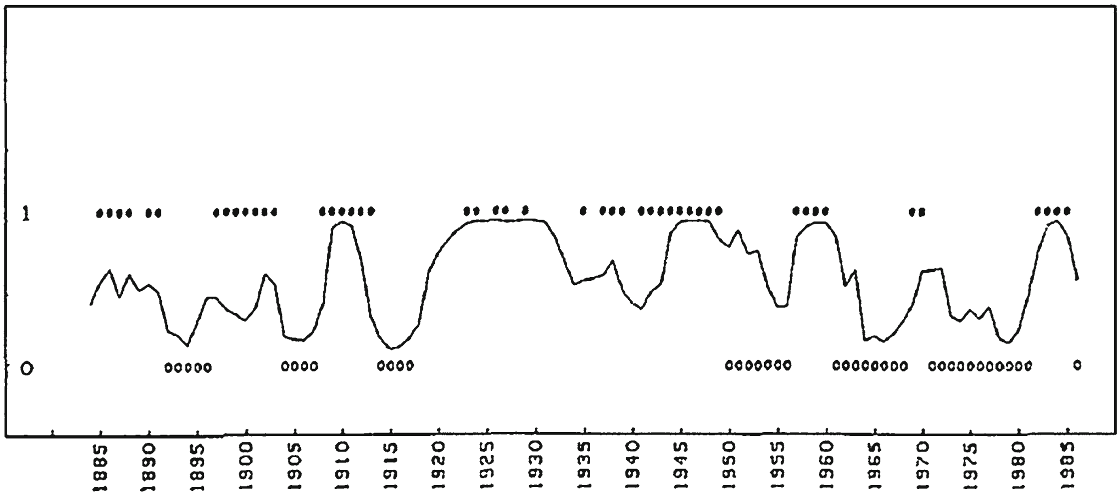


Fig. 11.2 Periodicity of *Pelagia noctiluca* blooms. *Open circles*: years without *P. noctiluca*. *Closed circles*: years with *P. noctiluca*. *Solid line*: probability of *P. noctiluca* blooms (After Goy et al. 1989)

food items of adults (Malej 1989). From analysis of gastric pouches of *P. noctiluca* ephyrae in the NW Mediterranean Sea, Sabatés et al. (2010) found positive selection for chaetognaths and larvae of mollusks during both day and night and for fish larvae during the night only. Recently, feeding experiments have revealed the potential of *P. noctiluca* to act as a control of the invasive ctenophore *Mnemiopsis leidyi* (Tilves et al. 2012).

11.1.2 History of Blooms of Pelagia noctiluca *in the Mediterranean Sea*

Intense interest in the dynamics of *Pelagia noctiluca* blooms started in the early 1980s when a massive occurrence of *P. noctiluca* affected the eastern Mediterranean Sea, the Adriatic Sea, and subsequently the western Mediterranean Sea (Malej and Malej 2004; Mariottini et al. 2008). The United Nations Environmental Program (UNEP), through the Mediterranean Action Plan (MAP), launched a project to fund scientific research on jellyfish in the Mediterranean Sea. Research activities culminated in two workshops in 1983 and 1987 (UNEP 1984, 1991). In those and other publications, all available information on *P. noctiluca* blooms in the Mediterranean was assembled.

Trends in jellyfish populations (including *P. noctiluca*) in the Mediterranean have been recently reviewed (e.g., Brotz and Pauly 2012; Condon et al. 2013). The periodic occurrence of *P. noctiluca* in the western Mediterranean was first reported by Goy et al. (1989) who used archival data from the Station Zoologique at Villefranche-sur-Mer and various other sources to reconstruct a time series of the occurrence of *P. noctiluca* dating back to 1775. Blooms of *P. noctiluca* occurred 55 times between 1775 and 1987, with a periodicity of about 12 years (Fig. 11.2), and were related to climatic fluctuations. Analyses of more recent data from the Gulf of Tunis, the Balearic Islands (Daly Yahia et al. 2010), and Ligurian Sea (Bernard et al. 2011), however, indicate that blooms may now be occurring more frequently in the western Mediterranean Sea. The recent potential change in the periodicity of blooms of *P. noctiluca* in the western Mediterranean, however, does not appear to be occurring in the eastern Mediterranean. Kogovšek et al. (2010) reconstructed a 200-year time series of the occurrence of *P. noctiluca* in the northern Adriatic Sea and identified three periods when *P. noctiluca* formed conspicuous blooms, around 1915, during the late 1970s and early 1980s, and from 2004 to 2007, but there was no evidence of a recent change in the periodicity of blooms although other species in the region do appear to have increased. Furthermore, there is limited evidence for a general increase in the periodicity of blooms of *P. noctiluca* in the southern Adriatic or Aegean seas (Daly Yahia et al. 2010).

11.2 Climatic, Oceanographic, and Biological Drivers of Jellyfish Blooms in the Mediterranean Sea

Possible relationships between environmental factors and blooms of *Pelagia noctiluca* have been studied since the establishment of the framework of the Long-Term Programme for Pollution Monitoring and Research in the Mediterranean Sea (MED POL – PHASE II) (UNEP 1984). Nevertheless, few clear associations have been determined, and final conclusions about the environmental variables controlling the distribution of this species are still under study (Kogovšek et al. 2010; Ferraris et al. 2012; Rosa et al. 2013).

The complex occurrence patterns of *P. noctiluca* associated with a lack of precise data on occurrence of blooms and the associated environmental variables make the prediction of *P. noctiluca* blooms difficult (UNEP 1984). We propose that factors that correlate with the occurrence of *P. noctiluca* be classified into the following four different types: physical, physicochemical, biological, and climatic forcing (Table 11.1).

11.2.1 Climatic Forcing

Long-term climate fluctuations have been correlated with jellyfish abundance in Mediterranean waters (Table 11.1). Molinero et al. (2005, 2008) using the most important modes of atmospheric circulation over the Northern Hemisphere (i.e., Northern Annular Mode [AO/NAO], East Atlantic pattern [EA], Gulf Stream/Northern Current Index, East Atlantic Western Russian pattern, and the Northern Hemisphere temperature [NHT]) established the first principal component (accounting for 47 % of the total variance) as a proxy of the Atlantic climate variability. This North Atlantic climate variability is significantly related to long-term changes in zooplankton functional groups, including *Pelagia noctiluca*, in the NW Mediterranean (Molinero et al. 2008). Daly Yahia et al. (2010) showed that abundances of *P. noctiluca* in 2004, 2005, and 2007 were positively associated with variations of the Northern Hemisphere

Table 11.1 Literature review on proposed forcings that explain jellyfish blooms in the Mediterranean Sea

Forcing	Environmental variable	Effect on	Relationship	Location	References
Climatic	Northern hemisphere temperature (NHT)	Abundance	Positive	Mediterranean Sea	Daly Yahia et al. (2010)
		Reproduction	Positive	SW Mediterranean Sea	Gislaso and Gorsky (2010)
	Atmospheric average annual temperature (AAT)	Abundance	Negative	Mediterranean Sea	Daly Yahia et al. (2010)
	Regional atmospheric index (RAI)	Abundance	Negative	Mediterranean Sea	Daly Yahia et al. (2010)
		Reproduction	Negative	SW Mediterranean Sea	Gislaso and Gorsky (2010)
	Rainfall	Co-occurrence	Negative	Mediterranean Sea	Goy et al. (1989)
	North Atlantic Oscillation (NAO)	Abundance	Neutral	Mediterranean Sea	Daly Yahia et al. (2010)
	North Atlantic climate variability	Abundance	Positive	Western Mediterranean Sea	Molinero et al. (2005, 2008)
Physical	Current direction	Accumulation and transport	Positive	Northern Adriatic Sea	Maretić (1984), Zavodnik (1987), Benović (1991), Legović and Benović (1984), Malej and Malej (2004), Kogovšek et al. (2010)
	Wind direction	Accumulation and transport	Positive	Adriatic and Maltese waters	Maretić (1984), Zavodnik (1987), Zavodnik (1991), Axiak et al. (1991), Legović (1991), Malačič et al. 2007
	Water masses	Transport	Positive	Mediterranean Sea	Vučetić (1984)
	Tidal	Accumulation	Positive	Adriatic Sea	Zavodnik (1987)
	Front structure	Accumulation	Positive	NW Mediterranean Sea	Sabatés et al. (2010)

Physicochemical	Dissolved oxygen	Co-occurrence	Negative	Northern Adriatic Sea	Vučetić (1991)
	Light intensity	Activity (pulsation rate)	Negative	Malta (experimental)	Axiak (1984)
	SST	Activity	Negative	Experimental	Malej and Malej (2004), Rosa et al. (2013)
		Co-occurrence	Positive	Strait of Messina (Italy)	Rosa et al. (2013)
		Growth	Negative	Experimental	Rosa et al. (2013)
		Transport	Negative	Adriatic Sea	Benović (1991)
		Co-occurrence	Positive	Mediterranean Sea	Goy et al. (1989), Vučetić (1991)
		Activity (pulsation rate)	Positive	Northern Adriatic Sea	Avian et al. (1991)
		Reproduction	Positive	Adriatic Sea	Legović (1991)
		Survival	Positive	Northern Adriatic Sea	Vučetić (1984)
	Salinity	Co-occurrence	Positive	Northern Adriatic Sea	Vučetić (1991)
		Reproduction	Positive	Mediterranean Sea	Vučetić (1984)
	Eutrophication	Survival	Positive	Northern Adriatic Sea	Legović (1987), Malej and Malej (2004)
	Nutrient load	Survival	Positive	Adriatic Sea	Legović (1991)
	Toxicants	Reproduction	Positive	Mediterranean Sea	Vučetić (1984)
Biological	Competition	Survival	Negative	Adriatic Sea	Legović (1991)
	Productivity (Chla)	Growth	Positive	Northern Adriatic Sea	Kogovšek et al. (2010)
		Reproduction	Positive	Northern Adriatic Sea	Kogovšek et al. (2010)
	Zooplankton (biomass)	Co-occurrence	Positive	Northern Adriatic Sea	Kogovšek et al. (2010)

temperature (NHT) and, conversely, abundances were negatively correlated with the Regional Atmospheric Index (RAI) and the atmospheric Average Annual Temperature (AAT); however, the North Atlantic Oscillation (NAO) index was not significantly related to abundances. These climatic conditions correspond to mild winters, low rainfall, high temperature, and high-atmospheric pressure, which seem to favor *P. noctiluca* reproduction and probably determine optimal conditions for the formation of *P. noctiluca* blooms and their maintenance for several months and even years (Daly Yahia et al. 2010; Rosa et al. 2013). Thus, *P. noctiluca* may be an indicator of climate variability in the Mediterranean Sea.

11.2.2 Physical Forcing

Physical forcing (wind and current direction and velocity, and also tidal effects) was thought to determine the presence of *Pelagia noctiluca* in inshore and offshore waters in the northern Adriatic Sea (Vučetić 1984). Physical forcing has also been responsible for coastal or inshore aggregations in the Adriatic Sea (Maretić 1984; Benović 1991; Legović 1991; Zavodnik 1991; Malej and Malej 2004) and in Maltese waters (Axiak et al. 1991). In these cases in shallow coastal waters wind, currents and tides have been the main drivers, allowing for big (sometime huge) accumulations of medusae (Zavodnik 1987). Some smaller-scale characteristics may explain certain locations for aggregation, such as in embayments, gulfs, islands, and ports.

The first record of *P. noctiluca* in the northern Adriatic Sea was principally due to advection by a strong southeastern Adriatic current (Malej and Malej 2004). Benović (1991) demonstrated that *P. noctiluca* enters into the Adriatic Sea only during the colder seasons with incoming surface currents from the Ionian Sea. A modeling study showed that the pathways of water parcels through the Adriatic Sea depended on the origin of the particles and suggested that this jellyfish enters the Adriatic Sea at the eastern side of the Otranto Strait (Malačič et al. 2007). This suggested connection between Adriatic and Mediterranean metapopulations and is supported by genetic evidence (Ramšak et al. 2007).

11.2.3 Physicochemical Forcing

Relationships between physicochemical forcing variables and the presence, demography, and behavior of *Pelagia noctiluca* have been assessed using field and experimental data. Sea surface temperature and salinity have a positive relationship with the presence of *P. noctiluca*. Survival of *P. noctiluca* increased with increased nutrient concentrations and eutrophication (Legović 1991; Malej and Malej 2004). Conversely, negative associations of the presence of this scyphozoan with dissolved oxygen have been shown (Vučetić 1991). Experiments reveal that temperature affects the activity (pulsation rate) of this species; specifically extreme temperatures, <11 °C and >26 °C, cause decreased activity (Malej and Malej 2004). Light intensity (lux shone on the jellyfish) also has a negative effect on pulsation rate

(Axiak 1984). This result is consistent with the nocturnal migration behavior of this species, where high abundances of large medusae are found only in deep waters (at least 400–600 m) during the daytime and in surface waters at night (Stiasny 1921; Axiak 1984; Ferraris et al. 2012). Vučetić (1984) also showed that survival of *P. noctiluca* was positively related to sea surface temperature (SST). A SST above the winter average enabled *P. noctiluca* to remain in surface waters and, in association with eutrophication and high-nutrient levels, resulted in more food being available and thus increased survival of the species (Table 11.1). Finally, reproduction was positively correlated with SST, salinity, and coastal toxic agents. Vučetić (1984) hypothesized that sublethal contamination levels of North Adriatic coastal waters had boosted *P. noctiluca* proliferations from 1977 onwards through "hormesis" (i.e., the increase of sexual reproduction as well as the stimulation of jellyfish growth rate by exposure to low concentrations of toxicants), as reported for several hydrozoans and other taxa (Loomis 1957; Braverman 1962, 1963; Muller 1965; Stebbing 1980, 1981; Piraino 1991). Temperatures higher than 10 °C in winter and lower than 27 °C in summer and salinities of 35–38 (reflecting low rainfall) are positively associated with good conditions for *P. noctiluca* occurrence (Goy et al. 1989; Purcell et al. 1999; Purcell 2005; Molinero et al. 2005; Licandro et al. 2010).

11.2.4 Biological Forcing

Although the temporal dynamics of this species seems to be controlled by large-scale factors (Daly Yahia et al. 2010; Kogovšek et al. 2010; Condon et al. 2013) local-scale features promote the retention of *P. noctiluca* medusae for extended periods, thus increasing their local abundance and survival (Legović 1991; Rosa et al. 2013). The local-scale factors relate to high primary production (Chl-*a* levels) increasing the availability of animal prey (zooplankton biomass), individual growth, and reproduction (Kogovšek et al. 2010) and ultimately leading to local *P. noctiluca* blooms. Biological interactions like competition have been suggested (Legović 1991; Brotz and Pauly 2012), but this kind of interaction is difficult to assess.

11.3 Impact of *Pelagia noctiluca* on Human Activities

Pelagia noctiluca is the most important species of scyphozoan in the Mediterranean Sea due to its high abundance, its distribution throughout the Mediterranean Sea, and because of its painful sting (Mariottini et al. 2008). Thus, negative interactions between this species and humans are diverse (Purcell et al. 2007). We classified the impacts of *P. noctiluca* blooms as "direct" or "indirect." Direct impacts have an immediate effect with direct repercussions for humans (and/or human activity); indirect impacts are related to reduction of the profit that humans receive from the activity (Table 11.2). *P. noctiluca* blooms negatively affect five main human activities, here presented in the order of decreasing scientific coverage: tourism, fisheries, aquaculture, energy, and ecosystem functioning.

Table 11.2 Literature review of the impacts of *Pelagia noctiluca* blooms on human activities in the Mediterranean Sea

Human activity	Impact type	Effect	Year	Location	References	Comments
Tourism	Direct	Stinging	1976	Italy	UNEP (1984)	
			1978	Pula, Croatia	Maretić (1984)	±50 % of bathers affected
			1977–1978	Istrian Coast (Yugoslavia)	Malej and Vuković (1984), UNEP (1991), Maretić et al. (1987)	
			1978–1983	Adriatic Sea (Trieste)	Legović (1991)	
			1983	Portoroz (Slovenia)	Malej and Vuković (1984)	
			1991	Yugoslavia	Axiak et al. (1991)	110 (52 %) of bathers affected
			1982	Greece	Axiak et al. (1991)	1,500 affected (2–3 stings per day)
			1981–1983	Athens	Axiak et al. (1991)	240 cases per year (720 total)
				Adriatic Sea	Legović (1991)	
			1984–1987	Monaco	Bernard 1991, Purcell et al. 2007	45,000 people affected
			2007	French Riviera	Purcell et al. (2007)	2,500 people affected
				Spain	Purcell et al. (2007)	More than 14,000 persons affected
			2008	Italy	Mariottini et al. (2008)	
			2010	Adriatic Sea	Nastasi (2010)	Review
			2011	Mediterranean Sea	Bernard et al. (2011)	
Fisheries	Indirect	Predation on fish eggs and larvae	1987	Ligurian Sea	Morand et al. (1987)	
			1991	Adriatic Sea	Legović (1991)	Review
			2001	Mediterranean Sea	CIESM (2001)	Review
			2007	Mediterranean Sea	Purcell et al. (2007)	Review
		Predation on fish larvae	2010	NW Mediterranean Sea	Sabatés et al. (2010)	
		Predation on fish food	1991	Adriatic Sea	Legović (1991)	Review
			2001	Mediterranean Sea	CIESM (2001)	Review
			2004	Adriatic Sea	Malej and Malej (2004)	
			2010	NW Mediterranean	Sabatés et al. (2010)	

	Direct	Stinging	1978	Pula (Croatia)	Maretić (1984)	During 1978
			1977–1980	Istrian Coast (Yugoslavia)	Malej and Vuković (1984)	From 1977 to 1980
			1985	Gulf of Trieste (Adriatic Sea)	Axiak et al. (1991)	700 fishermen in 192 days of fishing
			1987	Mediterranean Sea	Maretić et al. (1987)	
			1991	Adriatic Sea	Legović (1991)	Review
			2001	Mediterranean	CIESM (2001)	Review
			2008	Adriatic Sea	Mariottini et al. (2008)	Review
			2010	Adriatic Sea	Nastasi (2010)	Review
		Net clogging	1977	Istrian Coast (Yugoslavia)	Malej and Vuković (1984)	
			1978	Pula (Croatia)	Maretić (1984)	
			1983	Portoroz (Slovenia)	Malej and Vuković (1984)	
			1983–1984	Adriatic Sea	Legović (1991), Malej and Malej (2004)	Review
			2007	Mediterranean Sea	Purcell et al. (2007)	Review
			2010	Mediterranean	Nastasi (2010)	Review
		Boat engine clogging	1985	Istrian Coast (Yugoslavia)	Malej and Vuković (1984)	From 1977 to 1980
		Bycatch and economic impact	1983	Gulf of Trieste (Adriatic Sea)	Axiak et al. (1991)	Bycatch of 0.5 kgh^{-1} (review)
			2012	Israel Coast	Nakar et al. (2012)	Loss of 8 % “Trawl fish” profit
			2012	Israel Coast	Nakar et al. (2012)	Loss of 46.3 % “Gillnet” profit
		Capture damage	1985	Portoroz (Slovenia)	Malej and Vuković (1984)	Summer of 1983
			1987	Gulf of Trieste (Adriatic Sea)	Axiak et al. (1991)	
			1991	Adriatic Sea	Legović (1991)	Review
Aquaculture	Direct	Stinging	2010	Mediterranean Sea	Nastasi (2010)	Review
		Capture damage	2011	Spanish Coast	Baxter et al. (2011)	
		Fish mortality	1995	Brittany (France)	Merceron et al. (1995)	
			2007	Mediterranean Sea	Purcell et al. (2007)	Review
Energy	Direct	Clog cooling-water intake	1985	Istrian Coast (Yugoslavia)	Malej and Vuković (1984)	From 1977 to 1980

11.3.1 Tourism

Stings from pelagic cnidarians cause discomfort and sometimes medical emergencies for swimmers, primarily in warm marine waters worldwide (Fenner and Williamson 1996). When the jellyfish form blooms, stings can reach epidemic levels (Purcell et al. 2007). *Pelagia noctiluca* stings are usually limited to the skin's surface and cause only topical lesions with localized pain that persists for 1–2 weeks. Systemic complications or cutaneous infections are infrequent (Mariottini et al. 2008). Most people are stung during summer. Mariottini et al. (2008) reviewed the earliest reports of *P. noctiluca* stinging swimmers. The earliest reports originate from the coast of Italy in 1976 (UNEP 1984), followed by the Istrian coast, Yugoslavia, during 1977–1978 (Malej and Vuković 1984; UNEP 1991), the northern Adriatic (Trieste) during 1978–1983 (Legović 1991), and Slovenia (Portoroz) in 1983 (Malej and Vuković 1984).

The negative impacts of *P. noctiluca* have been reviewed over a larger scale from the Levantine to southern Spanish coast and for the whole Mediterranean basin (CIESM 2001; Nastasi 2010; Bernard et al. 2011). Quantitative data on stings are available for the coast of Pula, Croatia, in the summer of 1978, where *P. noctiluca* stung 50 % of the bathers (Maretić 1984). Similarly, 52 % of the bathers were stung during the same season along the coast of Yugoslavia (Maretić et al. 1987). During 1981 and 1983, 720 people were affected on the coast of Athens, with almost 250 people stung each summer (Vlachos and Kontoes 1987, cited in Axiak et al. 1991). During 1982, a total of 1,500 incidents were reported for Greece (Papathanassiou and Anagnostaki 1987, cited in Axiak et al. 1991). During the following years (1984–1987), the French Riviera reported that 2,500 people required treatment, reaching a peak along the coast of Monaco in 2004 with 45,000 people treated for stings (Bernard 1991). Two years later, the east and south coasts of Spain reported that more than 14,000 people were treated (Pingree and Abend 2006, cited in Purcell et al. 2007). These reports include only people who received medical treatment, so the total amount of people stung, but not attended by the first aid services, could be even larger. Mostly tourists were stung and the risk of being stung discouraged people from spending holidays at places where *P. noctiluca* is known to be abundant. Thus beaches affected by blooms of *P. noctiluca* will have less tourist appeal (Purcell et al. 2007).

11.3.2 Fisheries

Fisheries also have been negatively affected by their interaction with *Pelagia noctiluca*. The level of impact depends on the type of fishing gear being used and on the abundance of jellyfish. Fishers are directly affected by *P. noctiluca* when they are stung while removing the jellyfish from the nets (CIESM 2001; Purcell et al. 2007; Mariottini et al. 2008; Nastasi 2010). The first reported case of fishermen being stung comes from the Istrian coast, Yugoslavia during 1977–1980 (Malej and Vuković 1984), followed by a report from Pula, Croatia in 1978 (Maretić 1984).

Kokelj and Scarpa (1987, cited in Axiak et al. 1991) reported that in the Gulf of Trieste, 700 fishers were stung over a period of 192 days of fishing in 1985. Overall, the Adriatic Sea seems to be the most impacted (and/or reported) location for this type of interaction (reviewed in Legović 1991).

Other direct impacts of jellyfish on fisheries include jellyfish clogging the nets and the engines of fishing vessels (CIESM 2001; Purcell 2005; Nastasi 2010). Most reports come from the Adriatic Sea, where the first cases of net and engine clogging were described in 1977 along the Istrian coast, Yugoslavia (Malej and Vuković 1984). Maretić (1984) reported that in 1978 fishing nets became clogged by *P. noctiluca* along the coast of Pula, Croatia, and similar events occurred during the summer of 1983 along the coast of Portoroz, Slovenia (Malej and Vuković 1984). It seems that the clogging of fishing nets by jellyfish, for the period of the 1983 and 1984, was common in the Adriatic Sea (Legović 1991; Malej and Malej 2004). Little information is available for the rest of the Mediterranean basin, but clogging of fishing nets has been described as a recurrent and cyclic phenomenon (Bernard 1991; Purcell et al. 2007). Associated with clogging of nets is damage to the captured fish which reduces the value of the catch and the subsequent cost of cleaning the nets. The economic losses, however, have not yet been quantified. The Adriatic Sea again seems to be the most affected area (Malej and Vuković 1984; Legović 1991). Kokelj and Scarpa (1987, cited in Axiak et al. 1991) reported a total of 0.5 kg h^{-1} of *P. noctiluca* in fishing nets during trawling activities, in the Gulf of Trieste, northern Adriatic Sea, which together with the accumulation of jellyfish (mostly *Rhizostoma pulmo*) reduced the total fish catch and even caused the rupture of fishing nets. Recently, economic valuation models of the impact of jellyfish blooms on local economies have been presented for the Mediterranean Sea (Nakar et al. 2012; Nastav et al. 2013). Nakar et al. (2012) modeled the interaction of jellyfish with different fishery activities and showed annual reductions of 8% in net fishery income for trawl fishing and a 46.3 % reduction in net profit for the trammel and gillnet fisheries for the coast of Israel.

The case of the alien ctenophore *Mnemiopsis leidyi* in the Black Sea demonstrated that this gelatinous plankter can deplete fish populations by direct predation on fish eggs and larvae and indirectly by preying on the crustacean food of juvenile fish. In this way, gelatinous predators affect fisheries by depleting fish populations. This kind of impact, well quantified in the Black Sea for *Mnemiopsis*, has not been evaluated for *P. noctiluca*, but chances are that, due to the features of this species, its impact on fish populations is even greater than that of *Mnemiopsis*.

11.3.3 Aquaculture

Aquaculture activities also suffer from the effects of *Pelagia noctiluca* and are similar to those for fisheries. The main effects are stinging of the aquaculture operators (Purcell et al. 2007, Rutter 2010, cited in Nastasi 2010) and damage to, or mortality of, the fish inside of the pens (Merceron et al. 1995). On the Spanish coast, *P. noctiluca* inflicted gill damage to the marine-farmed fish *Dicentrarchus* *labrax*, resulting in stress to the fish that reduced their growth and even caused their death (Baxter et al. 2011). Impacts of jellyfish on aquaculture activities are summarized by Purcell et al. (2007, 2013) and Nastasi (2010).

11.3.4 Energy

Jellyfish proliferations also affect the energy industry by clogging cooling-water intake screens (CIESM 2001; Purcell et al. 2007). The only documented case of cooling-water intake screens being clogged by *P. noctiluca* in the Mediterranean Sea happened during 1977–1980 along the Istrian coast of Yugoslavia (Malej and Vuković 1984). However, *P. noctiluca* was also reported to have affected the functioning of the cooling systems of Maltese power plants during June 2009 (Schembri P and Deidun A pers. comm.).

11.4 Impacts of *Pelagia noctiluca* and Other Jellyfish Species on Planktonic Communities, Especially Fish Larvae and Eggs

In the Mediterranean, fisheries have existed since ancient times. Fishery resources have been long considered exploited or overexploited, and at present, forage fishes represent around 50 % of the total landings (Lleonart and Maynou 2003). Thus, the reduction of the finfish populations may result in important structural and functional changes in the marine ecosystem (Coll et al. 2008). In the Adriatic Sea, the proliferation of some jellyfish species since the 1980s has occurred in parallel with the decrease of small pelagic fish.

In the Mediterranean Sea, the highest abundance of *P. noctiluca* occurs in spring and summer (Morand et al. 1992; Licandro et al. 2010), when the majority of fish species reproduce. Indeed, spawning of most neritic fish species (families Sparidae, Labridae, Mullidae, Serranidae, Scombridae), as well as the small pelagic fish, anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*), takes place during this period of the year (Sabatés et al. 2007). Thus both ichthyoplankton abundance and diversity are high during spring-summer and coincide with large populations of jellyfish. As a consequence, the predation pressure of *P. noctiluca* on fish eggs and larvae can be high. In fact, Sabatés et al. (2010) reported that *Pelagia noctiluca* ephyrae would be an important predator on summer ichthyoplankton because fish larvae represented up to 12 % of the total prey captured by young jellyfish.

Gelatinous zooplankton can aggregate at hydrodynamic discontinuities (e.g., Arai 1976; Gili et al. 1988; Graham et al. 2001), and in the NW Mediterranean Sea, the most dense populations of gelatinous zooplankton and fish larvae have been associated with the northern current, along the shelf break, and its associated front (Sabatés et al. 2010; Ferraris et al. 2012). The particular hydrodynamic conditions of that area enhance and maintain high levels of biological production (Estrada and Margalef 1988; Sabatés et al. 2004; Stemmann et al. 2008), providing ideal conditions for feeding, growth, and reproduction of the jellyfish. Indeed, Sabatés et al. (2010) reported that predation on anchovy larvae by *P. noctiluca* ephyrae was higher in the frontal area than in the surrounding waters. Furthermore, during the night, when both groups of organisms co-occur in surface waters, *P. noctiluca* exhibited a positive selection for fish larvae. Thus, the temporal and spatial overlapping of *P. noctiluca* with early life stages of fish suggests that it may be an important predator of summer ichthyoplankton and potentially affect fish recruitment. Recently, Purcell et al. (2012) used a combination of data of jellyfish and fish larvae abundances, in situ jellyfish gut contents, experimentally measured digestion rates, and temperature and estimated that between 18 % and 32 % of the available fish larvae were consumed daily by *P. noctiluca* ephyrae.

Positive interactions between jellyfish and fish also exist. A large variety of fish associate with jellyfish among which, Carangidae are often the most abundant. Some benefits of these associations include predator avoidance, provisioning of food, and shelter for juvenile fish (Arai 1988; Purcell and Arai 2001; Masuda 2009). Associations between *P. noctiluca* and jack mackerel *Trachurus* spp. have been observed in the Mediterranean waters. Nevertheless, there are few systematic, quantitative data on the frequencies or durations of these positive associations, and their effect on the survival and recruitment of these fish species is not known.

Finally, it must be considered that natural predators of jellyfish, i.e., turtles, birds, and large carnivorous fish, have dramatically decreased due to overfishing, ingestion of floating plastics, and loss of essential habitats, therefore decreasing the control they perhaps once exerted over the jellyfish populations (Purcell et al. 2007). *P. noctiluca* has been identified as prey of a number of apex Mediterranean predators, including tuna, swordfish, sunfish, and loggerhead turtles (Cardona et al. 2012). If stocks of these predators were not depleted, they could potentially control the abundance of gelatinous zooplankton across the Mediterranean (Cardona et al. 2012).

11.5 *Pelagia noctiluca* Along the Catalan Coast (NW Mediterranean)

11.5.1 The Medusa Project

In 2007, the Catalan Water Agency (ACA, Agència Catalana de l’Aigua), in collaboration with the Marine Science Institute of Barcelona (ICM-CSIC), underwrote the “Medusa Project,” which constituted a network of organizations that contribute information about jellyfish observations. The aim of the Medusa Project was to monitor the presence of jellyfish along the entire Catalan coast. The ACA recorded the presence of jellyfish daily at more than 240 beaches, covering the 69 Municipalities of Catalonia during the summer season. Inspectors recorded the presence of stranded jellyfish on beaches, in nearshore water, and at 200 m offshore by means of a boat. The project also involves participation of Emergency Services from 26 Municipalities

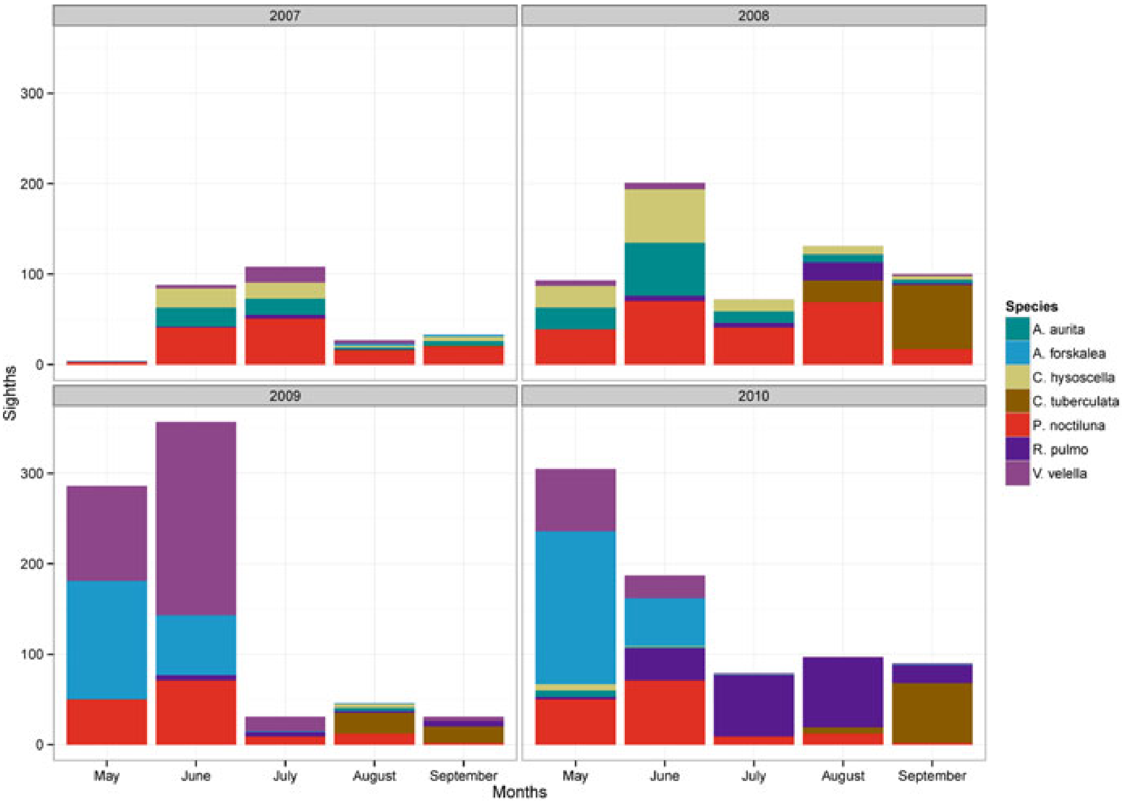


Fig. 11.3 Temporal variability of conspicuous jellyfish species stranded along the Catalan coasts, for the period 2007–2010. *Pelagia noctiluca* is shown in *red* at the base of the bars

and the Fisherman Associations of Catalonia, which report the presence of jellyfish daily. All of the information is summarized on the ACA web page (http://www.gencat.cat/aca/). Technical descriptions of the results and conclusions are presented in Gili et al. (2010).

11.5.2 Preliminary Results on Spatiotemporal Variability of Pelagia noctiluca

Data on stranded *Pelagia noctiluca* at 243 beaches along the Catalan coast were collected by beach inspectors daily from May to September, 2007–2010. Stranding records were grouped into three abundance categories: **“1”**< 10 medusae per beach (85 % of the reports), **“2”**< 1 medusa m^{-2} (12%), and **“3”**> 1 medusa m^{-2} (only 3.3 %). This last category is recognized as a “bloom” situation. Spatiotemporal variability is presented as the number of reports of stranded *P. noctiluca* medusae along the coast.

Six species of jellyfish were frequently observed on Catalan beaches (Fig. 11.3). Characteristic species observed during spring (May and June) were *Chrysaora hysoscella*, *Aurelia aurita*, *Aequorea forskalea*, and *Velella velella*. Interestingly, in 2007 and 2008, spring records were dominated by *C. hysoscella* and *A. aurita*, but in 2009 and 2010 the hydrozoans *A. forskalea* and *V. velella* were most commonly observed. The summer season (July and August) was characterized by the overlap of some

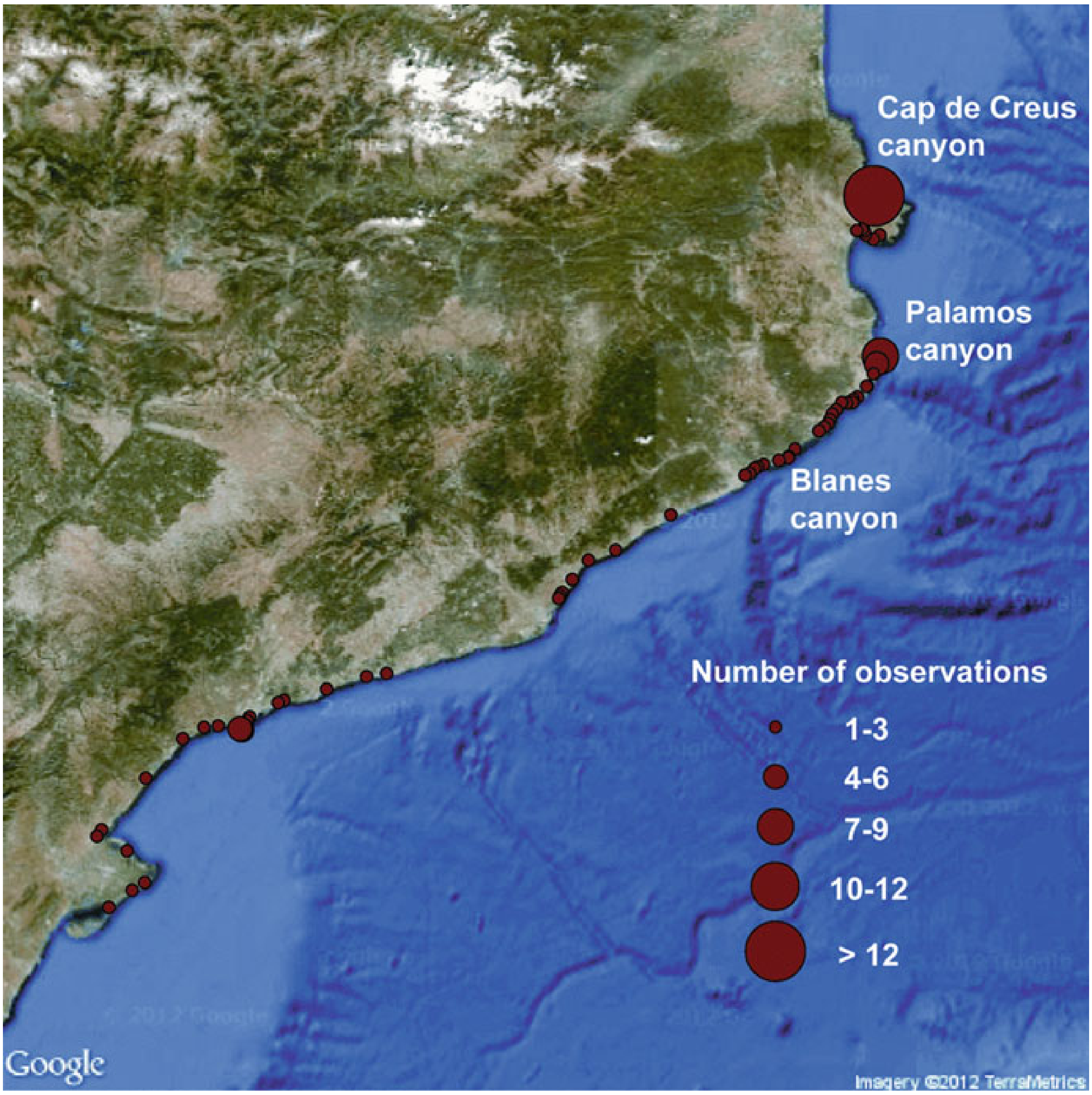


Fig. 11.4 Observations of stranded individuals of *Pelagia noctiluca* along the Catalan coast. Data represents mean annual values (2007–2010)

individuals of the spring species with the scyphozoan *Rhizostoma pulmo*, whose occurrence seemed to increase over time, especially in 2011 and 2012 (Fuentes et al. 2011). Finally, in late summer (September), the scyphozoan *Cotylorhiza tuberculata* appears. Stranded individuals of *Pelagia noctiluca* appear throughout the sampling period (May–September). In 2007, 2009, and 2010, stranded *P. noctiluca* were more abundant during June and July, with fewer reports during August, and September 2008 was an unusual year with high numbers of strandings for the entire study period. Even though the life cycle of *P. noctiluca* could lead to it occurring throughout the year, a clear pattern occurred in the stranded individuals, with the most strandings occurring during the spring-summer seasons, which may reflect its response to spring warming, increasing production, and local wind patterns.

Stranded *P. noctiluca* are widespread along the Catalan coast, but the highest concentrations of observations are along the northern Catalan coast every year (Fig. 11.4). Stranded jellyfish appear to occur most frequently on beaches close to marine canyons, particularly “Palamós” and “Cap de Creus” canyons. The association

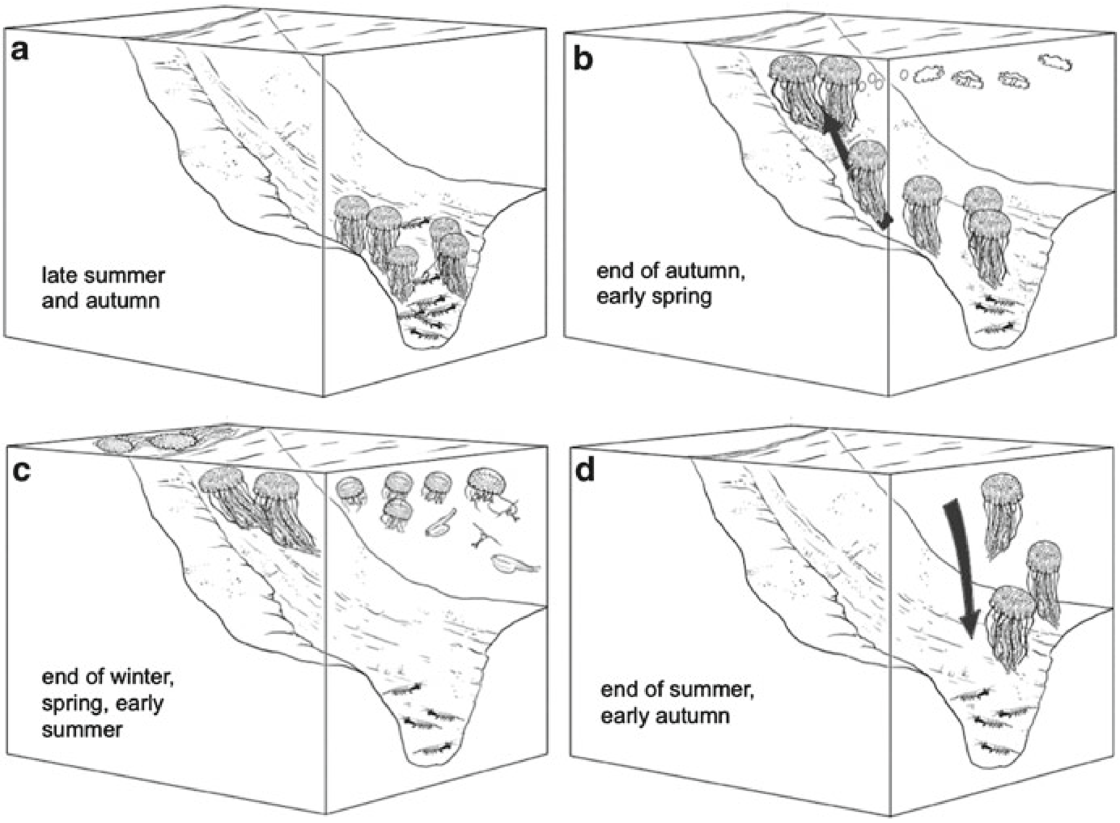


Fig. 11.5 (**a**–**d**) Hypothesis for seasonal vertical migration of *Pelagia noctiluca*. (**a**) Jellyfish overcome the warmer months at colder, mid-water levels; (**b**) by mid-autumn or early winter, jellyfish migrate upward for sexual reproduction; (**c**) throughout spring to early summer, at shallow levels jellyfish feed on the seasonal spring plankton bloom, with rapid somatic growth; (**d**) by the end of summer, jellyfish migrate downward to escape shortage of plankton food and warmer temperatures (Art: Alberto Gennari, concepts: Ferdinando Boero)

between stranding events and proximity to marine canyons along the Catalan coast is corroborated by similar findings along the Italian coasts. Analysis of data from a citizen science program from 2009 to 2012 (*Occhio alla Medusa*, F Boero unpublished data) and from experimental sampling campaigns in the Ionian, Tyrrhenian, and Ligurian seas revealed coastal outbreaks of *P. noctiluca* recurring in the proximity of canyons and upwelling areas, such as the Strait of Messina (NE Sicily) (Rosa et al. 2013). Marine canyons are known as "superhighways" because of the high-speed circulation of water masses, sediments, and organisms during active or passive movements from shallow to deeper waters and vice versa (Palanques et al. 2005; Würtz 2012). *P. noctiluca* is a mid-water jellyfish, and its life cycle may incorporate extensive vertical migration. Indeed, canyons may act as circulation pumps favoring the seasonal zonation of *P. noctiluca* from mid-water levels to surface waters and vice versa (Fig. 11.5). In summer, warm temperatures and the reduction of zooplankton prey make surface waters unfavorable to *P. noctiluca*, and records of *P. noctiluca* along shorelines become increasingly rare. Boero (in Sacchetti 2012) hypothesized that, during summer, jellyfish migrate down to cooler mid-water depths, possibly along canyon corridors (Fig. 11.5a).

Fig. 11.6 Formation of individual pairs during *Pelagia noctiluca* swarms: a behavior to enhance the success of sexual reproduction (Photo: Alejandro Olariaga. Galicia, Spain, summer 2010)

Mid-waters may also provide alternative, abundant crustacean resources (e.g., euphausiid shrimps) to *P. noctiluca*. Thus, this jellyfish may spend the warmer months at deeper habitats along the continental slope with abundant food sources and invest more energy towards future sexual reproduction by germ cell differentiation and gonad maturation (Fig. 11.5b). After surface waters have cooled by the late autumn or early winter, massive outbreaks of *P. noctiluca* occur at localities along the coastline nearest to the upper margins of marine canyons and upwelling areas, such as around the Aeolian Islands archipelago and the Strait of Messina, NE Sicily, the Island of Elba, Tuscany, and the continental platform of the Ligurian Sea. At this time of the year, large *P. noctiluca* can be found in surface waters even in daytime, where they also exhibit an uncommon swimming behavior, with frequent formation of couples (Fig. 11.6).

In late autumn-winter, outbreaks of *P. noctiluca* at the surface may be associated with sexual reproduction, leading to formation of a new cohort of planulae and ephyrae (Fig. 11.5c), followed by rapid somatic growth (Giacomo Milisenda, unpublished data). Indeed, swarms of juvenile jellyfish are encountered throughout winter. During the following months, the juvenile medusae will feed in surface waters on the spring zooplankton and ichthyoplankton (Fig. 11.5d). A new round of sexual reproduction may occur in late spring or early summer. Following the increase of sea surface temperatures and the formation of water mass stratification, *P. noctiluca* will leave the surface waters, starting a new annual migratory cycle (Fig. 11.5a).

11.5.3 Association with Physical Variables

Pelagia noctiluca medusae along the Catalonian coast are associated with particular oceanographic features. Sabatés et al. (2010) examined the role of a front associated with the shelf-slope in aggregating *P. noctiluca*. The front runs from north to south along the continental slope of the northwestern Mediterranean and reaches a depth of ~400 m. The increased primary and secondary productivity in the frontal area could contribute to the high abundances reported for *P. noctiluca* in the region. Jellyfish and other plankton also could be concentrated in the convergence associated with the front (e.g., Graham et al. 2001). Oceanographic conditions associated with the variability of this front were analyzed by Rubio and Muñoz (1997), who developed the first predictive model from physical variables for the arrival of *P. noctiluca* to the coastline of Barcelona. Their model indicated that the following conditions lead to a coastal bloom of *P. noctiluca*. First, if there is little or no rain at the beginning of winter and high solar radiation maximizes primary productivity in offshore waters of the Catalan Sea, an "offshore bloom" of *P. noctiluca* occurs at the front. If the wind fetch is perpendicular to the coastline of Barcelona during the early spring, the first individuals arrive at the coast at the beginning of April. High temperature and low precipitation at the start of summer then provide the ideal conditions for maximum dispersion, because the front is weak and allows transport of the accumulated medusae to the coastal area. These conditions thus cause a "coastal bloom" of *P. noctiluca* (Fig. 11.7) (Rubio and Muñoz 1997). Once the medusae reach the coast, their fate depends on other variables, such as the availability of zooplankton that will allow *P. noctiluca* medusae to increase its survival. Finally, wind and surface currents distribute the individuals to the shore. Thus, the study of stranded jellyfish is important to elucidate patterns of seasonality and population dynamics of jellyfish species (Houghton et al. 2007).

The association between jellyfish strandings and the prevailing wind direction and speed were analyzed from May to September, 2007–2010. Weekly averages of the number of strandings recorded were calculated to elucidate any quantitative pattern. Wind direction and velocity data were obtained from the meteorological service of Catalonia (http://www.meteo.cat). The meteorological stations were often located away from the beaches surveyed for stranding events. To correct for this, different portions of the coast were integrated to match the wind data resolution. This step was critical because coastlines that have different orientations and morphologies will be affected differently by any given wind direction. The relationship between stranded jellyfish and wind direction was analyzed using Generalized Additive Models (GAMs). Results showed a general pattern of stranding events associated with southerly winds. Low stranding category "1" and "2" showed a flattened kernel density distribution associated with winds (Fig. 11.8a upper and central panel). The first general pattern shown by the kernel density function was that more stranding events coincided with wind directions between 100° and 250° (east southeast to west southwest); the second, less obvious group of observations

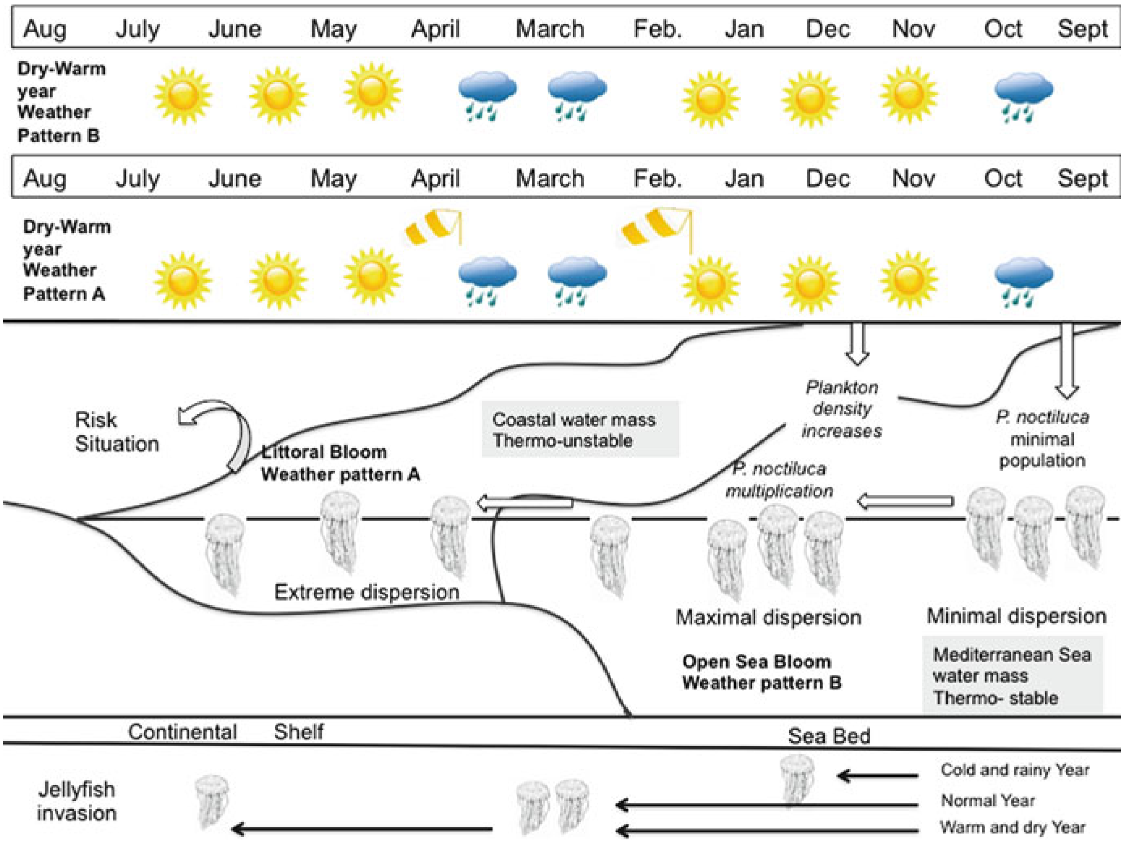


Fig. 11.7 Scheme of the proposed model by Rubio and Muñoz (1997), showing the different conditions leading a coastal bloom of *Pelagia noctiluca* (see text for interpretation)

coincide with northerly winds (0°–20°). For the jellyfish bloom category "3," more stranding events were only associated with southeast to south southwest (140°–200°) winds as seen from the kernel density distribution (Fig. 11.8a). In this category there were fewer observations because such large stranding events happened only occasionally (3.3 % of all records).

Weekly stranding events also revealed the variability in the association with southeastern winds (Fig. 11.9); the different magnitude axis on each circular plot illustrates the temporal variation of the stranding events. For all years, weeks with low abundances of jellyfish had a wider spread of wind direction (Fig. 11.9). Conversely, high weekly average abundances of jellyfish and blooms were particularly restricted to the southeastern winds.

The association between jellyfish strandings and wind speed needs to be interpreted with care, because jellyfish also can be "washed ashore" by waves generated by strong winds. Figure 11.8b shows the relationship between the stranding events according to abundance categories and wind speed. For all categories, stranding events increased with slow winds up to five knots, and then stranding events decreased at higher wind velocities.

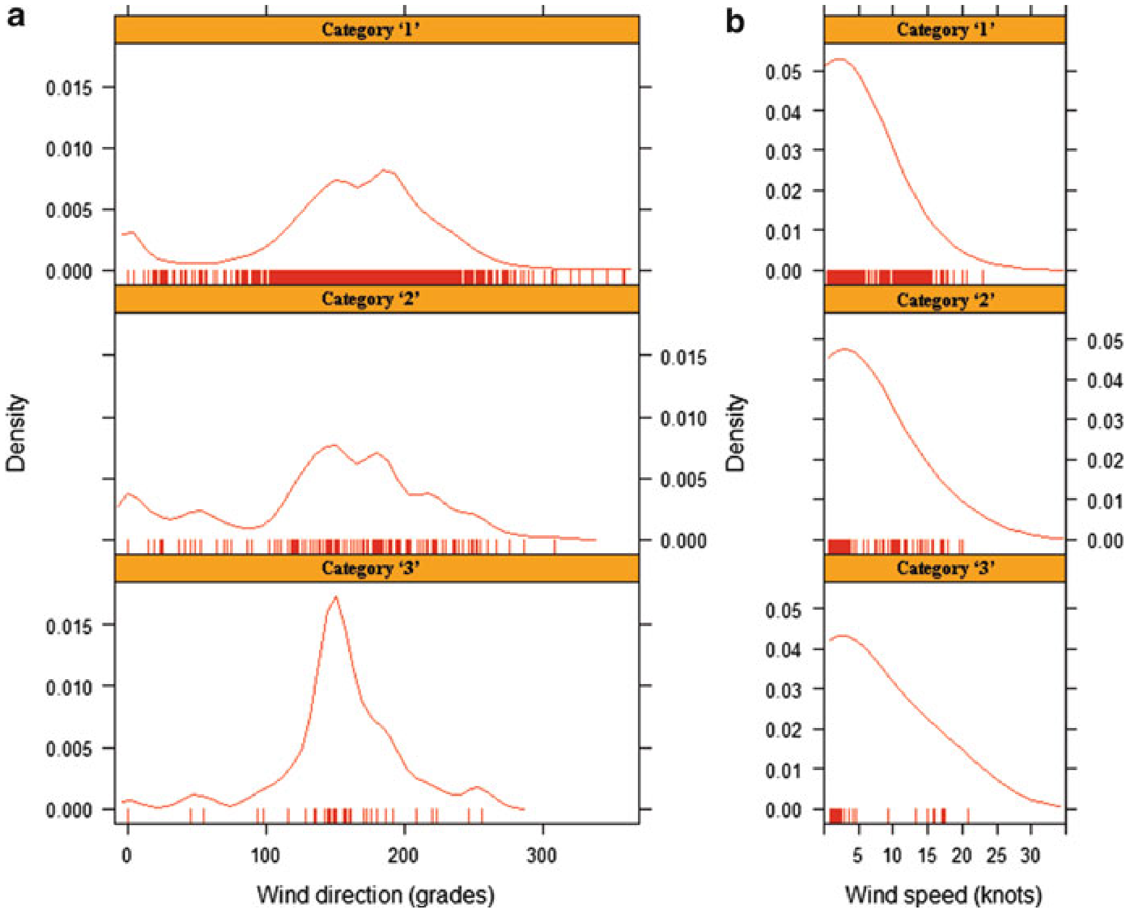


Fig. 11.8 (**a**–**b**) Relationship between stranded jellyfish species along the Catalonian coast with (**a**) wind direction and (**b**) speed. *Vertical lines* above the x-axis represent the raw stranded data. *Continuous line* represents the kernel density function used to model the relationship between stranded individuals and environmental factors

In summary, jellyfish strandings are associated with southeastern winds, which, due to the coastal orientation, are winds that blow mostly shoreward and push the water and the jellyfish to the coast. Nevertheless, the arrival of medusae to the coast will be ultimately limited by their presence along the coastal waters of Catalonia.

11.5.4 *Effects on Human Activities*

Along the Catalan coast one of the most important economic activities is beach-associated tourism. Nearly four million people visit Catalonia and use its beaches every year. During the summer season, *Pelagia noctiluca*, *Rhizostoma pulmo*, *Olindias phosphorica*, and *Carybdea marsupialis* (in decreasing order of importance based on their abundance) are responsible for stings that require first aid attention. Reports of the number of people affected by jellyfish stings recorded by the Red Cross service have provided useful data to understand the temporal patterns

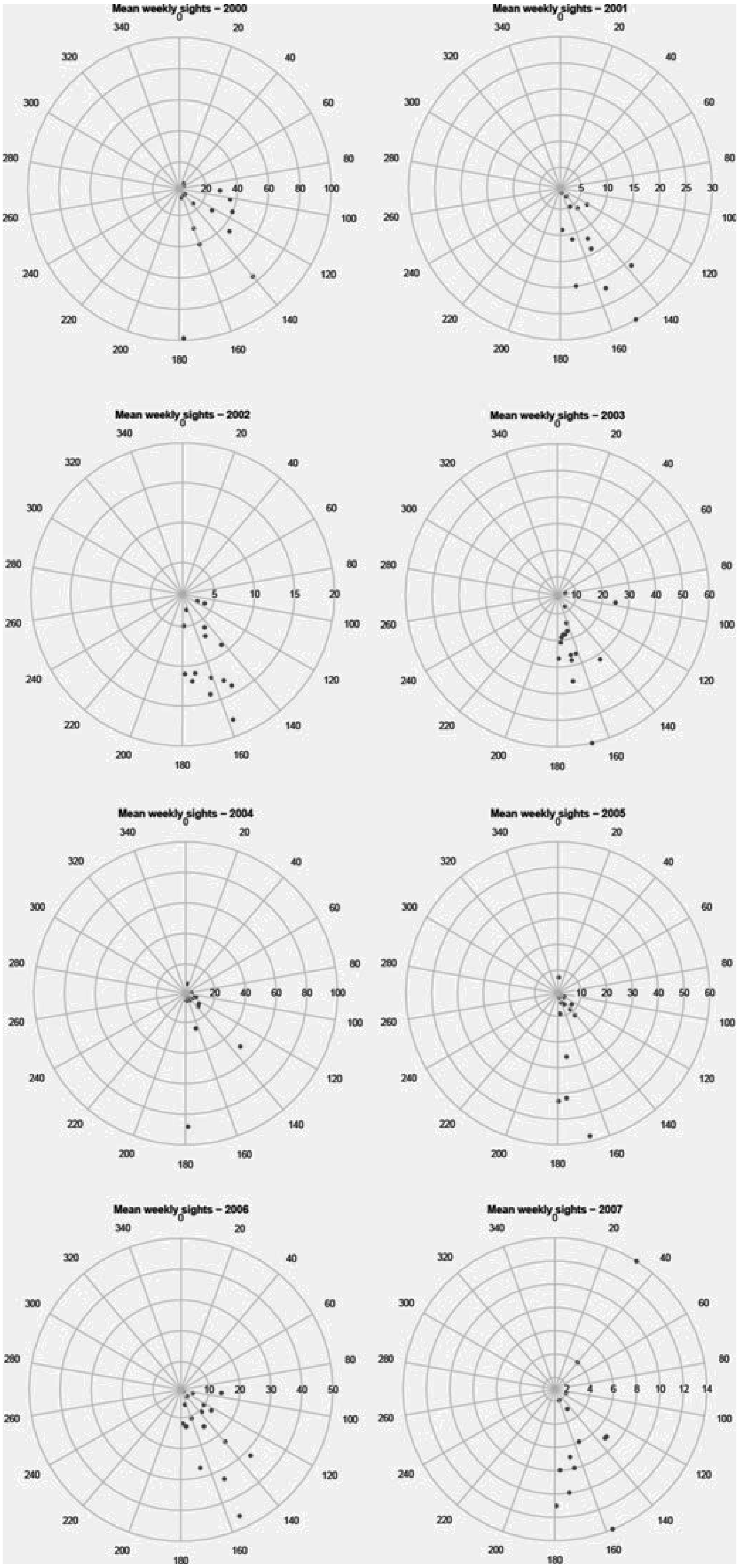


Fig. 11.9 Average weekly stranded jellyfish during May–Oct 2001–2007. *Degrees* represent compass directions, with north = 0°. Different magnitude scales in each year reflects differences in the total records

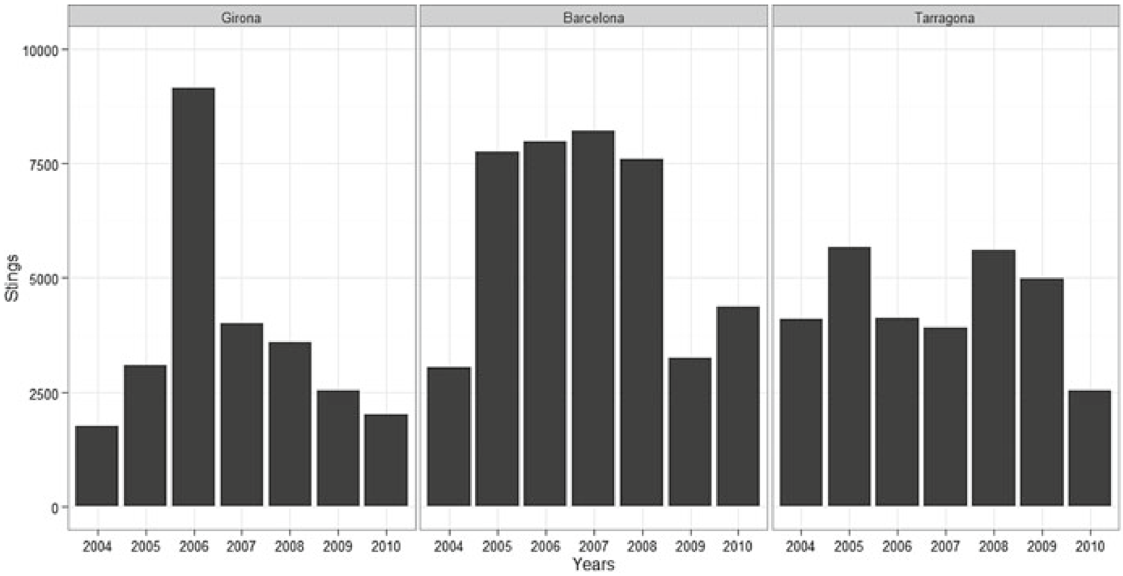


Fig. 11.10 Temporal distribution of people stung by jellyfish in the three provinces along the Catalan coast. Data showed the maximum number of assistances

and the magnitude of the stinging events. The information collected by the Red Cross for 2004–2010 was divided among the three provinces of Catalonia, from north to south: Girona, Barcelona, and Tarragona.

In the northern province of Girona, the number of people stung showed a strong peak during 2006, when 9,155 cases were registered (Fig. 11.10). The Barcelona province had a more extended peak, with an average of 7,880 cases recorded annually from 2005 to 2008 (Fig. 11.10). The southern province of Tarragona showed no clear pattern with two small peaks during the years 2005 and 2008 when 5,661 and 5,605 cases were registered, respectively (Fig. 11.10).

For the Catalan coast, jellyfish stings represent about 60% of all the requests for assistance from the Red Cross service. Reports of jellyfish stings included no information about the species responsible, and bathers usually do not know which species have stung them. Identification of the species that has stung a patient is very difficult and can be achieved only for a few species and within a few minutes of the patient being stung (Mariottini et al. 2008). Thus, to try to determine which species of jellyfish was responsible for most stings, in Barcelona province we correlated abundances of each species of jellyfish (as reported by the ACA beach inspectors) with the numbers of stings (as reported by the Red Cross). Among all recorded stinging jellyfish species, *P. noctiluca* was the only species with a significant correlation between abundance and first aid attention (Fig. 11.11).

The Medusa Project in Catalonia is an attempt to understand the spatiotemporal dynamics of the jellyfish populations along the Catalan coast. With a high temporal and spatial coverage, this project is a useful tool for elucidating answers to many of the questions surrounding jellyfish. *Pelagia noctiluca* is the most important jellyfish

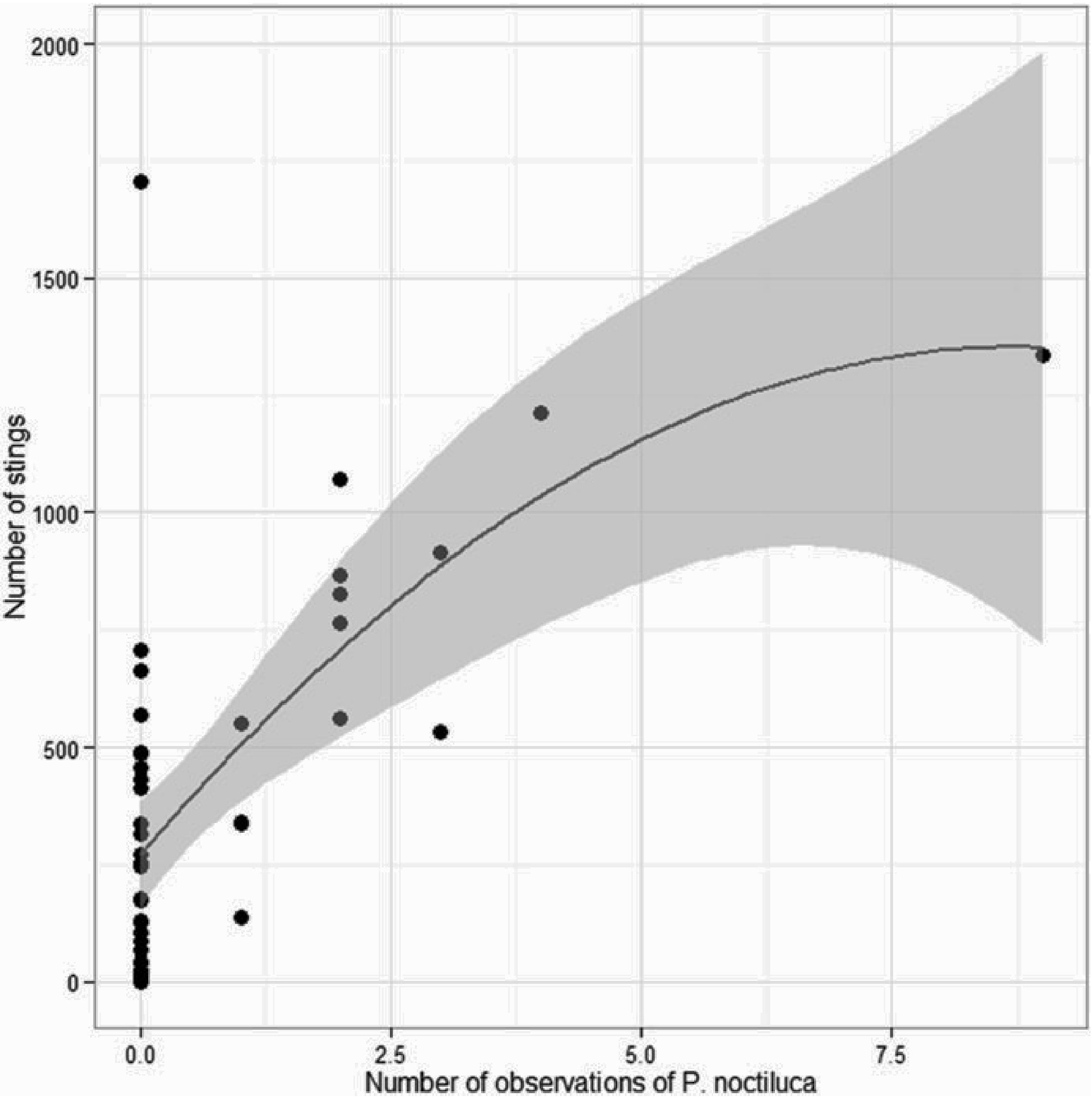


Fig. 11.11 Relationship between number of stings and strandings of *Pelagia noctiluca* along the coast of Barcelona (Catalonia)

species due to its distribution, abundance, and ecological role and also because it is the main species responsible for the negative interaction with humans. Finally, we recommend that similar efforts should be undertaken elsewhere to expand our knowledge about blooming patterns of dangerous jellyfish species.

Acknowledgments A. Canepa was funded by CONICYT (PFCHA/Doctorado al Extranjero 4ª Convocatoria, 72120016). The research leading to these results has received funding from the European Community's Seventh Framework Programme (FP7/2007–2013) under Grant Agreements n° 266445 for the project "Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors (VECTORS)," n° 287844 for the project "Towards COast to COast NETworks of marine protected areas (from the shore to the high and deep sea), coupled with sea-based wind energy potential" (CoCoNET), and n° 287600 for the project "Policy-oriented marine Environmental Research for the Southern European Seas (PERSEUS)" and from the ENPI CBC

MED program under Grant Agreement n° I-A/1.3/098 for the project "Integrated monitoring of jellyfish outbreaks under anthropogenic and climatic impacts in the Mediterranean Sea (coastal zones): trophic and socio-economic risks (MED-JELLYRISK)." A. Sabatés thanks Fishjelly project MAR-CTM2010-18874. Special thanks go to Jennifer Purcell for reviewing the manuscript and for her valuable comments on it.

References

Arai MN (1976) Behavior of planktonic coelenterates, *Sarsia tubulosa*, *Phialidium gregarium* and *Pleurobrachia pileus* in salinity discontinuity layers. J Fish Res Bd Can 30:1105–1110

Arai MN (1988) Interactions of fish and pelagic coelenterates. Can J Zool 66:1913–1927

Avian M, Rottini-Sandrini L, Stravisi F (1991) The effect of seawater temperature on the swimming activity of *Pelagia noctiluca* (Forsskål). B Zool 58:135–143

Axiak V (1984) Effect of decreasing light intensity on the activity of the scyphomedusa, *Pelagia noctiluca* (Forskal). UNEP: Report on the workshop on jellyfish blooms in the Mediterranean, Athens, 31 Oct–4 Nov 1983, pp 121–127

Axiak V, Galea C, Schembri PJ (1991) Coastal aggregations of the jellyfish *Pelagia noctiluca* (Scyphozoa) in Maltese coastal waters during 1980–1986. UNEP: Jellyfish blooms in the Mediterranean. In: Proceedings of the II workshop on jellyfish in the Mediterranean Sea. MAP Tech Rep Ser, 47. UNEP, Athens, pp 32–40

Bastian T, Stokes D, Hays GC, Davenport J, Doyle TK (2011) Fisheries bycatch data provide insights into the distribution of the mauve stinger (*Pelagia noctiluca*) around Ireland. ICES J Mar Sci 68:436–443

Baxter EJ, Albinyana G, Girons A, Isern MM, García AB, Lopez M, Canepa A, Olariaga A, Gili J-M, Fuentes V (2011) Jellyfish-inflicted gill damage in marine-farmed fish: an emerging problem for the Mediterranean? In: XIII Congreso Nacional de Acuicultura. Castelldefels, Barcelona

Benović A (1991) The aspect of jellyfish distribution in the Adriatic Sea. UNEP: Jellyfish blooms in the Mediterranean proceedings of the II workshop on jellyfish in the Mediterranean Sea MAP Tech Rep Ser, No. 47. UNEP, Athens, pp 41–50

Bernard P (1991) Recapitulation des résultats de la surveillance des proliférations de méduses sur les côtes méditerranéennes françaises durant l'été 1987. UNEP: Jellyfish blooms in the Mediterranean proceedings of the II workshop on jellyfish in the Mediterranean Sea MAP Tech Rep Ser, No. 47. UNEP, Athens, pp 51–57

Bernard P, Berline L, Gorsky G (2011) Long term (1981–2008) monitoring of the jellyfish *Pelagia noctiluca* (Cnidaria, Scyphozoa) on the French Mediterranean coasts. J Oceanogr Res Data 4:1–10

Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T, Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299–310

Braverman M (1962) Studies in hydroid differentiation. I. *Podocoryne carnea* culture methods and carbon dioxide induced sexuality. Exp Cell Res 26:301–306

Braverman M (1963) Studies in hydroid differentiation. II. Colony growth and initiation of sexuality. J Embryol Exp Morph 11:239–253

Brotz L, Pauly D (2012) Jellyfish populations in the Mediterranean Sea. Acta Adriat 53:211–230

Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. Hydrobiologia 690:3–20

Cardona L, de Quevedo IA, Borrell A, Aguilar A (2012) Massive consumption of gelatinous plankton by Mediterranean apex predators. PLoS ONE 7:e31329

CIESM (2001) Gelatinous zooplankton outbreaks: theory and practice. CIESM Workshop Series, no 14, Monaco, 112 pp. Available on-line at www.ciesm.org/publications/Naples01.pdf

Coll M, Palomera I, Tudela S, Dowd M (2008) Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978–2003. Ecol Model 217:95–116

Condon RH, Graham WM, Duarte CM, Pitt KA, Lucas CH, Haddock SHD, Sutherland KR, Robinson KL, Dawson MN, Decker MB, Mills CE, Rhode JE, Malej A, Hermes M, Uye S-I, Belcich S, Madin LP (2012) Questioning the rise of gelatinous zooplankton in the world's oceans. BioScience 62:160–169

Condon RH, Duarte CM, Pitt KA, Robinson KL, Lucas CH, Sutherland KR, Mianzan HW, Bogeberga M, Purcell JE, Deckerj MB, Uye S, Madin LP, Brodeur RD, Haddock SHD, Malej A, Parry GD, Eriksen E, Quiñones J, Acha M, Harvey M, Arthur JM, Graham WM (2013) Recurrent jellyfish blooms are a consequence of global oscillations. Proc Natl Acad Sci U S A 110:1000–1005

Daly Yahia MN, Batistic M, Lucić D, Fernández de Puelles ML, Licandro P, Malej A, Molinero J-C, Siokou-Frangou I, Zervoudaki S, Prieto L, Goy J, Daly Yahia-Kéfi O (2010) Are the outbreaks of *Pelagia noctiluca* (Forsskål, 1775) more frequent in the Mediterranean basin? In: Gislason A, Gorsky G (eds) Proceedings of the joint ICES/CIESM workshop to compare zooplankton ecology and methodologies between the Mediterranean and the North Atlantic (WKZEM), ICES Cooperative Research Report, pp 8–14

Doyle TK, De Haas H, Cotton D, Dorschel B, Cummins V, Houghton JDR, Davenport J, Hays GC (2008) Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. J Plankton Res 30:963–968

Estrada M, Margalef R (1988) Supply of nutrients to the Mediterranean photic zone across a persistent front. Oceanol Acta 9:133–142

Fenner PJ, Williamson JA (1996) World-wide deaths and severe envenomation from jellyfish stings. Med J Aust 165:658–661

Ferraris M, Berline L, Lombard F, Guidi L, Elineau A, Mendoza-Vera JM, Lilley MKS, Taillandier V, Gorsky G (2012) Distribution of *Pelagia noctiluca* (Cnidaria, Scyphozoa) in the Ligurian Sea (NW Mediterranean Sea). J Plankton Res 34:874–885

Forsskal P (1775) Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium, quae in itinere orientale observavit Petrus Forsskal. Post mortem auctoris edidit Carsten Niebuhr. Adjuncta est materia medica Kahirina atque tabula maris rubri geographica. pp 1–20, I-XXXIV, 1–164, 1 map. Hauniae

Franqueville C (1971) Macroplacton profond (Invertébrés) de la Méditerranée nord-occidentale. Tethys 3:11–55

Fuentes V, Straehler-Pohl I, Atienza D, Franco I, Tilves U, Gentile M, Acevedo M, Olariaga A, Gili JM (2011) Life cycle of the jellyfish *Rhizostoma pulmo* (Scyphozoa: Rhizostomeae) and its distribution, seasonality and inter-annual variability along the Catalan coast and the Mar Menor (Spain, NW Mediterranean). Mar Biol 158:2247–2266

Gili J-M, Pagès F (2005) Les proliferacions de meduses. Bolletí de la Societat d'Història Natural de les Balears 48:9–22

Gili JM, Pagès F, Sabatès A, Ros JD (1988) Small-scale distribution of a cnidarian population in the western Mediterranean. J Plankton Res 10:385–401

Gili JM, Fuentes V, Atienza D, Lewinsky I (2010) Report of the Medusa Project. Tech Rep No. 8, Agencia Catalana de l'Aïgua, Generalitat de Catalunya, Barcelona

Giorgi R, Avian M, De Olazabal S, Rottini-Sandrini L (1991) Feeding of *Pelagia noctiluca* in open sea. Jellyfsh blooms in the Mediterranean. In: Proceedings of II workshop on jellyfsh in the Mediterranean Sea. MAP Tech Rep Ser, No. 47. UNEP, Athens, pp 102–111

Gislason A, Gorsky G (eds) (2010) Proceedings of the "Joint ICES/CIESM Workshop to Compare Zooplankton Ecology and Methodologies between the Mediterranean and the North Atlantic (WKZEM)". ICES Cooperative research report No. 300. 91 pp

Goy J, Morand P, Etienne M (1989) Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. Deep-Sea Res 36:269–279

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

Graham WM, Martin DL, Martin JC (2003) In situ quantification and analysis of large jellyfish using a novel video profiler. Mar Ecol Prog Ser 254:129–140

Houghton JDR, Doyle TK, Davenport J, Lilley MKS, Wilson RP, Hays GC (2007) Stranding events provide indirect insights into the seasonality and persistence of jellyfish medusae (Cnidaria: Scyphozoa). Hydrobiologia 589:1–13

Kokelj F, Scarpa C (1987) Pelagia noctiluca in the Gulf of Trieste: epidemiologic and clinical observations. (unpublished)

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

Larson RJ (1987) A note on the feeding, growth, and reproduction of the epipelagic Scyphomedusa *Pelagia noctiluca* (Forsskål). Biol Oceanogr 4:447–454

Legović T (1987) A recent increase in jellyfish populations: a predator–prey model and its implications. Ecol Model 38:243–245

Legović T (1991) Causes, consequences and possible control of massive occurrences of jellyfish *Pelagia noctiluca* in the Adriatic Sea. UNEP: Jellyfish blooms in the Mediterranean proceedings of the II workshop on jellyfish in the Mediterranean Sea MAP Tech Rep Ser, No. 47. UNEP, Athens, pp 128–132

Legović T, Benović A (1984) Transport of *Pelagia noctiluca* swarrns in the south Adriatic. UNEP: report on the workshop on jellyfish blooms in the Mediterranean. Athens, pp 185–193, 31 Oct–4 Nov 1983

Licandro P, Conway DVP, Daly Yahia MN, Fernandez de Puelles ML, Gasparini S, Hecq JH, Tranter P, Kirby RR (2010) A blooming jellyfish in the northeast Atlantic and Mediterranean. Biol Lett 6:688–691

Lleonart J, Maynou F (2003) Fish stock assessments in the Mediterranean: state of the art. Sci Mar 67(Suppl):37–49

Loomis WF (1957) Sexual differentiation in hydra. Science 126:735–739

Malačič V, Petelin B, Malej A (2007) Advection of the jellyfish *Pelagia noctiluca* (Scyphozoa) studied by the Lagrangian tracking of water mass in the climatic circulation of the Adriatic Sea. Geophys Res Abs 9:02802

Malej A (1989) Behaviour and trophic ecology of the jellyfish *Pelagia noctiluca* (Forsskål, 1775). J Exp Mar Biol Ecol 126:259–270

Malej A, Malej AJ (2004) Invasion of the Jellyfish *Pelagia noctiluca* in the Northern Adriatic: a non-success story, In: Dumont H, Shiganova TA, Niermann U (eds) Aquatic invasions in the Black, Caspian, and Mediterranean Seas: the ctenophores *Mnemiopsis leidyi* and *Beroe* in the Ponto-Caspian and other aquatic invasions. Nato Science Series: 4. Earth and Environmental Sciences. Springer, Netherlands, pp 273–285

Malej A, Vuković A (1984) Some data on the occurrence and biology of the scyphomedusa *Pelagia noctiluca* in the Gulf of Trieste, and the impact of jellyfish swarming on human activities. UNEP: Report on the workshop on jellyfish blooms in the Mediterranean, Athens, 31 Oct–4 Nov 1983, pp 89–94

Malej A, Faganeli J, Pezdič J (1993) Stable isotope and biochemical fractionation in the marine pelagic food chain: the jellyfish *Pelagia noctiluca* and net zooplankton. Mar Biol 116:565–570

Maretić Z (1984) The bloom of jellyfish *Pelagia noctiluca* along the coasts of Pula and Istria 1977-1983, with special reference to epidemiology, clinics and treatment. UNEP: Report on the workshop on jellyfish blooms in the Mediterranean, Athens, 31 Oct–4 Nov 1983, pp 83–88

Maretić Z, Matic-Piantanida D, Ladavac J (1987) The blooms of the jellyfish *Pelagia noctiluca* in the Mediterranean and Adriatic and its impact on human health. In: Proceedings of the 2nd workshop on jellyfish in the Mediterranean, Trieste, pp 260–267

Mariottini GL, Giacco E, Pane L (2008) The Mauve Stinger *Pelagia noctiluca* (Forsskål, 1775). Distribution, ecology, toxicity and epidemiology of stings. A review. Mar Drugs 6:496–513

Masuda R (2009) Ontogenetic changes in the ecological function of the association behavior between jack mackerel *Trachurus japonicus* and jellyfish. Hydrobiologia 616:269–277

Merceron M, Fevre-Lehoerff GL, Bizouarn Y (1995) Fish and jellyfish in Brittany (France). Equinoxe 56:6–8

Molinero JC, Ibanez F, Nival P, Buecher E, Souissi S (2005) North Atlantic climate and northwestern Mediterranean plankton variability. Limnol Oceanogr 50:1213–1220

Molinero JC, Ibanez F, Souissi S, Buecher E, Dallot S, Nival P (2008) Climate control on the long-term anomalous changes of zooplankton communities in the Northwestern Mediterranean. Global Change Biol 14:11–26

Morand P, Carré C, Biggs DC (1987) Feeding and metabolism of the jellyfish *Pelagia noctiluca* (Scyphomedusae, Semaeostomae). J Plankton Res 9:651–665

Morand P, Goy J, Dallot S (1992) Recrutement et fluctuations à long-terme de *Pelagia noctiluca* (Cnidaria, Scyphozoa). Institut océanographique, Paris

Muller W (1965) Experimentelle Untersuchungen fiber Stockentwicklung, Polypdifferenzierung und Sexual chimaerenbei *Hydractinia echinata*. Wilhelm Roux Arch Entw Mech Org 155:181–268

Nakar N, DiSegni DM, Angel D (2012) Economic valuation of jellyfish bloom on the fishery sector. In: Proceedings of the 13th annual BIOECON conference, Genève, Sept 2012

Nastasi A (2010) Algal and jellyfish blooms in the Mediterranean and Black Sea: a brief review. GFCM workshop on algal and jellyfish blooms in the Mediterranean and Black Sea, Istanbul, 6th/8th Oct 2010, 59 pp

Nastav B, Malej M, Malej A Jr, Malej A (2013) Is it possible to determine the economic impact of jellyfish outbreaks on fisheries? A case study – Slovenia. Mediterr Mar Sci 14(1):214–223

Palanques A, García-Ladona E, Gomis D, Martin J, Marcos M, Pascual A, Puig P, Gili J-M, Emelianov M, Monserrat S, Guillén J, Tintoré J, Segura M, Jordi A, Ruiz S, Basterretsea G, Font J, Blasco D, Pagès F (2005) General patterns of circulation, sediment fluxes and ecology of the Palamòs (La Fonera) submarine canyon, northwestern Mediterranean. Prog Oceanogr 66:89–119

Papathanassiou E, Anagnostaki K (1987) Occurrence of *Pelagia noctiluca* in Greek waters during summer 1983. Biol Gallo-Hellenica 12:149–158

Pingree G, Abend L (2006) Spain's beaches and flora feel the heat. Available at http://www.csmonitor.com/2006/0914/p07s02-woeu.html

Piraino S (1991) The adaptive pattern of growth and reproduction of the colonial hydroid *Clavopsella michaeli*. Hydrobiologia 216(217):229–234

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. J Mar Biol Assoc UK 85:461–476

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:27–44

Purcell JE, Malej A, Benović A (1999) Potential links of jellyfish to eutrophication and fisheries. In: Malone TC, Malej A, Harding LW Jr, Smodlaka N, Turner RE (eds) Ecosystems at the land-sea margin. Drainage basin to coastal sea. American Geophysical Union, Washington, DC, p. 381

Purcell JE, Uye S, Lo W (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar Ecol Prog Ser 350:153–174

Purcell JE, Sabatés A, Fuentes V, Pagès F, Tilves U, Olariaga A, Gili J-M (2012) Predation potential of blooming jellyfish, *Pelagia noctiluca*, on fish larvae in the NW Mediterranean Sea PICES annual meeting, Hiroshima

Ramšak A, Stopar K, Malej A (2007) Dispersal ecology of scyphomedusae *Pelagia noctiluca* and *Rhizostoma pulmo* in the European Southern Seas. International Biogeography Society, Tenerife, Canary Islands, 9–13 Jan 2007

Rosa S, Pansera M, Granata A, Guglielmo L (2013) Interannual variability, growth, reproduction and feeding of *Pelagia noctiluca* (Cnidaria: Scyphozoa) in the Straits of Messina (Central Mediterranean Sea): linkages with temperature and diet. J Mar Syst 111–112:97–107

Rubio P, Muñoz JM (1997) Predicción estival del riesgo de blooms de *Pelagia noctiluca* (litoral central catalán). In: Novau JC (ed) Situaciones de riesgo climático en España. Instituto Pirenaico de Ecología, Jaca (Huesca), pp 281–287

Russell FS (1970) The Medusae of the British Isles volume II: pelagic scyphozoa, with a supplement to the first volume of Hydromedusae. Cambridge University Press, Cambridge. ISBN 521 07293 X, 284 p

Rutter T (2010) Managing risk and uncertainty. Workshop on advancing the aquaculture agenda. Paris 15th/16th April 2010. http://www.oecd.org/dataoecd/11/3/45400772.pdf

Sabatés A, Gili JM, Pagès F (1989) Relationship between zooplankton distribution, geographic characteristics and hydrographic patterns off the Catalan coast (Western Mediterranean). Mar Biol 103:153–159

Sabatés A, Salat J, Masó M (2004) Spatial heterogeneity of fish larvae across a meandering current in the northwestern Mediterranean. Deep-Sea Res I 51:545–557

Sabatés A, Olivar MP, Salat J, Palomera I, Alemany F (2007) Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Prog Oceanogr 74:355–376

Sabatés A, Pagès F, Atienza D, Fuentes V, Purcell JE, Gili J-M (2010) Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. Hydrobiologia 645:153–165

Sacchetti F (2012) Il ritorno di MeteoMedusa. Focus 237:92–94

Sandrini LR, Avian M (1989) Feeding mechanism of *Pelagia noctiluca* (Scyphozoa: Semaeostomeae); laboratory and open sea observations. Mar Biol 102:49–55

Stebbing ARD (1980) Increase in gonozooid frequency as an adaptive response to stress in *Campanularia flexuosa*. In: Tardent P, Tardent R (eds) Developmental and cellular biology of coelenterates. Elsevier North-Holland Biomedical Press, Amsterdam, pp 27–32

Stebbing ARD (1981) Hormesis – stimulation of colony growth in *Campanularia flexuosa* (Hydrozoa) by copper, cadmium and other toxicants. Aquat Toxicol 1:227–238

Stemmann L, Prieur L, Legendre L, Taupier-Letage I, Picheral M, Guidi L, Gorsky G (2008) Effects of frontal processes on marine aggregate dynamics and fluxes: an interannual study in a permanent geostrophic front (NW Mediterranean). J Mar Syst 70:1–20

Stiasny G (1921) Mittheilungen über Scyphomedusen. I Zool Meded Rijks Mus nat Hist Leiden 6:109–113

Tilves U, Purcell JE, Marambio M, Canepa A, Olariaga A, Fuentes V (2012) Predation by the scyphozoan *Pelagia noctiluca* on *Mnemiopsis leidyi* ctenophores in the NW Mediterranean Sea. J Plankton Res 35:218–224

UNEP (1984) UNEP: Report on the workshop on jellyfish blooms in the Mediterranean, Athens, 31 Oct–4 Nov 1983, 221 pp

UNEP (1991) Jellyfish blooms in the Mediterranean. In: Proceedings of the II workshop on jellyfish in the Mediterranean Sea. MAP Technical Reports Series No 47. UNEP, Athens

Vlachos P, Kontoes P (1987) Epidemiology and therapeutic methods of jellyfish poisoning in Greece. In: Proceedings. IInd workshop on jellyfish in the Mediterranean, Trieste, pp 302–308

Vučetić T (1984) Some causes of the blooms and unusual distribution of the jellyfish *Pelagia noctiluca* in the Mediterranean (Adriatic). UNEP: Report on the workshop on jellyfish blooms in the Mediterranean; Athens, 31 Oct–4 Nov 1983, pp 167–176

Vučetić T (1991) Hydrobiological variability in the Middle Adriatic in relation with the unusual distribution or behavior of *Pelagia noctiluca*. UNEP: Jellyfish blooms in the Mediterranean proceedings of the II workshop on jellyfish in the Mediterranean Sea MAP Tech Rep Ser, No 47. UNEP, Athens, pp 188–201

Würtz M (2012) Mediterranean submarine canyons: ecology and governance. IUCN, Gland/ Málaga, 216 pp

Zavodnik D (1987) Spatial aggregations of the swarming jellyfish *Pelagia noctiluca* (Scyphozoa). Mar Biol 94:265–269

Zavodnik D (1991) On the food and feeding in the northern Adriatic of *Pelagia noctiluca* (Scyphozoa). UNEP: Jellyfish blooms in the Mediterranean proceedings of the II workshop on jellyfish in the Mediterranean Sea MAP Tech Rep Ser, No 47. UNEP, Athens, pp 212–216

EXTREME ECOLOGICAL EVENTS: THE IMPORTANCE OF DETERMINISTIC AND STOCHASTIC DRIVERS OF JELLYFISH OUTBREAKS

EXTREME ECOLOGICAL EVENTS: THE IMPORTANCE OF DETERMINISTIC AND STOCHASTIC DRIVERS OF JELLYFISH OUTBREAKS

Running Head: JELLYFISH OUTBREAKS

Lisandro Benedetti-Cecchi*[1], Antonio Canepa[2], Veronica Fuentes[2], Laura Tamburello[1], Pat Halpin[3], Stefano Piraino[4], Jennifer E. Purcell[5] and Jason Roberts[3]

[1]Department of Biology, University of Pisa, CoNISMa, Via Derna 1, Pisa, Italy

[2]Institut de Ciencies del Mar, Consejo Superior de Investigaciones Científicas, ICM-CSIC.
Passeig Marítim de la Barceloneta, 37-49. 08003 Barcelona, Spain

[3]Marine Geospatial Ecology Laboratory, Nicholas School of the Environment, Duke University, Durham, NC, USA

[4]Università del Salento, CoNISMa via Monteroni, 73100 Lecce, LE, Italy

[5]Western Washington University, Shannon Point Marine Center, Anacortes, WA 98221, USA.

*Correspondence to:
Lisandro Benedetti-Cecchi; e-mail lisandro.benedetti.cecchi@unipi.it
Address: Department of Biology, University of Pisa, Via Derna 1, 56126 Pisa, Italy

KEYWORDS: climate change, environmental extremes, environmental bootstrap, species outbreaks, jellyfish blooms, *Pelagia*

Type of paper: Primary Research Article

Abstract

Jellyfish outbreaks are increasingly viewed as a deterministic response to escalating levels of environmental degradation and climate extremes. However, a comprehensive understanding of the influence of deterministic drivers and stochastic environmental fluctuations favouring population renewal processes has remained elusive. This study quantifies the deterministic and stochastic components of environmental change that lead to favourable conditions for jellyfish outbreaks. Using data of jellyfish abundance collected at 243 sites along the Catalan coast from 2007 to 2010 we: (1) tested alternative hypotheses about the influence of time-varying and spatial predictors of jellyfish outbreaks; (2) evaluated the relative importance of stochastic vs. deterministic forcing of outbreaks through the environmental bootstrap method (EBM) and (3) quantified return times of extreme events. An important contribution of our work is extension of the EBM by allowing a statistical model to determine the likelihood that an extreme outbreak will occur, which can make this method applicable to a wide range of ecological problems. Outbreaks were common in May and June and less likely in other summer months, which resulted in a negative relationship between outbreaks and SST. Cross-shore advection by geostrophic flow was an important concentrating force of jellyfish, whereas outbreaks were associated with proximity of canyons. This result supported the recently proposed hypothesis that canyons can funnel jellyfish blooms during upwelling. Return time values indicated that extreme outbreaks were likely to be encountered in a century or millennium only slightly more frequently than in a decade. Thus, the rate of jellyfish outbreaks should not increase along the Catalan coast as a consequence of environmental fluctuations. Overall, deterministic processes were more important than the stochastic component of environmental variation, suggesting that alignment in space and time of the environmental variables selected had little influence on jellyfish outbreaks. Our ability to anticipate these extreme events future will require a better understanding of how environmental drivers affect demographic and population processes in jellyfish species.

Introduction

Extreme events such as droughts, storms and floods are becoming more frequent with climate change (IPCC, 2012). These environmental changes may provoke extreme ecological responses in populations and species assemblages that may result in severe impacts to natural ecosystems (Gaines & Denny, 1993; Katz *et al.*, 2005; Kreyling *et al.*, 2011; Thompson *et al.*, 2013). Species outbreaks are examples of extreme ecological events that may be driven by extreme climate conditions (Danovaro *et al.*, 2009; Nelson *et al.*, 2013). Outbreaks occur when the alignment in space and time of certain environmental drivers (abiotic and biotic), result in particularly favourable conditions for population renewal processes (Boero, 1994; Denny *et al.*, 2009). Defining these conditions quantitatively and understanding when and where they will occur are key tasks to forecast species outbreaks.

The environmental envelope that provides favourable conditions for population renewal is just one realization of a virtually infinite number of possible combinations of environmental conditions (Denny *et al.*, 2009). Each realization is the result of a combination of deterministic and chance events. Deterministic events reflect what is known about population responses to environmental drivers. The relationship between temperature and organismal growth and development is an example (Chown & Gaston, 1999). Thus, global warming provides a deterministic vector of environmental change. Unfortunately, for many other drivers our understanding of how they impinge on natural populations is limited, let alone our understanding of the compounded effects of multiple drivers (Crain *et al.*, 2008; Darling & Côté, 2008). Chance events reflect our unknowns, which can be treated as stochastic vectors of environmental change.

Deterministic events can be identified by relating environmental drivers to species outbreaks through appropriate statistical techniques such as multiple regression and related approaches (Dormann *et al.*, 2007; Lima *et al.*, 2007). Addressing stochastic events requires randomization procedures, so that observed probabilities of occurrence of outbreaks can be compared to those expected from chance alone. The environmental bootstrap method (EBM) has been specifically designed for this purpose (Denny *et al*., 2009). The method consists of bootstrapping relatively short (5-10 yrs) time series of environmental variables to determine the probability that a particular set of conditions (e.g. the combination of high nutrients and extreme temperatures that can favour outbreaks of exotic species) will occur by chance alone. In its original formulation the procedure used mechanistic response functions to translate environmental extremes into meaningful biological responses. In principle, the method is not restricted to mechanistic response functions, but can be extended to any class of models that relate biological variables to environmental data. For example, one might use a multiple regression approach to determine the circumstances under which species outbreaks becomes more likely and couple this statistical model with the EBM to determine the probability that the event will occur by chance alone, at any place and time for which a short history of environmental data is available.

Jellyfish blooms are examples of species outbreaks that may have adverse effects on fisheries and tourism and are therefore of great concern to scientists, policy makers and the public at large (Richardson *et al.*, 2009; Purcell, 2012). Although the drivers of jellyfish blooms are not fully understood, they likely involve a combination of climate events and local anthropogenic stressors. Recent findings have documented decadal oscillations in jellyfish blooms, which may be explained by climatic oscillations, lunar cycles and internal population dynamics (Purcell, 2005, 2012; Condon *et al.*, 2013). Local drivers that may favour jellyfish blooms include changes in food web structure owing to the depletion of potential predators and competitors from overfishing, human modification of coastal habitats, including the proliferation of artificial structures that may provide habitats for jellyfish benthic stages, species introductions from shipping and eutrophication (Purcell, 2012; Duarte *et al.*, 2013). These effects can be exacerbated by global change events such as warming temperatures, which may positively affect jellyfish population processes and vital rates (Purcell *et al.*, 2012; Lucas & Dawson, 2014).

This study quantifies the deterministic and stochastic components of environmental change that lead to favourable conditions for jellyfish outbreaks along the Catalan coast in Spain. We employed a Bayesian analysis to relate jellyfish spatio-temporal dynamics to a set of explanatory environmental variables and coupled the resulting model with the EBM to assess the relative importance of deterministic vs. stochastic chance events leading to jellyfish outbreaks. We used sea surface temperature (SST), chlorophyll *a*, geostrophic current velocities and distance from the nearest canyon as environmental predictors of jellyfish outbreaks. SST provided a surrogate measure for environmental energy, which is important for many metabolic functions (Lucas *et al.*, 2012; Purcell *et al.*, 2012). Chlorophyll *a* was a surrogate for local productivity and food availability (Attrill *et al.*, 2007). Zonal and meridional current velocities were included as potentially important predictors of jellyfish advection. Distance from the nearest canyon was included as a covariate to examine the recently proposed hypothesis that when occurring near the cost, these physiographic features of the deep sea environment can operate as a convey belt driving jellyfish blooms during upwelling (Canepa *et al.*, 2014). This hypothesis applies more specifically to holoplanktonic jellyfish species, such as *Pelagia noctiluca*. The specific objectives of this study were: (1) To test alternative hypotheses about the influence of time-varying and spatial predictors of jellyfish outbreaks; (2) to evaluate the relative importance of stochastic vs. deterministic forcing of outbreaks and (3) to quantify return times of extreme jellyfish outbreaks along the Catalan coast.

Materials and methods

Data

We use a dataset consisting of semi-quantitative measures of the abundance of eight species of jellyfish collected at 243 sites along the Catalan coast (Spain). Monitored species were: *Aequorea forskalea* Péron & Lesueur, *Aurelia aurita* (Linnaeus), *Chrysaora hysoscella* (Linnaeus), *Cotylorhiza tuberculata* (Macri), *Pelagia noctiluca* (Forsskål), *Physalia physalis* (Linnaeus), *Rhizostoma pulmo* (Macri) and *Velella velella* (Linnaeus). The data have been collected through a Citizen Science program under the supervision of the Catalan Water Agency on a daily basis from May to September from 2007 to 2010. Further details of this dataset can be found in Canepa *et al.* (2014). We defined an outbreak as the occurrence of at least one jellyfish m^{-2}, corresponding to an abundance class of two in the dataset. We downloaded daily values of SST, chlorophyll *a* and geostrophic current velocities from publically available databases from May 1 to September 30 for the years 2004-2010 (Table S1). These data matched the seasons of jellyfish sampling, but extended backwards in time to enable the characterization of the recent environmental history of each site. Distance from the nearest canyon was determined for each site using the *marmap* library in R (Pante & Simon-Bouhet, 2013).

The dataset based on daily occurrence of jellyfish blooms had too many zeros, precluding a meaningful spatio-temporal analysis of daily outbreaks. To mitigate this problem we combined data across species and computed the number of days with outbreaks over monthly periods for each year at each site. This resulted in 20 data points (four years x five months) for each of the 243 sites. Although jellyfish blooms that are observed over short time intervals (days or weeks) may be part of the same outbreak, we will refer to the number of days in a month in which an outbreak was observed just as the number of outbreaks, for simplicity. Pooling data across species was not ideal, because of differences in life-history traits and ecology. For example, *P. noctiluca*, which alone accounted for 34% of the recorded outbreaks, differs from the other species in that it lacks a benthic stage. However, aggregation by species eliminated possible problems of species misidentification due to the involvement of non-specialists in sampling activities.

Bayesian hierarchical analysis

We modelled the number of outbreaks through a Bayesian hierarchical analysis based on the INLA approach (Integrated Nested Laplace Approximation) that ensured efficient computation (Rue *et al.*, 2009). We compared the performance of three models of increasing complexity with respect to how spatial and temporal information was used. The simplest model considered only random spatial variation among sites. The model of intermediate complexity accounted for temporal autocorrelation through a first order AR (1) autoregressive process, in addition to random spatial variation. Finally, the more complex analysis modelled spatial dependencies through a Gaussian Markov Random Field (GMRF) and temporal autocorrelation as an autoregressive AR (1) process. We implemented the GMRF representation using the SPDE method (Stochastic Partial Differential Equation) (Lindgren *et al.*, 2011; Cameletti *et al.*, 2013).

Briefly, a GMRF is a spatial process that models the spatial dependence of data through the definition of a neighbourhood structure based on geographic coordinates, so that only sites within a certain distance from each other are spatially correlated, whereas sites further distances apart are spatially independent. The SPDE approach represents the GMRF through a fine mesh triangulation (e.g., using Delaunay triangulation) of the study area where the latent variable (the true unobserved value of the response variable) is modelled at the vertices of the triangles. Sampling locations that fall within a triangle (i.e. that are not on a vertex) take the average value of the three nearby vertices. We specified a mesh with 721 vertices with the largest density of triangles located along the coast in correspondence of the sampling sites (Fig. S1). The outer triangles were uninformative and had lower resolution. Obviously, triangles falling on land were meaningless.

Spatial dependencies were modelled through the Matérn spatial covariance function with scale and smoothness parameters κ and ν that define the empirically derived relation $\rho = \sqrt{8\nu/\kappa}$, where ρ is the distance at which spatial correlation becomes close to 0.1, for each ν (with ν=1 in calculations).

In the spatio-temporal context, the GMRF $\boldsymbol{\zeta}_t = (\zeta(s_1, t), \ldots, \zeta(s_n, t))$, with s_1 to s_n sampling sites, is modelled as a first order autoregressive process:

$$\boldsymbol{\zeta}_t = a\boldsymbol{\zeta}_{t-1} + \omega_t, \qquad \boldsymbol{\omega}_t \sim N(\mathbf{0}, \mathbf{Q}^{-1}) \tag{1}$$

where $\mathbf{Q}_s$ is a sparse precision matrix of size *n*, corresponding to the number of vertices of the domain triangulation and with $\boldsymbol{\zeta}_1 \sim N(\mathbf{0}, \mathbf{Q}_s^{-1}/(1-a^2))$. $\mathbf{Q}_s = \boldsymbol{\Sigma}^{-1}$, where $\boldsymbol{\Sigma} = \boldsymbol{\sigma}_w^2 C(h)$ is the covariance matrix with *C(h)* being the Matérn spatial correlation function for the Euclidean distance lags *h*. This formulation assumes that $\mathbf{Q}_s$ does not change through time, which means that the GMRF has a constant correlation structure and changes through time according at a first order autoregressive process.

Thus, for the most complex of our models, the number of outbreaks at time *t* (with time defined by a specific year x month combination) at the *i*-th site, was modelled as a Poisson process y_{it} ~ Poisson (λ_{it}), with mean λ_{it} and with the linear predictor defined on the logarithmic scale as:

$$\eta_{it} = \log(\lambda_{it}) = \mathbf{z}_{it}\boldsymbol{\beta} + \sum_{j=1}^{G}\mathbf{B}_{ij}\boldsymbol{\zeta}_t \qquad (2)$$

where $\mathbf{z}_{it}$ is a vector of p covariates for site i at time t, $\boldsymbol{\beta}$ is the vector of p coefficient parameters (including the intercept) and $\mathbf{B}_{ij}$ is the sparse matrix that maps the GMRF $\boldsymbol{\zeta}_t$ from the individual sites to the G triangulation nodes (j=1,….,G).

In addition to SST, chlorophyll *a*, geostrophic current velocities and distance from the nearest canyon, models included year and month of sampling as covariates. We employed non informative priors in Bayesian computation and used the Deviance Information Criterion (DIC) and the Root-Mean-Square-Error (RMSE) from 10-fold cross validation to compare the model in Eq. 2 with simpler formulations based on spatial and temporal random effects. We also explored variants of each of these models that considered the presence/absence rather than the number of outbreaks in each month (with binomial errors and logit link function), zero-inflated versions of the Poisson and binomial distributions and the zonal and meridional components of wind velocities instead of current velocities. These models yielded very similar results, so we will present results based on the Poisson distribution and geostrophic current velocities. This analysis was done using the *inla* library in R (Martino & Rue, 2010).

The environmental bootstrap

The selected model was used iteratively with the EBM to determine the probability of observing a jellyfish outbreak under stochastic environmental fluctuations. The procedure started by smoothing the time series of environmental variables with a sliding window of 15 days (other choices of smoothing windows in the range of 9-31 days did not affect the results). The sliding window combined environmental observations for the same period across years (for example, from the 1 to 15 January for all years from 2004 to 2010) from which a mean and a standard deviation were obtained for the focal day of 7 January in this case. The mean was subtracted from the observed value and the difference was divided by the standard deviation to obtain a standardized residual for the focal day. The sliding window then moved to the next day and so on until the whole series of observations was smoothed (the first and last observations were repeated to fill the series at its boundaries).

The core of the EBM is the separation of the deterministic part of the signal from the stochastic component, the residuals, so that they can be randomized over time. Randomization is possible if residuals are statistically interchangeable, which implies that they are independent and identically distributed. Independence was assessed by estimating for each environmental variable the decorrelation time – i.e. the number of days at which the autocorrelation function reached zero. We used the number of days for the variable with the longest decorrelation time to define the length (in days) of the segments of standardized residuals to randomize. Standardized residuals had approximately mean zero and standard deviation of one within segments, so that they could be considered identically distributed for practical purposes. Another assumption is that the shape of the distribution of standardized residuals is not correlated with the smoothed means – i.e. the deterministic component of the signal. To assess this assumption we calculated an index of skewness as the ratio between the sample third central moment and the sample variance in each window of the series of standardized residuals, and inspected this index for any linear correlation with the smoothed means.

After randomization, the residuals were added back to the deterministic component of the signal. The first element in the randomized series was multiplied by the standard deviation calculated for the first point in the original time series and added to the expected value for that point, and so forth until a new hypothetical record of the time series was generated. This procedure was applied simultaneously to all the environmental variables and sampling sites, so that residuals were randomized in blocks to preserve the correlation structure among variables and the spatial correlation among sites.

One iteration of the procedure generated a hypothetical realization of environmental variables with the same predictable component of the original signal, but with environmental anomalies and extreme events reallocated randomly in time. A subset of the newly generated data matching the period of jellyfish sampling was then extracted from the randomized series and used as covariates to predict from the fitted model. Predictions were obtained by adding up the components of the linear predictor, the residuals and then back-transforming to the scale of the response variable.

We iterated the entire procedure 10000 times to calculate return times of jellyfish outbreaks using the generalized extreme value distribution (GEV) (Gaines & Denny, 1993; Katz *et al.*, 2005). The GEV distribution was fitted to the maximum value of jellyfish outbreaks observed over the 243 sites at each iteration, separately for each month. To compare the relative importance of deterministic and stochastic events, we randomized the deterministic component of the data in the same way as we did for the residuals. We then compared the standard deviations of jellyfish outbreaks obtained from the randomization of the stochastic and deterministic components of the environmental data. The rationale behind this analysis is that the randomization of a weak predictor will have little effect on the predicted values of the response, so that outcomes will be similar across bootstrapped replicates at any given site. In contrast, a strong predictor will generate more variability among bootstrapped replicates, with the predicted value of the response changing at any site in relation to the particular value of the predictor assigned to that site for each iteration. Standard deviations were obtained at the site level and compared between the two randomization schemes with the Wilcoxon signed-rank test, matching data by site. Analyses were done in R (R Core Team 2013).

Results

Jellyfish outbreaks were more frequent in May and June, particularly in the years 2009 and 2010 (Fig. 1). Data provided greater support to a GMRF spatio-temporal model than did the spatial GMRF and random-effect models (Table1). Outbreaks were negatively associated with SST and distance to the nearest canyon, and positively associated with the meridional component of geostrophic current velocities; all the posterior mean estimates of these covariates differed significantly from zero (Table 2). There was also a significant negative association between jellyfish outbreaks and month of sampling, reflecting the larger frequency of outbreaks in spring-early summer than in late summer (Fig. 1, Table 2). In contrast, the posterior coefficients for chlorophyll, the zonal component of geostrophic currents and year of sampling did not differ significantly from zero (Table 2).

A map of the posterior mean of jellyfish outbreaks (on the logarithmic scale) indicated that the locations most affected were those in the northern and southern parts of the study region, with considerable spatial heterogeneity at intermediate locations (Fig. 2). Further evidence of spatial heterogeneity was provided by a weak correlation coefficient (ρ) which, albeit significant, decreased sharply to 0.1 at the distance of 0.044 km (Table 2). In contrast, the analysis estimated a first-order temporal autocorrelation coefficient (a) of 0.32, which did not differ significantly from zero (Table 2).

The EBM enabled us to calculate the cumulative probability function and the probability density curves of annual maxima (over the 243 sites) of jellyfish outbreaks. Outbreaks were most frequent in May and June (Fig. 3a, b). Outbreaks were more likely in June than May, but the difference was less than one event. This analysis also suggested that the return time for the maximum number of outbreaks (6 outbreaks observed in a month) was 6.5 years (Fig. 3c).

The 100- and 1000-years return values were very close to the observed maximum number of outbreaks (Fig. 3c).

Randomization of standardized residuals, as implemented in the EBM, resulted in lower standard deviations among bootstrap replicates than observed in the residuals of the deterministic component of the environmental predictors (Fig. 4). The Wilcoxon signed-rank test of the null hypothesis that the data came from the same population was rejected (W=4209, $P<0.0001$).

Discussion

Jellyfish outbreaks may be a deterministic response to escalating levels of environmental degradation exacerbating their intrinsic oscillations (Purcell, 2012; Condon *et al.*, 2013; Duarte *et al.*, 2013). A global rising trend in SST is a point in case. Several studies have reported the coincidence of greater abundances of jellyfish with warm conditions and experiments have shown how increasing temperatures may enhance asexual production in several gelatinous species (Purcell, 2012 supplement Table 2; Purcell *et al.*, 2012). This evidence has raised concern that jellyfish outbreaks may become more frequent with global warming. Global climate change, however, includes many factors in addition to warming, including increased frequency and intensity of extreme precipitation events, runoff and storms. In addition to climate change, other potentially important drivers of jellyfish outbreaks, such as nutrient pollution, habitat modification and overfishing are increasing globally in coastal regions (reviewed in Purcell, 2012). While all these potential causes of jellyfish outbreaks have been widely acknowledged, a comprehensive understanding of the influence of individual drivers and their potential synergistic or antagonistic interactions has remained elusive. In principle, multiple causality should make compounded effects and chance events more likely.

Our results indicated that deterministic processes were more important than the stochastic component of environmental variation, suggesting that alignment in space and time of the selected environmental variables, *i.e.* the compounded effects among environmental variables, had little influence on jellyfish outbreaks. SST and the meridional component of geostrophic currents were significant time-varying predictors, but their signal was not strong enough to avert deterministic effects. The negative relationship we found between jellyfish outbreaks and SST reflected seasonal effects, with outbreaks being more frequent in cool waters during spring and early summer than in the warmer months. By contrast, the positive relationships between jellyfish abundance and SST in the literature reflect interannual variability or regional effects (reviewed in Purcell, 2012). Our results were constrained by the sampling, which excluded fall and winter months. The seasonal patterns documented here were consistent with evidence that *P. noctiluca* declines during the summer (Boero, 1994; Rosa, 2013; Canepa *et al*., 2014); however, they were inconsistent with evidence on other species, whose populations peak during summer in the same region (Purcell *et al*., 2012).

The meridional component of geostrophic currents was positively associated with jellyfish outbreaks, indicating that advection by geostrophic flow was an important cross-shore concentrating force. Although the role of currents as drivers of concentration of gelatinous plankton has been widely recognized (Graham *et al.*, 2001; Ferraris *et al.,* 2012), the predominant flow in the study area is determined by the position of the Northern Current in the Ligurian Sea and it is in the along-shore direction (Birol *et al.*, 2010). While cross-shore transport has been inferred from modelling studies (Berline *et al.*, 2013), the effect of onshore displacement over the main flow due to submarine canyons and its effects on mass transportation have poorly been assessed (Jordi *et al.*, 2005) . As with any other regression analysis, the effect of a particular covariate was evaluated after adjusting for the effects of the other covariates in our Bayesian model. This analysis accounted for the effect of another important spatial predictor, distance from the nearest canyon, for spatiotemporal gradients in SST and also modelled spatial dependencies explicitly through the Matérn covariance function. Thus, by taking into account different sources of spatiotemporal variation, the analysis was able to detect cross-shore advection patterns that might have gone undetected by looking at geostrophic currents in isolation from other drivers of jellyfish outbreaks.

A similar argument may explain the lack of a significant association between chlorophyll a and jellyfish outbreaks. Chlorophyll *a* concentration is a surrogate for phytoplankton abundance, and more chlorophyll *a* could lead to greater availability of zooplankton prey to jellyfish. Some evidence of such food-web interactions comes from the North Sea, where nematocyst occurrence was positively related to the phytoplankton colour index (Attrill *et al.*, 2007). Opposite effects have shown the effect of trophic cascades where the presence of jellyfish predators consumed and reduced herbivores, leading to higher levels of phytoplankton or chlorophyll *a* (Feigenbaum & Kelly, 1984; Daskalov *et al.*, 2007). Nevertheless, phytoplankton typically peaks before zooplankton populations in spring (Boero, 1994). As our results showed, the corresponding peak in jellyfish outbreaks had already occurred by spring months of sampling in the statistical analysis.

Jellyfish outbreaks declined as distance from the canyons increased. This result supported the recent hypothesis that canyons promote *P. noctiluca* aggregation and vertical migration so that outbreaks should be more frequent in coastal areas near these physiographic features of the sea floor (Canepa *et al.*, 2014). This hypothesis applies particularly to *P. noctiluca*, which undergoes a deep daily vertical migration (Franqueville, 1971). Our analysis combined all species; nevertheless, the effect of canyons was significant. This probably reflected the fact that many (34%) of outbreaks events in the dataset involved *P. noctiluca*. It is noteworthy, however, that important outbreaks also occurred in the southwest part of the study region where canyons were not present (Fig. 2a). Possibly, this pattern reflected the deflections associated with the predominant along-shore current that increases retention in the southern Catalan Sea (Salat, 1995), although the zonal component of geostrophic velocities was not significant in the analysis. The considerable patchiness of jellyfish outbreaks along the coast also underscored the influence of local oceanographic features and hydrological patterns that likely interacted with topography or coastal prominences (Gili *et al.*, 1988). Location of sites did not affect these results because analysis modelled spatial dependencies through a GMRF or setting spatial autocorrelation as random.

The EBM was developed to investigate the effects of stochastic extreme environmental fluctuations on ecological and biological response variables (Denny *et al.*, 2009; Denny & Dowd, 2012). They used this procedure to assess the effect of extreme wave forces on mussel dislodgment and the influence of heat stress on limpet mortality on rocky intertidal shores. These analyses used mechanistic response functions to translate the distribution of maximum values of physical variables into meaningful biological responses.

Instead of using a mechanistic response function, which was unavailable for jellyfish outbreaks, we used a statistical model to determine the likelihood that an extreme outbreak will occur by chance alone in a random year. This is a potentially important extension of the EBM that can make this method applicable to a wide range of ecological problems, not only those for which mechanistic response functions or physiological models are available. Our results indicated that outbreaks were more likely in June and May than in any other summer month of a random year, as observed in the empirical data. Return time values also indicated that extreme outbreaks likely occurrence within a century or millennium were only slightly more likely than within a decade, in accord with periodicity previously reported by Kogovšek *et al* (2010), for the Adriatic Sea. Thus, the frequency of jellyfish outbreaks should not increase along the Catalan coast as a consequence of environmental fluctuations.

Jellyfish populations often show a cyclic pattern of temporal variation with periods varying among species and locations, but that involve decadal oscillations related to climate (Goy *et al.*, 1989; reviewed in Purcell, 2005, 2012, Condon *et al.*, 2013). The data available to us did not allow trends or periodicities to be evaluated; however, we observed jellyfish outbreaks throughout the study period with peaks varying between May or June depending on the year of sampling. These short term, often irregular events are less emphasized in the literature than the more regular temporal patters, but interannual variation is often dramatic in jellyfish populations (Purcell, 2012).

As an alternative to stochastic environmental fluctuations, which were of limited importance in our study, demographic processes provided a valid explanation for irregular outbreaks (Boero *et al.*, 2008). Most jellyfish species reproduce asexually from benthic polyps, have exceptionally high growth rates and can tolerate stressful environmental conditions (e.g. anoxia) (Purcell *et al.*, 1999; Lucas *et al.*, 2012; Purcell, 2012). While deterministic factors such as canyons, currents and possibly other local hydrological processes can explain the occurrence and distribution of jellyfish, population-level processes are the proximate cause of outbreaks. Thus, a better understanding of how environmental factors affect population and demographic processes in jellyfish species, can greatly improve our ability to anticipate their outbreaks in the future.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge financial support by the European Community Seventh Framework Programme (FP7/2007–2013) for the project VECTORS (grant agreement no. 266445). A.C. was supported by a doctoral fellowship from the Chilean National Commission for Scientific and Technological Research (CONICYT – PFCHA/Doctorado al Extranjero 4a Convocatoria, 72120016).

REFERENCES

Attrill MJ, Wright J, Edwards M (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography,* **52**, 480-485.

Berline L, Zakardjian B, Molcard A, Ourmières Y, Guihou K (2013) Modeling jellyfish *Pelagia noctiluca* transport and stranding in the Ligurian Sea. *Marine Pollution Bulletin,* **70**, 90-99.

Birol F, Cancet M, Estournel C (2010) Aspects of the seasonal variability of the Northern Current (NW Mediterranean Sea) observed by altimetry. *Journal of Marine Systems,* **81**, 297-311.

Boero F (1994) Fluctuations and variations in coastal marine environments. *Marine Ecology,* ***15***, 3-25.

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

Cameletti M, Lindgren F, Simpson D, Rue H (2013) Spatio-temporal modeling of particulate matter concentration through the SPDE approach. *Asta-Advances in Statistical Analysis,* **97**, 109-131.

Canepa A, Fuentes V, Sabatés A, Piraino S, Boero F, Gili J-M (2014) *Pelagia noctiluca* in the Mediterranean Sea. In: *Jellyfish Blooms.* (eds Pitt Ka, Ch L) pp Page., Springer Netherlands.

Chown SL, Gaston KJ (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Reviews of the Cambridge Philosophical Society,* **74**, 87-120.

Condon RH, Duarte CM, Pitt KA *et al.* (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences of the United States of America,* **110**, 1000-1005.

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters,* **11**, 1304-1315.

Danovaro R, Umani SF, Pusceddu A (2009) Climate change and the potential spreading of marine mucilage and microbial pathogens in the Mediterranean Sea. *Plos One,* **4**.

Darling ES, Côté IM (2008) Quantifying the evidence for ecological synergies. *Ecology Letters,* **11**, 1278-1286.

Daskalov Georgi M, Grishin Alexander N, Rodionov Sergei, and Mihneva Vesselina (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceeding of the National Academy of Sciences of the United States of America,* **104**, 10518-10523.

Denny MW, Dowd WW (2012) Biophysics, environmental stochasticity, and the evolution of thermal safety margins in intertidal limpets. *Journal of Experimental Biology,* **215**, 934-947.

Denny MW, Hunt LJH, Miller LP, Harley CDG (2009) On the prediction of extreme ecological events. *Ecological Monographs,* **79**, 397-421.

Dormann CF, Mcpherson JM, Araujo MB *et al.* (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography,* **30**, 609-628.

Duarte CM, Pitt KA, Lucas CH *et al.* (2013) Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment,* **11**, 91-97.

Feigenbaum D, Kelly M (1984) Changes in the lower Chesapeake Bay food chain in presence of the sea nettle *Chrysaora quinquecirrha* (Scyphomedusa). *Marine Ecology Progress Series*, **19**, 39-47.

Ferraris M, Berline L, Lombard F *et al.* (2012) Distribution of *Pelagia noctiluca* (Cnidaria, Scyphozoa) in the Ligurian Sea (NW Mediterranean Sea). *Journal of Plankton Research*.

Franqueville C (1971) Macroplancton profond (invertébrés) de la Méditerranée nord-occidentale. *Tethys,* **3**, 11–56.

Gaines SD, Denny MW (1993) The largest, smallest, highest, lowest, longest, and shortest - Extremes in ecology. *Ecology,* **74**, 1677-1692.

Gili JM, Pagès F, Sabatés A, Ros JD (1988) Small-Scale Distribution of a Cnidarian Population in the Western Mediterranean. *Journal of Plankton Research,* **10**, 385-401.

Goy J, Morand P, Etienne M (1989) Long-Term Fluctuations of Pelagia-Noctiluca (Cnidaria, Scyphomedusa) in the Western Mediterranean-Sea - Prediction by Climatic Variables. *Deep-Sea Research Part a-Oceanographic Research Papers,* **36**, 269-279.

Graham WM, Pages F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia,* **451**, 199-212.

IPCC (2012) Managing the risk of extreme evnts and disasters to advance climate change adaptation In: *A special report of working groups I and II of the Intergovernmental Panel on climate change.* (eds Field CB, Barros V, Stocker TF, Dahe Q, Dokken DJ, Ebi KL, Mastrandrea MD, Mach KJ, Plattner G-K, S.K. A, Tignor M, Midgley PM) pp Page., Cambridge University Press, Cambridge.

Jordi A, Orfila A, Basterretxea G, Tintoré J (2005) Shelf-slope exchanges by frontal variability in a steep submarine canyon. *Progress in Oceanography,* **66**, 120-141.

Katz RW, Brush GS, Parlange MB (2005) Statistics of extremes: Modeling ecological disturbances. *Ecology,* **86**, 1124-1134.

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

Kreyling J, Jentsch A, Beierkuhnlein C (2011) Stochastic trajectories of succession initiated by extreme climatic events. *Ecology Letters*, **14**, 758-764.

Lima FP, Ribeiro PA, Queiroz N, Xavier R, Tarroso P, Hawkins SJ, Santos AM (2007) Modelling past and present geographical distribution of the marine gastropod Patella rustica as a tool for exploring responses to environmental change. *Global Change Biology,* **13**, 2065-2077.

Lindgren F, Rue H, Lindstrom J (2011) An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. *Journal of the Royal Statistical Society Series B-Statistical Methodology,* **73**, 423-498.

Lucas C H, Graham W M, & Widmer C (2012) Jellyfish life histories : role of polyps in forming and maintaining scyphomedusa populations. *Advances in Marine Biology,* **63**, 133-196.

Lucas C H & Dawson M N (2014) What are jellyfishes and thaliaceans and why do they bloom? In K A Pitt & C H Lucas (Eds.) *Jellyfish Blooms* (pp. 9–44). Springer Netherlands. doi:10.1007/978-94-007-7015-7_2

Martino S, Rue H (2010) Case studies in Bayesian computation using INLA. *Complex Data Modeling and Computationally Intensive Statistical Methods*, 99-114.is the volume missing?

Nelson WA, Bjornstad ON, Yamanaka T (2013) Recurrent insect outbreaks caused by temperature-driven changes in system stability. *Science,* **341**, 796-799.

Pante E, Simon-Bouhet B (2013) Marmap: A package for importing, plotting and analyzing bathymetric and topographic data in R. *Plos One,* **8,** e73051. doi:10.1371/journal.pone.0073051.

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review.Journal of the Marine Biological Association of the United Kingdom, 85, 461-476.

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. In: *Annual Review of Marine Science,* **4**, 209–235. Purcell JE, Atienza D, Fuentes V, Olariaga A, Tilves U, Colahan C, Gili JM (2012) Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. *Hydrobiologia,* **690**, 169-180.

Purcell JE, Malej A. Benović A (1999) Potential links of jellyfish to eutrophication and fisheries. In: *Ecosystems at the land-sea margin: drainage basin to coastal sea*, Malone TC, Malej A, Harding, LW Jr., Smodlaka N, Turner RE (eds.), *Coastal and Estuarine Studies*, **55**, 241-263.

R Core Team (2013) R: A language and environment for statistical computing. pp Page, R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution*, **24**, 312-322.

Rosa S, Pansera M, Granata A, Guglielmo L (2013) Interannual variability, growth, reproduction and feeding of *Pelagia noctiluca* (Cnidaria: Scyphozoa) in the Straits of Messina (Central Mediterranean Sea): Linkages with temperature and diet. *Journal of Marine Systems*, **111–112,** 97–107.

Rue H, Martino S, Chopin N (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, **71**, 319-392.

Salat J (1995) The interaction between the catalan and balearic currents in the southern Catalan Sea. *Oceanologica Acta*, **18**, 227-234.

Thompson RM, Beardall J, Beringer J, Grace M, Sardina P (2013) Means and extremes: building variability into community-level climate change experiments. *Ecology Letters*, **16**, 799-806.

SUPPORTING INFORMATION

Table S1. Sources and spatial and temporal extents of environmental data for the Catalan coast

Fig. S1. Constrained refined Delanuay triangulation of the study region. Red dots are jellyfish sampling sites along the Catalan coast.

Table 1. Model comparisons of jellyfish outbreaks along the Catalan coast

Model	DIC	$\overline{D}$	p_D	RMSE
Spatial (random effect)	3406.6	3331.3	75.3	0.538
Spatial (random effect), AR(1)	3339.8	3320.3	19.6	0.580
Spatio-temporal (GRMF), AR(1)	2967.5	2868.1	99.4	0.481

DIC: Deviance Information Criterion; $\overline{D}$: posterior mean of the deviance; p_D: effective number of parameters; GMRF: Gaussian Markov Random Field;AR(1); autoregressive temporal effect; RMSE: root mean square error

Table 2. Spatio-temporal Bayesian model of jellyfish outbreaks along the Catalan coast

Covariate	Mean	SD	Quantiles (95% credible interval)		
			0.025	0.5	0.975
Intercept	-0.4024	0.1679	-0.7319	-0.4024	-0.0730
Distance from nearest canyon	-0.0043	0.0021	-0.0086	-0.0043	-0.0002
SST	-0.0198	0.0072	-0.0340	-0.0198	-0.0056
Chl	-0.1238	0.1650	-0.4480	-0.1238	0.1998
Current zonal	0.0042	0.0048	-0.0052	0.0042	0.0137
Current meridional	0.0116	0.0050	0.0018	0.0116	0.0213
Month	-0.0769	0.0231	-0.1223	-0.0769	-0.0315
Year	-0.0002	0.0001	-0.0004	-0.0002	0.0000
σ_t^2	0.6564	0.2556	0.3123	0.6017	1.3034
σ_w^2	0.4366	0.0848	0.2946	0.4286	0.6270
ρ	0.0441	0.0124	0.0247	0.0423	0.0733
a	0.3420	0.1958	-0.0493	0.3452	0.7034

FIGURE LEGENDS

Fig. 1. Timing of jellyfish outbreaks along the Catalan coast. Bars from black to light grey correspond to sampling months from May to September in each year.

Fig. 2. Posterior mean (a) and standard deviation (b) of the Gaussian Markov Random Field on the logarithmic scale. Arrows indicate the approximate location of canyons near the coast: Cape De Creus (CC), Fondera (FC), Blanes (BC) and Tarragona (TC) canyons. Cyan color away from the coastline has little predictive value since it corresponds to the low resolution area of the triangulation mesh (see Fig. S1).

Fig. 3. Empirical cumulative (a) and probability density (b) distributions and return time plot (c) for extreme jellyfish outbreak events obtained from the environmental bootstrap analysis. Calculations are done for the month of May (dash-dot line) and June (continuous line) of a random year.

Fig. 4. Frequency distributions of site standard deviations of jellyfish outbreaks over 10000 bootstrapped replicates for the stochastic (grey bars) and deterministic (black bars) components of the environmental data.

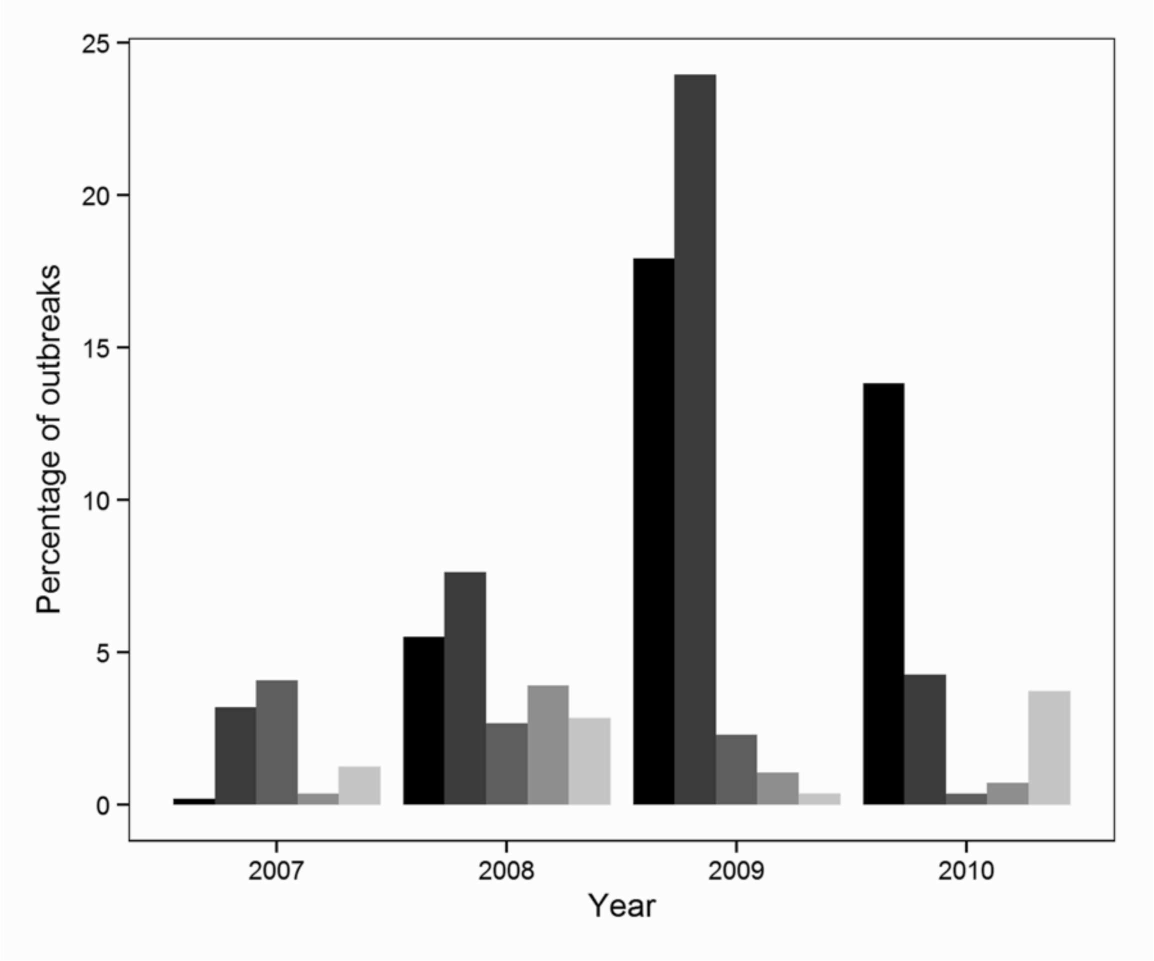


Fig. 1. Benedetti-Cecchi et al.

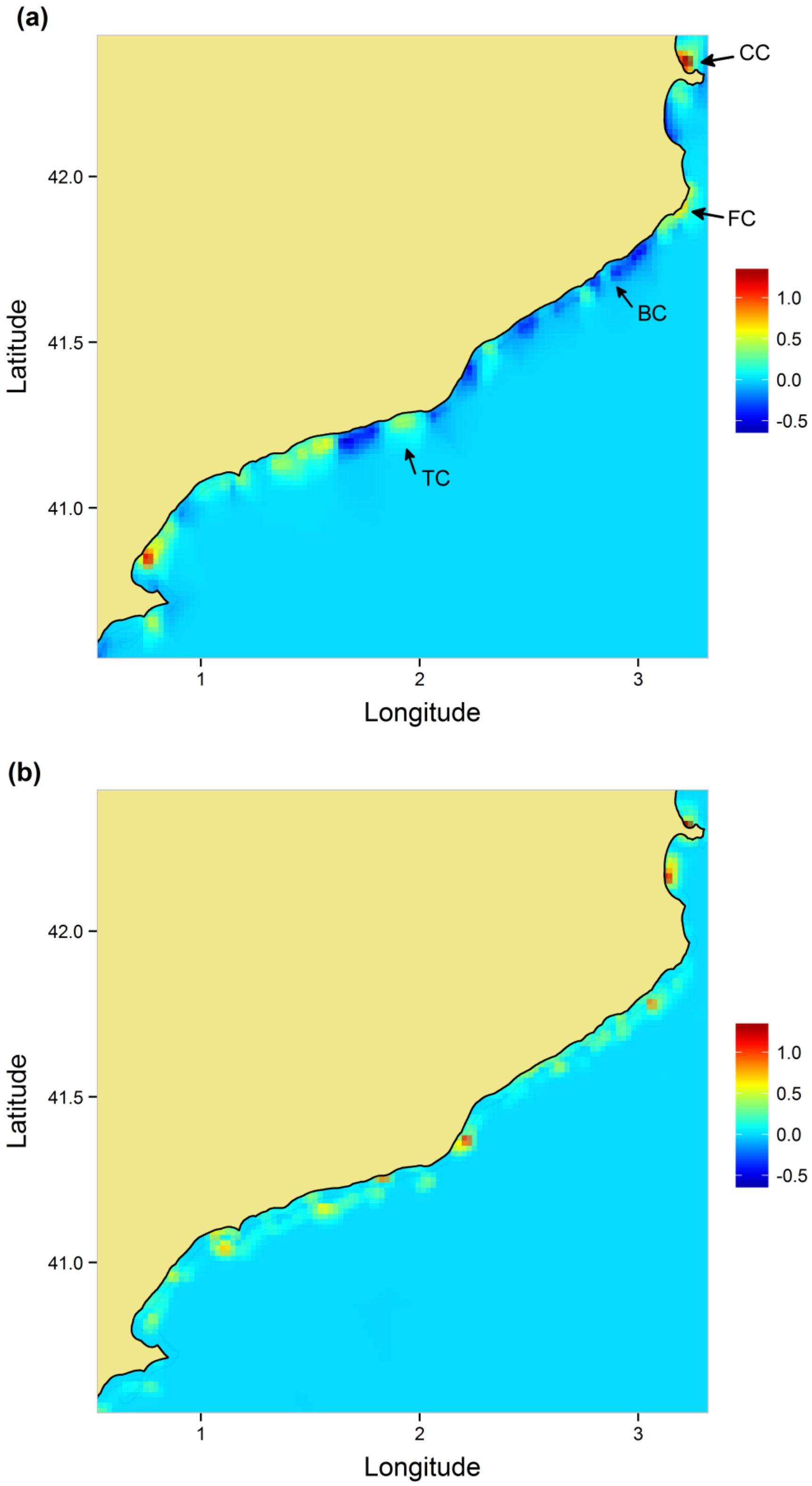


Fig. 2. Benedetti-Cecchi et al.

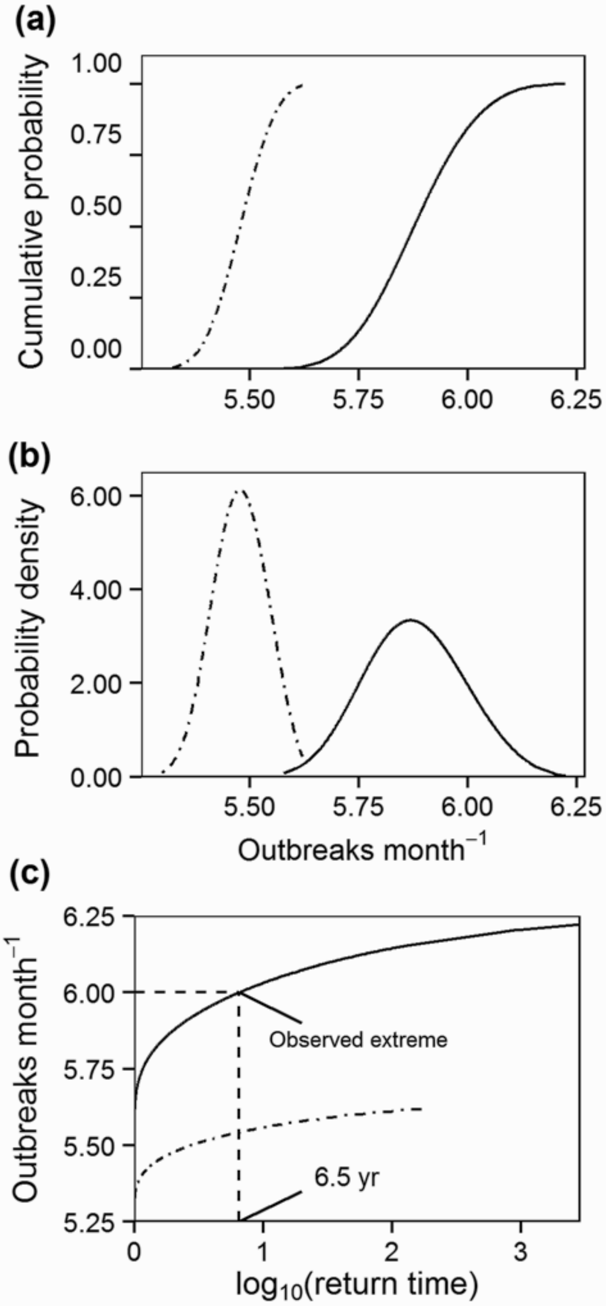


Fig. 3. Benedetti-Cecchi et al.

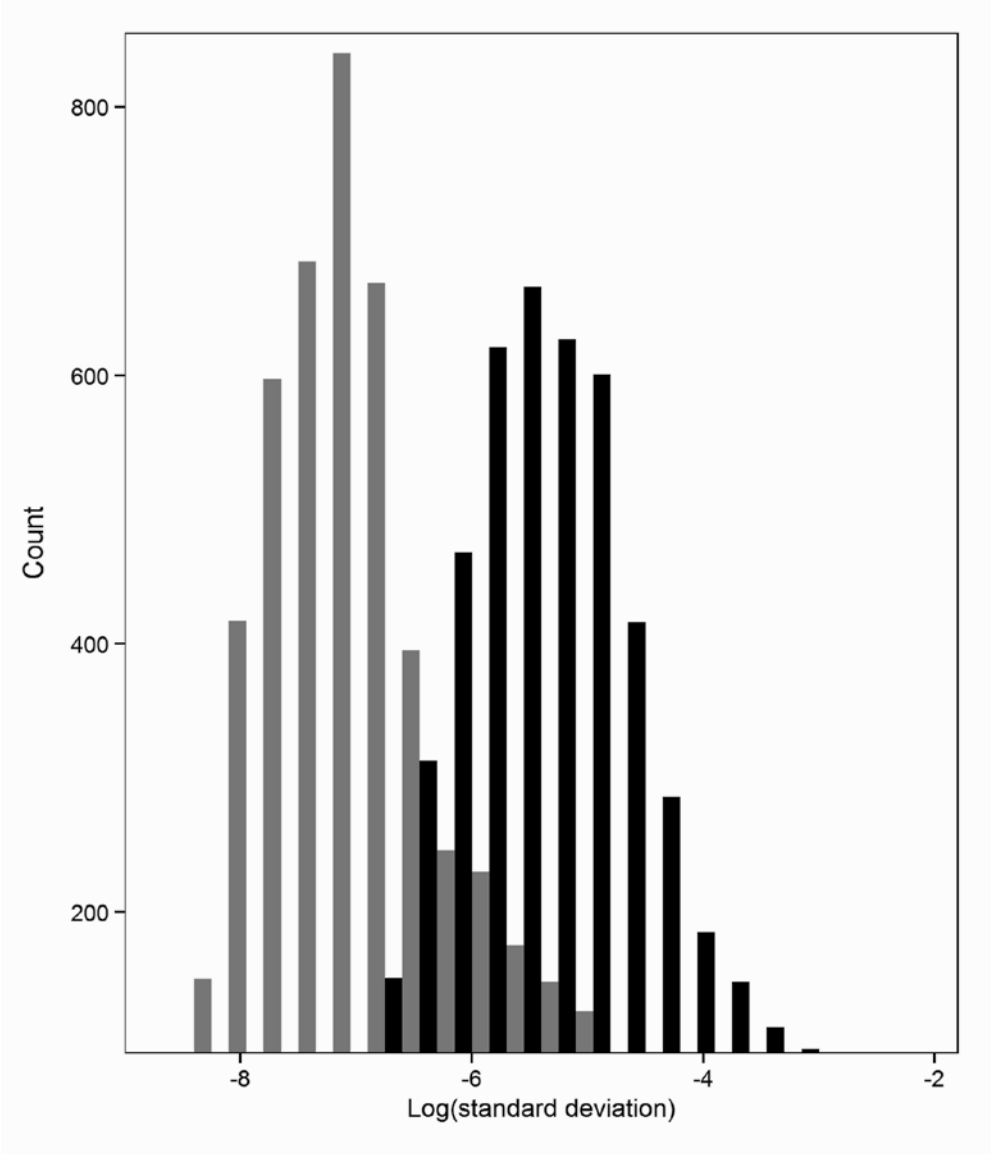


Fig. 4. Benedetti-Cecchi et al.

Table S1. Source and extent of environmental data

Variable	Source	Temporal extent	Spatial resolution
Sea Surface Temperature	GHRSST Level 4 MUR http://podaac.jpl.nasa.gov/dataset/JPL-L4UHfnd-GLOB-MUR	01/05/2004 30/09/2010	1 km
Chlorophyll *a* concentration	Ocean Color MEaSUREs project http://wiki.icess.ucsb.edu/measures/index.php/GSM	01/05/2004 30/09/2010	9 km
Geostrophic currents	AVISO product http://www.aviso.oceanobs.com/index.php?id=1275	01/05/2004 30/09/2010	1/8°x1/8° (14 km)

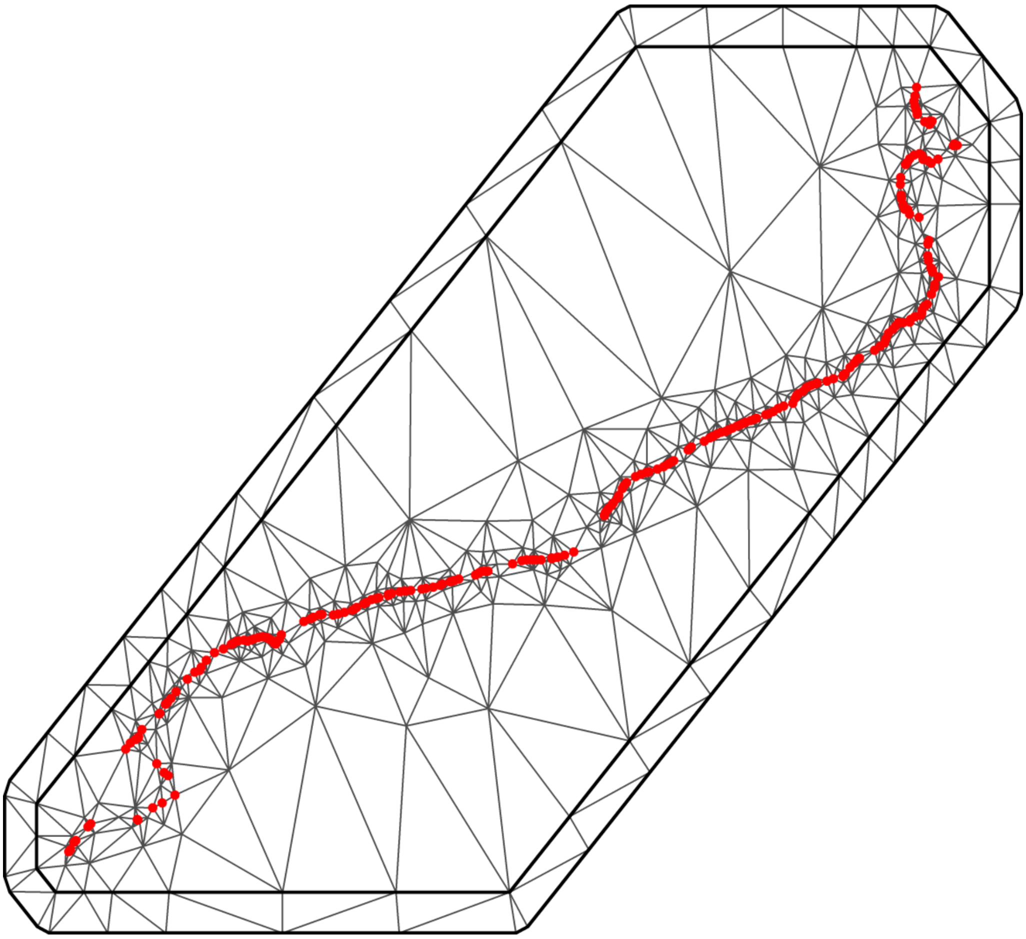


Fig. S1. Constrained refined Delanuay triangulation of the study region. Red dots are jellyfish sampling sites.

Beach recreationist's preferences for lower risk of jellyfish outbreaks: economic results from a stated-choice experiment in Catalonia, Spain

Beach recreationist’s preferences for lower risk of jellyfish outbreaks: economic results from a stated-choice experiment in Catalonia, Spain

Paulo A.L.D Nunes[1, 2], Maria Loureiro[3], Laia Piñol[4], Sergio Sastre[2], Louinord Voltaire[5] and Antonio Canepa[2]

[1]Policy and Technical Experts Committee– WAVES Wealth Accounting and Valuation of EcosystemServices,Agriculture and Environment Services Department, TheWorld Bank

[2]Institut de Ciencies del Mar – CSIC, 37-49 PasseigMarítim de la Barceloneta, 08013Barcelona, Spain

[3]Departamento de Fundamentos da Análise Económica, Facultade de Ciencias Económicas, Universidade de Santiago de Compostela, 15782 Campus Norte, Avda Burgo das Nacións, 15704 Santiago de Compostela, Spain

[4]LEITAT Technological Center – MaritimeDivision, 2, Carrer de la Innovació, 08225 Terrassa, Spain

[5]UMR-AMURE, Université de BretagneOccidentale (UBO) 12, rue de Kergoat, 29200 Brest,France

ABSTRACT: The painful and sometimes dangerous stings of pelagic cnidarians are an increasing problem around the world. Jellyfish blooms and their consequences appear to be increasing around the Mediterranean Sea. The Spanish coast of Catalonia is 580 km long and constitutes a world-leading coastal tourist destination. In 2012, 263.7 million recreational beach visits were registered. In 2012, qualified interviewers administered an in situ socio-economic questionnaire to 644 tourists to determine their preferences for beach recreation. We used a state-choice questionnaire and a Random Utility Model to estimate how much respondents were willing to spend, in terms of reported extra travel time, for lower risk of jellyfish outbreaks. The estimation results indicated that respondents were willing to spend an additional 23.8% of their travel time to enjoy beach recreation is areas with a lower risk of jellyfish outbreak. Economists interpret this result as reiterating the importance of reducing the risk of jellyfish outbreaks in the consumption of beach recreation activities. This estimate, combined with the respondents' mean income, yielded annual economic gains associated with reduction of jellyfish outbreaks on the Catalan coast ranging between €312 and €322 million, approximately 9% of the tourism expenditures in 2012. From the policy perspective, this study confirms the urgency to provide daily information by use of the wide set of social media applications. The current lack of knowledge about jellyfish suggests that providing such information to beach recreationists is the only effective policy instrument to minimize the impact of jellyfish outbreaks.

Keywords: socio-economic questionnaire, stated choice survey, economic valuation, jellyfish outbreaks, risk perception, travel time, econometrics, welfare.

INTRODUCTION

Although jellyfish are a natural feature of the Mediterranean Sea, “jelly blooms” are recurring events. Such events represent an inconvenience for swimmers and certain species even present a significant health hazard (Mariottini & Pane 2010). Media have increased people’s awareness about jellyfish blooms (Condon et al. 2012), thus intensifying reports about this phenomenon on the Catalan coast for the period 1980-2012 (reviewed in Canepa et al. 2014). Jellyfish are considered detrimental to fish and fishing, because they clog fishing nets, keep away fish and consume fish eggs and larvae (Purcell & Arai 2001, Sabatés et al. 2010). The resulting socio-economic impacts, both direct (tourism) and indirect (coastal development, fisheries), have become tangible and significant. Although overfishing, coastal habitat degradation and climate warming are amongst the most probable drivers (Purcell 2012), the economic impacts and consequences of such outbreaks remain poorly known.

Very few studies report the impacts of jellyfish outbreaks on the economic sectors. Some estimates exist in fisheries, as for the Gulf of Mexico shrimp fishery (Graham et al. 2003), the Black Sea anchovy fishery (Knowler 2005), the Peruvian anchovy fishery (Quiñones et al. 2012), and multiple fisheries in Korea (Kim et al. 2012) and Slovenia (Nastav et al. 2013). Kim et al. (2012) estimated that the impacts of jellyfish outbreaks in Korea´s various fisheries ranged between 2.1% and 25% of the total value of the catches. However, jellyfish outbreaks have many more consequences than those suffered by the fishing fleet, including potentially severe losses in recreational sectors. Economic valuation of tourism and recreational losses due to jellyfish outbreaks is very limited or nonexistent. The present paper addresses this gap and constitutes the first econometric valuation study of both market and non-market losses.

The objective of this paper is to assess the impact of jellyfish outbreaks in recreationists’ preferences in Catalonia (Spain). Catalonia is a region in northeastern Spain with 580km of coastline and constitutes a top coastal tourist destination. In 2012, 263.7 million beach recreational visits were reported (Catalunya Turística en Xifres 2012). We tested the impact of the risk of jellyfish outbreaks on beach recreationists by computing the implicit value of the additional time that visitors were willing to travel in order to reduce the probability of encountering a jellyfish outbreak at the beach.

MATERIALS AND METHODS

Survey design and implementation

The 221 beaches along the coast of Catalonia were classified according to a set of parameters including the municipality/location, the beach area, the water quality/visibility, the level of occupancy/congestion and the type of the surrounding environment, ranging from urban to natural. The combination of these elements allowed us to profile the beaches and helped to select beaches that are representative for the entire Catalan coastline for our study (Table 1).

The beaches selected had different profiles and, therefore, could attract different users, or consumers of beach recreation activities, as well as different uses of the beach. For example, Barceloneta is a semi-closed urban beach located in a highly touristic neighborhood in Barcelona with a high occupation level. Bogatell is a closed urban beach located in the urban area of Barcelona and highly occupied. Sabanell is a semi-closed beach located in a semi-urbanized area in Blanes. Blanes is a closed urban beach located in the city of Blanes. Gran de Palamós is a semi-closed beach located in the urban centre of Palamós with a high visitation, but a low occupation due to its large extent. Fosca is a closed beach located in La Fosca neighbourhood in Palamós with a high occupancy level. Castell is a closed natural beach located between the municipalities of Palamós and Palafrurgell, inside the Castell-Cap Roig, a natural area protected by the Plan for Spaces of Natural Interest. Golfet is a closed natural beach also located in the Castell-Cap Roig area, next to a low urbanized area south of Calella de Palafrurgell, highly occupied due to its small area.

In addition to the sampling of the beaches, we drafted and tested the survey protocol by means of several focus groups and a pilot experience held on the beach. Those activities allowed us to optimize the wording, the use of visual-aids and the overall understanding of the final questionnaire by the respondents. In addition, a training session of the surveyors was conducted in the Institut de Ciències del Mar, CSIC, in order to prepare them for the face-to-face survey. Each surveyor was debriefed about the nature and the objective of the questionnaire and given a toolbox for this operation, including a set of *verbatim* explanations of the questions. At this stage, the final questionnaire was ready for execution.

The final questionnaire consisted of six sections (Supplement 1). The first questions focused on profiling the respondent with respect to the set of recreational activities that they use on the beach, the size and the composition of people in their group, the number of the days on the beach during the 2011 summer season, the number of days expected during the 2012 summer season, the distance to the beach, whether nautical sports will be played, as well as the importance attached to recreational activities and other features in choosing the beach. The second section requested information regarding the travel cost and expenditures incurred to visit the beach (e.g. travel cost and travel time, accommodation cost on that day, meal cost on that day). Respondents were also asked to report the means of transportation they used to get to the beach, including walking. Among the non-residents, information was also collected on the respondents' type of accommodation, including holiday home, hotel or staying with friends/relatives. The third section focused on eliciting the socio-economic impacts of jellyfish outbreaks, including profiling the respondent's experience with respect to jellyfish stings and the potential economic cost of treatment.

In the fourth section, respondents faced the stated choice exercise or a choice experiment (CE). For this task, ten multiple choice cards consisting of three different options were presented to every respondent. The first two options, showed two beaches with different recreational opportunities. The third, as recommended by Adamowicz et al. (1998), was a non-choice option offering alternatives that included the opportunity to stay at home or do any recreational activity other than going to the beach. It was presented to participants because this is an obvious element of choice behavior. Recreational opportunities were characterized by four main attributes:(1) the risk of jellyfish outbreak at the beach, (2) the water quality of the beach, (3) the infrastructure and services available at the beach, (4) the proposed additional travel time (with respect to the reported travel time to reach the beach) that the respondent would incur to reach the beach being considered (Table 2). Respondents were presented with a given stated choice question (Fig. 1).

Respondents were placed in a hypothetical day of leisure situation, for which three recreational options were available on that particular day. The first two options were to visit either Beach A or Beach B, with beaches differing by attributes; the third option (status quo) provided the opportunity to do something else or stay at home. In order to reduce the dimensionality of the choice design (i.e. the multiple possible combinations), the discrete choice experiment was limited to four attributes: (1) the risk of jellyfish outbreak of the beach, (2) the water quality of the beach, (3) the infrastructure and services available at the beach, (4) the proposed additional travel time (with respect to the reported travel time to reach the beach) that the respondent would be incurring to reach the beach under consideration (Table 2). The first two attributes had two levels and the others had three levels. Attributes and their levels were selected from discussions with marine experts in Catalonia, focus groups and pilot studies. The number of hypothetical beach profiles generated was $2^2*3^2 = 36$. To reduce the cognitive burden for respondents, fractional factorial designs were used, which resulted in 18 profiles (i.e. 9 choice sets). These choice sets were blocked into Survey A and Survey B containing 4 and 5 choice sets, respectively. We followed state-of-the-art methodological protocol (Carson et al. 2009) randomly gave each respondent one survey type. The final section of the questionnaire had a set of socio-economic and demographic variables of the respondent, including age, nationality and the household income. At the end of the questionnaire, the respondent was given a cold soft drink as a sign of appreciation for their participation.

The questionnaire was administered in Catalan, Spanish and English through a face-to-face interview by a team of trained surveyors. The interviews were conducted in two distinct time frames, 10:00-14:00 and 15:00-19:00. The questionnaires were executed during weekdays and weekends from 14 June to 15 September 2012. Only beach visitors aged 18 years or over were interviewed. Surveyors used the shoreline as a reference line and walked ten meters straight along the shoreline or from the shoreline inland to randomly encounter each respondent. When possible, interviews were conducted only with beachgoers between the shoreline and the first 30 meters, which is considered to be the useful beach area (Sardá 2009). Beachgoers were mainly approached while they were laying and sunbathing on a towel, while they were coming out of the sea, and while they were walking along the shoreline. Surveyors were identified by a badge and were charged with giving the respondents the specific context, explaining the aim of the study as well as the estimated duration of the survey. Two teams of surveyors were established to cover the 4 southern and the 4 northern beaches studied, respectively. The questionnaire took about 15 min for each respondent to complete.

Economic model

In order to elicit individuals' preferences for the various beaches represented in the choice cards, we used a CE framework, which allowed individuals to select between different beach alternatives, as above. From the economic modeling view point, this attribute-based choice method has its theoretical grounding in Lancastrian consumer theory (Lancaster 1996), which proposes that individual welfare is based on the consumption of goods and services, which is expressed in terms of their characteristics and respective contribution to welfare or utility. The underlying fundamental assumption is that individuals act rationally, selecting the consumption bundle, and respective characteristics, that yields the highest utility (McFadden 1973, Hanemann & Kanninen 1999). In our study, we applied this economic model to analyze the behavior of the beach recreationist and, in particular, the demand for beach recreation opportunities. This was presented in terms of the selection of the beach to visit. The model is described in accordance with a set of characteristics and the respondents selected the beach destination according to the characteristics of the location. In formal terms, we can represent a beach recreationist as an individual *i*'s whose utility associated with the choice of a beach-alternative *j* is described as:

$$U_{ij} = V(Z_j, S_i) \qquad (1)$$

Where, for any respondent *i*, a given level of utility will be associated with any of the alternatives proposed *j*. The derived utility depends on the attributes of the proposed beach-scenarios (Z_j) and respondent's socio-economic characteristics (S_i).

From the individual's point of view, the selection of a beach scenario, as described in the survey, is the result of maximizing the utility; thus, the respondent's stated choice, as reported in the survey by selection of the beach scenario, is the one that yields the highest utility. In this context, the probability of any particular alternative *j* being chosen can be expressed as:

$$P_{ij} = \frac{exp[V(Z_{ij}, S_i)]}{\sum_{h \in C} exp[V(Z_{ih}, S_i)]} \qquad with\ j = 1, 2, \ldots J \qquad (2)$$

Bearing in mind the present beach attributes, we estimated the following empirical specification:

$$U_{ij} = \beta_1 additionaltime_{ij} + \beta_2 additionaltime_{ij}^2 + \beta_3 waterquality_{ij} + \beta_4 services_{ij} + \beta_5 riskofjellyfishoutbreak_{ij} + \varepsilon_{ij} (3)$$

In other words, the utility that the respondent *i* has from selecting beach *j* depends on the four attributes under consideration, including additional travel time, beach water quality, the services available at the beach, as well as the risk of a jellyfish outbreak. The indirect utility function was constructed to include all attributes that defined the choice elections, which contained a trade-off between traveling time and different beach characteristics. Furthermore, non-linear effects were explored. In particular, we tested for the possibility that additional travel time affected the choice behavior in a non-linear way. In other words, we tested empirically that the marginal impact of this characteristic was not constant.

Bearing in mind the respondents' answers to the stated choice survey, we estimated the parameters β_s. These parameters are random and unknown to the economist. Therefore, we proposed to estimate these exploring the use of a conditional logit model (McFadden 1973).

RESULTS

Data description

We received 644 completed questionnaires by respondents averaging 42 years old. Tourists in Catalonia constituted about 57% of our sample and reported planning to stay about 16 days on holidays at the coast. In addition, international tourists represented about 24% of the respondents (Table 3).

Three quarters of respondents planned to stay at the beach less than half a day, while 21% planned to stay at the beach half a day and 6% the whole day. This means that the consumption of beach recreation opportunities is concentrated in a couple of hours, and the median respondent spends less than half a day at the beach. About half of the respondents came to the beach on foot or bicycle; 39% used a car and 13% public transportation. The average time taken to reach the beach was around 22 min. We also observed a wide distribution of traveling time, ranging from about 5 min (first quartile) to 3 h (fourth quartile). In addition, about 61% of the respondents reported that were never stung by a jellyfish and did not know anyone who has been stung. About 22% had been stung by a jellyfish and 17% knew someone who had been stung. Finally, the median respondent had an education above high school, most had a job and a household income between 2,000€ and 4,000€ per month.

Estimation results

Estimation of the main effects model was reported in Equation 3. Model I refers to the main effects model because we only considered the direct effects of the characteristics in choice of the beach scenario. We interpreted this as our baseline model specification. All coefficients carried the expected sign and were statistically significant (Table 4).

In particular, we observed that the estimated coefficient with respect to jellyfish outbreaks was negative. This means that a beach scenario described in the questionnaire with a higher risk of jellyfish outbreak was associated with a negative impact on the utility of the respondent and therefore less likely to be chosen. The estimation results showed that increasing the risk of jellyfish outbreak reduced the probability of the choice of that beach by 34.5%. By contrast, increases in the water quality and the range of services provided at the beach increased the probability of that choice by 73% and 41%, respectively. Thus, we inferred that the most relevant characteristic to explain the respondent's choice was water quality, followed by surrounding services/infrastructure and then by lower risk of jelly fish outbreaks. These estimates were robust because the respective parameter estimates did not change according to Models II to IV.

The empirical data on additional travel time in this study did not reject the null hypothesis and showed the presence a non-linear effect of travel time on utility. The first additional minutes of travel time were associated with a utility gain and increased the probability of choice. We interpreted this result indicated that the travel time to reach the beach, which was seen mainly in trips by bicycle and on foot, was associated with a positive impact in the utility by the respondent. In other words, the respondent enjoyed the time spent to reach the beach. One of the first illustrations of this type of situation was presented by Walsh et al. (1990) who developed and applied a statistical procedure to estimate a demand function for the recreation activity of pleasure driving or sightseeing by car on scenic river highways in the Rocky Mountains. In our present study, the consumptive value of travel time was positive until a point. Mathematically, this point is computed from the equation:

$$\frac{dU}{dt} = \frac{d(0.079t - 0.001t^2)}{dt} = 0.079 - 0.002t = 0 \tag{4}$$

In our study, this occurred when t=39.5 min. Thus, after 39.5 min any additional traveling time produced a negative impact on utility. After this point, respondents considered that reaching the beach may require using other transport, such as a car or subway, which reduced the pleasure in walking or biking to the beach. Our estimates of travel time were robust because the parameter estimates did not change with respect to the Models II to IV.

In addition, we estimated the impact of beach and respondent characteristics on their stated choices. After many empirical checks, we assessed the impact of being at the beach Blanes, which had the lowest jellyfish risk, as recorded from 2006 to 2010 (Canepa unpublished data). This effect was captured by the variable Jellyfish risk * Blanes in see Model II (Table 4). We also assessed the impact of being stung. This effect was captured by the variable Jellyfish risk * Stunning Model III (Table 4). Finally, we also evaluated the impact in the stated choices of being a resident. This effect was captured by the variable Jellyfish risk * Resident in Model IV (Table 4). The estimation results showed that the respondents that chose the beach Blanes revealed preferences for which the risk of jellyfish was not important to their stated choices, when compared to the average respondent. The estimation results from Model II and III showed that increased risk of jellyfish outbreak reduced the probability of the choice of the beach by 37.4 to 40.0%, on average. These results may indicate that these respondents have already adapted to the risk of jellyfish outbreaks by selecting the beach with the lowest risk profile. Estimation results from Model III also showed that increased jellyfish risk reduced the probability of the choice of the beach by 28.9% amongst respondents who reported previously being stung. However, this marginal impact was not statistically significant at the 90% confidence interval. In other words, the empirical evidence supported a statistical difference of risk profiles, i.e. with respect to the impact of reduction of jellyfish risk on beach behavior, among the two respondent segments: stung vs. non-stung. Finally, Model IV showed that residents reported a slightly lower risk aversion to jellyfish outbreaks, but again this difference was not statistically significant.

From these estimation results, we inferred that respondents were willing to travel an average of 3.8 min more to travel from a beach described as having jellyfish outbreaks 5 or more days a week to another beach where the risk is ≤2 days per week. Given that the mean traveling time for the entire sample was 21 minutes, on average, recreationists were willing to travel 23.8% more minutes to reduce the risk of jellyfish outbreak. Furthermore, recreationists were willing to travel about 8 min more, equivalent to 38% of the average time more to find a beach with more services, including children's play area, toilets, parking and lifeguards, in comparison to only toilettes and parking areas, which were presented as basic services available in all scenarios. Water transparency was also significantly valued by beach recreationists, who were willing to travel an average of 4.5 min (21.28%) more to a beach with higher water transparency.

We also considered two sub-groups of the respondents: the frequent beach visitors that were below the median in reported travel time to the beach (t_1 = 5 min), and those near the median (t_2 = 21 min; t_3 = 37 min). Table 5 presents the econometric valuations of the set of attributes under consideration across three time segments. All coefficients carried the expected signs and were statistically significant. The valuation of the attributes (mean willingness to pay estimates) for the entire sample, without splitting into time segments showed that the most valuable attribute was water quality; on average, beachgoers were willing to travel about 8 min additional to find a beach with higher water transparency (Table 6). Beachgoers were willing to travel about 4.5 min extra to find a beach with additional services, including a play area for children and a first aid center. The importance of jellyfish was also significant in terms of beach selection, indicating that recreationists were willing to travel 3.8 min more to reduce the probability of encountering a jellyfish outbreak.

The well-being estimates were obtained by substituting specific values of the distribution of the variable traveled time in the utility function (Fig. 2). This allowed us to observe the relative changes on the respective valuations of attributes with respect to the time traveled to the beach. Thus, respondents were willing to incur different additional travel times for alternative beach consumption patterns, according to their characteristics. Figure 2 shows the marginal (or implicit) prices of the attributes, which depended on both the profile of the respondent in terms of reported travel time, as well as in terms of the beach characteristics considered. First, improvement in the beach water quality was, by far, the most valuable attribute and this ranking was valid across all types of respondents. Second, improvement in the beach infrastructure was ranked second and reduction in the risk of jellyfish outbreaks, third. Finally, from the econometric view point, the difference in ranking between infrastructure and jellyfish risk were not statistically significant, meaning that these attributes were seen as equally important by the respondents of this study.

DISCUSSION

Policy Analysis

As seen from the estimation results, the risk of jellyfish outbreaks plays an important role in explaining individual behavior with respect to the consumption of beach recreation opportunities. Nevertheless, this characteristic, or driving force, of beach recreation consumption, was not the most important one. The estimation results ranked the improvement of the water quality as first; therefore it is interpreted as the most important factor when choosing a beach. The estimation results also informed us that reduction of risk of jellyfish outbreaks ranked as important as the improvement of beach infrastructure, including the provision of additional services, such as playgrounds for children. Furthermore, we can also monetize the survey described lower risk of jellyfish outbreaks by using the concept of value of time. Our sample results indicated that the average household income per hour of our sample population was €19.23. The additional travel time an average consumer was willing to incur to move to a beach with the same characteristics but with lower risk of jellyfish outbreak equated to €1.22.

Because the sampling design of this study guaranteed the regional representativeness of the recreationists of this area, we could scale up this monetary value to the regional level. The 2012 tourist statistics released by the Catalan government showed a total of 263.7 millions of trips to the beach per year for all recreationists (local, domestic and international) in Catalonia. We calculated that the well-being gains associated with a reduction of jellyfish outbreaks in this area would range between €312 and €322 million annually, corresponding approximately to 19% of the tourism expenditures of the Catalan population in 2012. In this case, such significant value shows that preventive policy measures pass a cost benefit analysis as long as their corresponding implementation costs are below €312 million per year.

Similar exercises regarding recreational ecosystem services assessment based on questionnaires have been carried out worldwide. For instance, Hearne &Salinas (2002) evaluated several management options in the context of protected areas in Costa Rica. Nunes & Van den Bergh (2004) and Nunes & Markandya (2008) illustrated the use of alternative, non-market valuation methods to estimate the economic value of the social damage caused by marine bio-invasions on beach recreationists. Underlying economic value assessments were shown to be relevant in undertaking cost-benefit analyses and supported the selection of a policy management practice, including a ballast water treatment plant in the harbor of Rotterdam. In addition, Beaumont et al. (2008) assessed the goods and services resulting from marine biodiversity in the UK. The present exercise also constitutes a valid tool for informing the general public; Remoundou et al. (2009) gives a more comprehensive review on non-market valuation to estimate marine ecosystem services.

All in all, one can argue that from a policy perspective there is significant social relevance for the investment of public resources in mechanisms that deal with management of the jellyfish outbreaks, including daily reports informing the users about the presence or absence of a jellyfish outbreak at each beach. An example of this type of public policy mechanism is the MedJelly application (Marambio et al. 2013) that provides daily observations on the status of the Catalan beaches, including information on the presence of the jellyfish outbreaks[1]. Such informational and public awareness campaigns are useful to provide public jellyfish reports, and to explore the use of new technologies, such as mobile phones, internet and other social media applications, which can provide immediate and real-time information. Such campaigns may help to prevent stigmatization of certain beaches and jellyfish species by raising awareness and knowledge on such species among beach users and citizens. According to the scientific community this may be the most effective policy instrument for adaptation to jellyfish outbreaks.

CONCLUSIONS

In this study we conducted a survey of coastal recreationists in Catalonia in order to understand their preferences when selecting among various beaches that provided different recreational opportunities, with different chances to encounter jellyfish outbreaks. From this exercise, we computed the number of minutes that respondents were willing to travel to find, or avoid, some specific beach characteristics. After knowing the number of minutes that respondents were willing to travel for each beach characteristic, we expressed this value in monetary terms from their mean annual household income. On average, each recreationist was willing to pay €1.22 per trip to the beach to go to a beach with ≤2 days per week of jellyfish outbreaks (low risk) rather than one with jellyfish more than 5 days a week (high risk). By scaling up the implicit personal valuations to the regional level from the 2012 total of 263.7 million of trips to the beach annually for all recreationists in Catalonia, we estimated € 312 - € 322 million per year, which corresponds approximately to 19% of the tourism expenditures on the Catalan coast in 2012. Thus, significant

---

[1] Free download at IphoneAPP store and Google PlayStore as ‘iMedJelly’.

welfare gain associated with reduction of jellyfish outbreaks also shows that preventive and adaptive jellyfish measures pass a cost benefit analysis, as long as their corresponding implementation costs are below €312 million per year. Needless is to say, this pioneering study calls for further socio-economic investigation, including the mapping and distribution of the well-being impacts, discussion and evaluation of other alternative policy measures, including jellyfish fishing and the establishment of nets, as currently are under development and experimentation.

Acknowledgments.

The authors thank the comments and suggestions of three anonymous referees and especially to Jennifer Purcell for her guidance and comments to an earlier version of this manuscript. In addition, the authors are thankful to the feedback posted by the participants of the Fourth International Jellyfish Bloom Symposium,5-7 June, 2013, Hiroshima, Japan, where this work was first presented and to Camila Serra for her field assistance. Finally, the authors are thankful to the European Commission, under contract agreement no. 266445 Vectors–Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors, for its financial support. A. Canepa was funded by CONICYT (PFCHA/Doctorado al Extranjero 4a Convocatoria, 72120016).

LITERATURE CITED

Adamowicz W, Louviere J,SwaitJ(1998) Introduction to attribute-based stated choice methods. Available at http://wwwneronoaagov/hcd/statedchoicemethods.pdf

Beaud M, Blayac T, Stéphan M (2012) Value of travel time reliability: two alternative measures15th Edition of the Euro Working Group on Transportation - International Conference, Paris.

Beaumont NJ, Austen MC, Mangi SC, Townsend M (2008) Economic valuation for the conservation of marine biodiversity. Mar Pollut Bull 56:386–396

Canepa A, Sastre S, Piñol L, FuentesV (2013) Thirty years of jellyfish blooms in Catalonia: narratives and empirical evidences. Abstract Fourth International Jellyfish Bloom Symposium, Hiroshima, Japan

Carson RT, Louviere JJ, Wasi N (2009) Acautionary note on designing discrete choice experiments: acomment on Lusk and Norwood's "Effect of experiment design on choice-based conjoint valuation estimates". Amer J Agric Econ 91, :1056-1063

Catalunya Turística en Xifres (2012) Generalitat de Catalunya Departamentd'empresa i Ocupació Direcció General de Turisme, Available at http://www20.gencat.cat/docs/empresaiocupacio/20%20-%20Turisme/Observatori%20turisme/Estad%C3%ADstiques/Catalunya%20tur%C3%ADstica%20en%20xifres/Documents/Arxius/CTX_2012.pdf

CondonRH, GrahamWM, DuarteCM, PittKA, LucasCH, Haddock, SHD, SutherlandKR, RobinsonKL, DawsonMN, DeckerMB, MillsCE, PurcellJE, MalejA, MianzanH, Uye S-i, GelcichS, MadinLP(2012)Questioningtherise of gelatinouszooplankton in theworld'soceans.BioScience 62:160-169

Graham WM, Martin DL, Felder DL, Asper VL, Perry HM(2003) Ecological and economic implications of a tropical jellyfish invader in the Gulf of Mexico. Biol Invas 5:53-69

Hanemman M, KanninenB (1996) The statistical analysis of discrete-response CV Data. Available at http://are.berkeley.edu/~gh082644/wp798.pdf

Hearne RR, Salinas ZM (2002) The use of choice experiments in the analysis of tourist preferences for ecotourism development in Costa Rica. J Environ Manag 65:153-163

Kim DH, Seo JN, Yoon WD, Suh YS (2012)Estimating the economic damage caused by jellyfish to fisheries in Korea. Fish Sci 78:1147-1152

Lancaster K (1966) A new approach to consumer theory. J Polit Econ74:132-157

McFadden D (1973) Conditionallogitanalvsis of qualitative choice behavior. In: Zaremiibka P (ed) Frontiers in econometrics. Wiley, New York, pp 105-135

Marambio M, Nunes PALD, Fuentes V, Blasco D, Revke I (2013) Exploring the role of the social media platforms for providing public, real time information on jellyfish outbreaks: results from a worldwide première Iphone application in Catalonia, Spain. Abstract Fourth International Jellyfish Bloom Symposium, Hiroshima, Japan

Mariottini GL, Pane L (2010) Mediterranean jellyfish venoms: a review on scyphomedusae. Mar Drugs 8:1122-1152

Nastav B, MalejM, MalejA Jr, Malej A (2013) Is it possible to determine the economic impact of jellyfish outbreaks on fisheries? A Case Study – Slovenia. Medit Mar Sci 14: 214:223

Nunes PALD. Bergh JCJM(2004) Can people value protection against invasive marine species? Evidence from a joint TC-CV Survey in the Netherlands. Environ Res Econ 28:517-532

Nunes PALD, Markandya A (2008) Economic value of damage caused by marine bio-invasions: lessons from two European case studies. ICES JMarSci 65:775–780

Nunes PALD Blaiej AT BerghJCJM (2009) Decomposition of warm glow for multiple stakeholders: stated choice valuation of shellfishery policy.Land Econ85:485–499

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annu Rev Mar Sci 4:209–235

Quiñones J, Monroy A, Acha E, Mianzan H (2013). Jellyfish bycatch diminishes profit in an anchovy fishery off Peru. Fish Res 139:47-50

Remoundou K, Koundouri PK, Nunes PALD, Skourtos M (2009)Valuation of natural marine ecosystems: an economic perspective. Environ Sci Pol12:1040-1051

Sabatés A, Pagès F, Atienza D, Fuentes V, Purcell JE, Gili JM (2010) Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. Hydrobiologia 645:153–165

Sardá R, Mora J, Ariza E, Avila C, Jiménez JA (2009) Decadal shifts in beach user sand availability on the Costa Brava (Northwestern Mediterranean Coast).Tourism Manag30:158–168

Supplementary material: Survey

English version (also available in Catalan and Spanish)

*Good-morning/good-afternoon. My name is **[say your name]** and I am working on Marine Sciences at the CSIC/LEITAT, Barcelona, I would like to ask you some questions regarding your attitudes and opinions on marine environmental quality and recreational behavior at the Catalonian beaches. This is an anonymous interview and will take less than 10 minutes of your time.*
We appreciate very much your participation, so we would like to thank you for it. However, we cannot offer you any monetary reward; instead we would like to offer you a soft drink to refresh yourself after the survey.

1. Recreational data [do not read this]

Please think carefully about each question and give your best answer. There are no right or wrong answers, only personal answers.**1.1**How many persons are in your group (including yourself?)
1.2 During the **last summer season** (from June to September of 2011), how many times did you come to **this** beach?
1.3.1 During **this summer season** (from June to September of 2012), how many times have you come to **this** beach?
1.3.2 How many more times have you planned to go to **this** beach?
1.4 How important are these activities/factors to you to chose to **this** beach?
1.5 Which of the following nautical sports have you ever practiced in **this** beach?
1.6 How long do you plan to stay at **this** beach **today**?

2. Travel Cost Expenditures Data [do not read this]

2.1 Where are you staying?
In case he/she is staying in his first residence/home, skip to section C3.
In case he/she stays in another kind of accommodation, ask for its' typology and in case it's a hotel/camping…etc, ask for its' name and location.
2.2 ¿How many nights are you going to stay?
2.3 How much did it cost for you to stay in the Catalan coast **per person** with regard to:

Now we are going to talk about your stay at **this** beach only during the day of **today**:

2.4 How did you travel from the hotel/home to the beach **today**?
In case he/she answers by car or motorbike: how much have you spend on tolls and parking to and from your origin place?
In case he/she answers by public transport: how much did the ticket cost you?
2.5 How much time have you spent to arrive to **this** beach **today**?
2.6 Did you rent any equipment at the beach (sun-umbrella, sun bed, windbreak, boat, fishing material, etc.), paid any permits (anchoring, etc) or spend any money (e.g. meals) at **this** beach?
In case he/she answers yes: how much have you spend on it?

3. Socio-economic impact of a jellyfish outbreak [do not read this]

3.1 Have you or someone you know ever been stung by a jellyfish?
In case he/she answers NO, skip to section E.
In case he/she answers YES but in another beach, ask for the name of the beach.
In case he/she or the person who knows, has been stung several times, ask to answer the questions regarding to the last time he/she/the other person was stung.
3.2 How many times have you have been stung by a jellyfish?
3.3 How did you treat the pain?
In case you went to the first aid station/physician/family doctor: how many hours/day did you spend?
In case you went to the pharmacy: how much time and money did you spend?

3.4 Did you lose work time as a result of the sting?
In case he/she answers YES, ask for many hours.
3.5 Were you able to identify the species of jellyfish that stung you? **[Please show CSIC identification of the different jellyfish species]**

4. Contingent Behavior: impact of building of an offshore wind farm [do not read this]

I would like to ask you how your use of this beach may change with the building of an offshore wind farm for next year. The proposed changes are described in CARD 1. ***[Please show CARD 1]***

4.1 Suppose that next year the change described in this card takes place in this beach. Would you like it?
4.2 Would you change the number of trips you would do to this beach over the next years´ summer season?
In case that he/she would reduce the number of trips, ask how many fewer trips he/she would do.
In case he/she would not come to that beach again and that he/she would do something else, ask what she/he would do.

5. Choice experiment

Now, imagine you are planning to go to the beach. I'm going to show you some cards in which you will see two profiles of beaches according to different attributes and characteristics. Could you choose among the two possibilities shown? Please, take into consideration that if none of the two possibilities shown fits with your preferences and wishes, you can also decide not to go to the beach. ***[Please show CARD A]***

6. Socio-economic demographic questions [do not read this]

We are finishing the questionnaire. Before, I would need to ask you some additional questions about you.

6.1 Year of birth
6.2 Place of birth
6.3 Where do you live? Ask for postal code if he/she knows it.
6.4 What kind of form of education have you got?
6.5 ¿What is your job? **In case the person is unemployed, ask for his/her last job.**
6.6 ¿How many people live in your household?
6.7 In which interval is the **after tax income** of your household **monthly**? (In case that you don't share your income with the people you are living with, could you please tell me an approximated interval of your own income? **[Wait for a spontaneous answer]** Take into consideration if the respondent is a student without job or he/she is unemployed without receiving unemployment benefits.

7. FEEDBACK

Thank you very much for your time [**handle him/her the soft drink**]**,** We hope the survey was of your interest. Would you like to receive information and the results of this survey? If yes, could you please provide us with your email address?

TABLES:

Table 1.Beaches in Catalonia, Spain analyzed in the study (from SW to NE).

Beach name	Environment	Width (m)	Length (m)	Area (m²)	Jellyfish risk* (%)	Blue flag
Barceloneta	Urban	40	600	24,000	7.07	Yes
De Bogatell	Urban	32	625	18,676	12.96	Yes
De Sabanell	Mixed	32	2,380	75,921	0.75	Yes
De Blanes	Urban	44	610	26,170	0.37	Yes
Gran de Palamòs	Urban	55	990	48,650	9.52	No
De la Fosca	Mixed	37	514	16,461	3.96	Yes
El Castell	Natural	63	339	22,715	7.14	No
El Golfet	Natural	17	75	1,277	5.58	No

[*] This variable was delivered by the Catalan Water Agency and is constructed bearing in mind the observations of jellyfish outbreaks with respect to the number of inspections carried out between 2006 and 2010. [Risk = (No. of observations of jellyfish / No. of Inspections)*100]

Table 2.Possible choicesfor the jellyfish surveyadministered at beaches in Catalonia, Spain

Attributes	Levels		
Jellyfish risk outbreak	Low risk (≤2days/week)	High risk (> 5 days/week)	
Water transparency	Average (as regulated by the law)	Above average	
Services	Parking and toilettes	Parking, toilettes and children play area	Parking, toilettes, children play area and first aid center
Additional travel time	+5%	+10%	+15%

Table3.Characteristics of people answering the jellyfish surveyas beaches in Catalonia, Spain.Variables are presented as percentages (%)of 644 completed questionnaires

Description	Mean	Std. Dev.
Male	21.8	41.3
Respondent planned to stay at this beach < half a day	72.6	44.6
Respondent planned to stay at this beach half a day	21.0	40.8
Respondent planned to stay at this beach entire day	06.4	24.4
Respondent came to the beach on foot or bicycle	47.4	49.9
Respondent came to the beach by car or by motorbike	39.0	48.8
Respondent came to the beach by public transport	13.6	34.3
Respondent has been stung by a jellyfish	21.7	41.2
Respondent knows someone who has been stung by a jellyfish	17.2	37.7
Respondent has not been stung and does not know anyone who has been stung	61.1	48.8
Respondent has his/her primaryresidence in this place	43.7	49.6
Respondent is international	23.6	42.4
Respondent lives in Spain	17.8	38.3
Respondent lives in Catalonia	14.9	12.3
Respondent has above high school; 0 otherwise	49.6	50.0
Length of stay (days)	15.9	24.6
Age of respondent (years)	42.7	13.5
Respondent has a job; 0 otherwise	72.2	44.8
Respondent’s household income is below 2000€	36.7	48.2
Respondent’s household income is between 2000€-4000€	44.4	49.7
Respondent’s household income is above 4000€	18.9	39.2
Time taken to reach the beach (min)	21.3	24.4

Table 4. Estimation results (2892 observations were used for each model).

	Model I	Model II	Model III	Model IV
Variable	Coefficient	Coefficient	Coefficient	Coefficient
Jellyfish risk	-0.349*	-0.374*	-0.400*	-0.367*
Water quality	0.730*	0.737*	0.738*	0.733*
Services	0.409*	0.400*	0.401*	0.410*
Additional time	0.079*	0.081*	0.081*	0.078*
Additional time^2	-0.001*	-0.001*	-0.001*	-0.001*
Jellyfish risk * De Blanes	--	0.310**	0.312**	--
Jellyfish risk * Stung	--	--	0.111	--
Jellyfish risk * Resident	--	--	--	0.054
Log-likelihood	-1,970.409	-1,967.313	-1,966.448	-1,961.602
AIC	3,950.800	3,946.600	3,946.900	3,935.200

* statistically significant at 99%, ** statistically significant at 90%

Table 5.Willingness to pay estimates per quartile (measured in extra minutes of travel time). Quartile 1 = 5 min; Quartile 2 = 10 min; Quartile 3 = 37 min; SE = standard error; CI =Confidence Interval

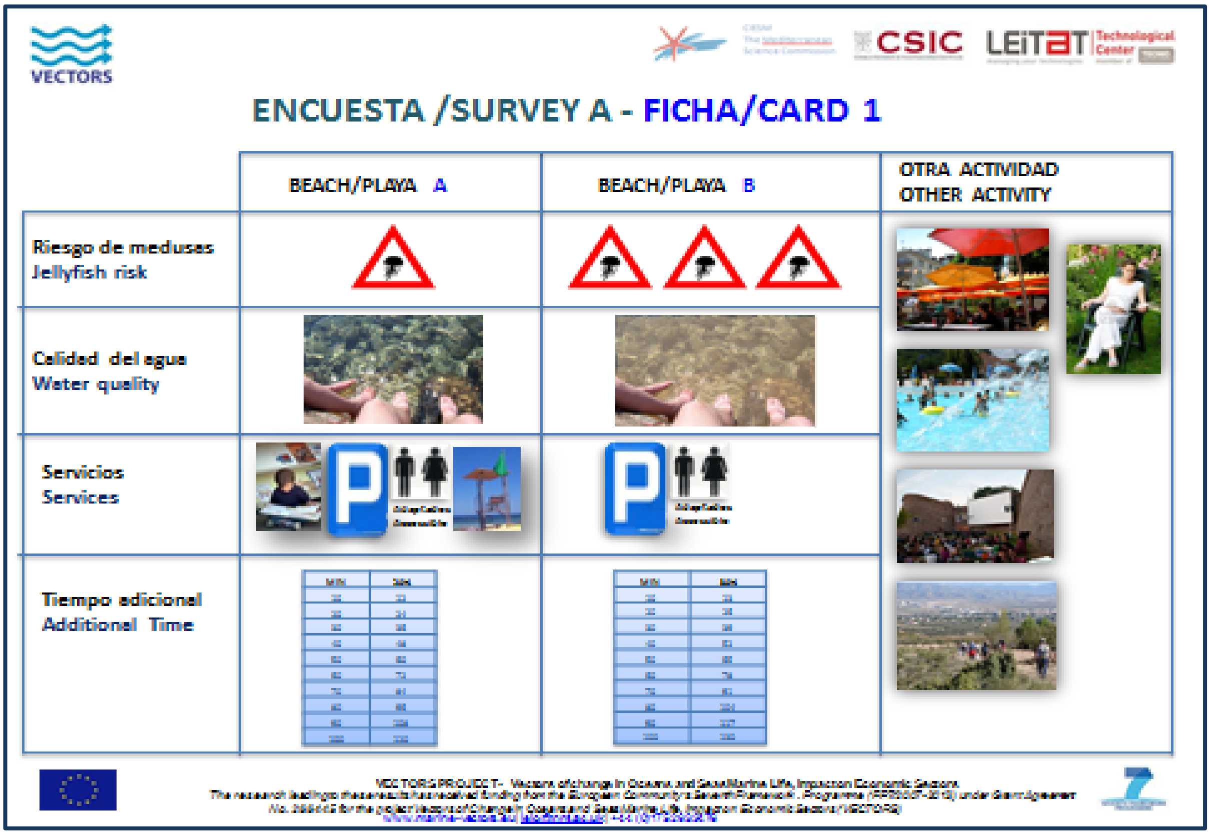
		Implicit value	SE	P|z|>Z*	95% CI	
	Quartile 1	5.374	0.753	0.000	-6.851	-3.898
	Quartile 2	6.866	0.962	0.000	-8.752	-4.980
Jellyfish risk	Quartile 3	-13.764	1.929	0.000	0.590	1.037
	Quartile 1	11.251	0.559	0.000	10.155	12.347
	Quartile 2	14.374	0.715	0.000	12.973	15.774
Water quality	Quartile 3	-28.816	1.432	0.000	-1.870	-1.538
	Quartile 1	6.309	0.579	0.000	5.175	7.444
	Quartile 2	8.060	0.740	0.000	6.611	9.510
Services	Quartile 3	-16.158	1.483	0.000	-1.127	-0.784

Table 6.Economic valuation of the selected beach attributes expressed as additional time to travel in minutes.

Willingness to pay					
Variable	Estimate*	Std. Err.	P |z|>Z*	95% Confidence Interval	
Jellyfish risk	3.81	0.890	0.000	-5.553	-2.066
Water quality	7.98	1.773	0.000	4.500	11.450
Services	4.47	1.104	0.000	2.309	6.635

*estimates are presented as absolute values

FIGURES



ENCUESTA /SURVEY A - FICHA/CARD 1

BEACH/PLAYA A

BEACH/PLAYA B

OTRA ACTIVIDAD
OTHER ACTIVITY

Riesgo de meduses
Jellyfish risk

Calidad del agua
Water quality

Servicios
Services

Tiempo adicional
Additional Time

Figure 1: Choice set card example

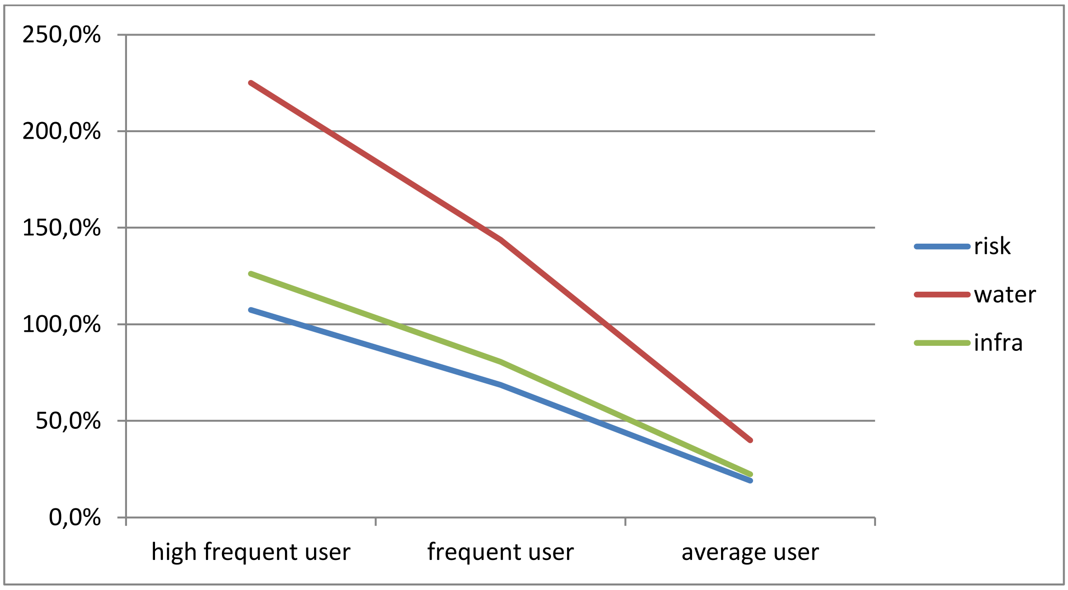


Figure 2: Relative WTP Estimates per User Intensity