

Kylie A. Pitt · Cathy H. Lucas
Editors

Jellyfish Blooms

 Springer

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)

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 Ciències 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

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

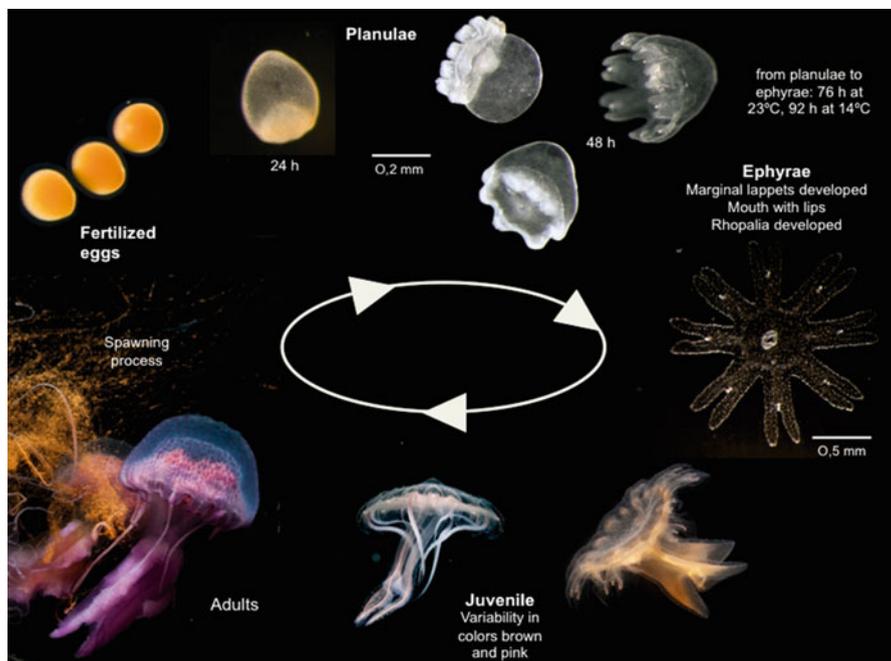


Fig. 11.1 Holoplanktonic life cycle of *Pelagia noctiluca* photographed at the ZAE (Experimental Aquaria Zone at ICM-CSIC in Barcelona) with indications on the sizes and times of developments (Photos Eduardo Obis Alberola)

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

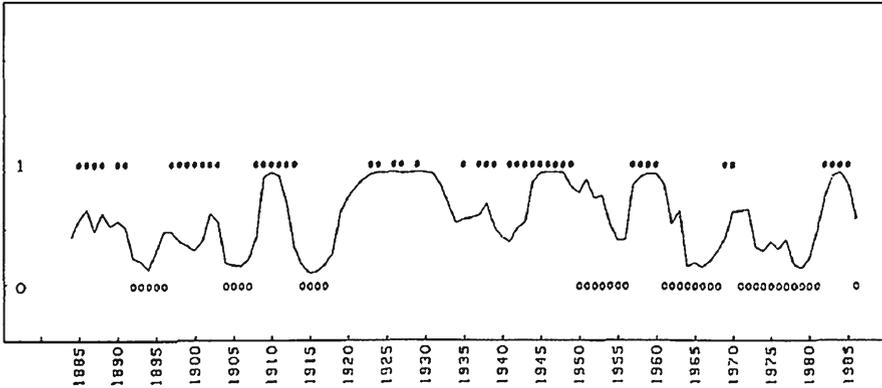


Fig. 11.2 Periodicity of *Pelagia noctiluca* blooms. Open circles: years without *P. noctiluca*. Closed circles: years with *P. noctiluca*. Solid line: probability of *P. noctiluca* blooms (After Goy et al. 1989)

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	Gislason 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	Gislason 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), Malačić 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)

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)	
			1977–1978	Istrian Coast (Yugoslavia)	Malej and Vuković (1984), UNEP (1991), Maretić et al. (1987)	±50 % of bathers affected
			1978–1983	Adriatic Sea (Trieste)	Legović (1991)	
			1983	Portoroz (Slovenia)	Malej and Vuković (1984)	
			1991	Yugoslavia	Axiak et al. (1991)	
			1982	Greece	Axiak et al. (1991)	
			1981–1983	Athens	Axiak et al. (1991)	
				Adriatic Sea	Legović (1991)	
				Monaco	Bernard 1991, Purcell et al. 2007	45,000 people affected
Fisheries	Indirect	Predation on fish eggs and larvae	1984–1987	French Riviera	Purcell et al. (2007)	2,500 people affected
			2007	Spain	Purcell et al. (2007)	More than 14,000 persons affected
			2008	Italy	Marriottini et al. (2008)	
			2010	Adriatic Sea	Nastasi (2010)	
			2011	Mediterranean Sea	Bernard et al. (2011)	
			1987	Ligurian Sea	Morand et al. (1987)	
			1991	Adriatic Sea	Legović (1991)	
			2001	Mediterranean Sea	CJESM (2001)	Review
			2007	Mediterranean Sea	Purcell et al. (2007)	Review
			2010	NW Mediterranean Sea	Sabatés et al. (2010)	Review
	Adriatic Sea	Legović (1991)	Review			
	Mediterranean Sea	CJESM (2001)	Review			
	Adriatic Sea	Malej and Malej (2004)	Review			
	NW Mediterranean	Sabatés et al. (2010)	Review			

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 kg hr ⁻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
		2010	Mediterranean Sea	Nastasi (2010)	Review
Aquaculture	Direct	2011	Spanish Coast	Baxter et al. (2011)	
	Capture damage	1995	Brittany (France)	Merceron et al. (1995)	
	Fish mortality	2007	Mediterranean Sea	Purcell et al. (2007)	Review
Energy	Direct	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 (Leonart 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

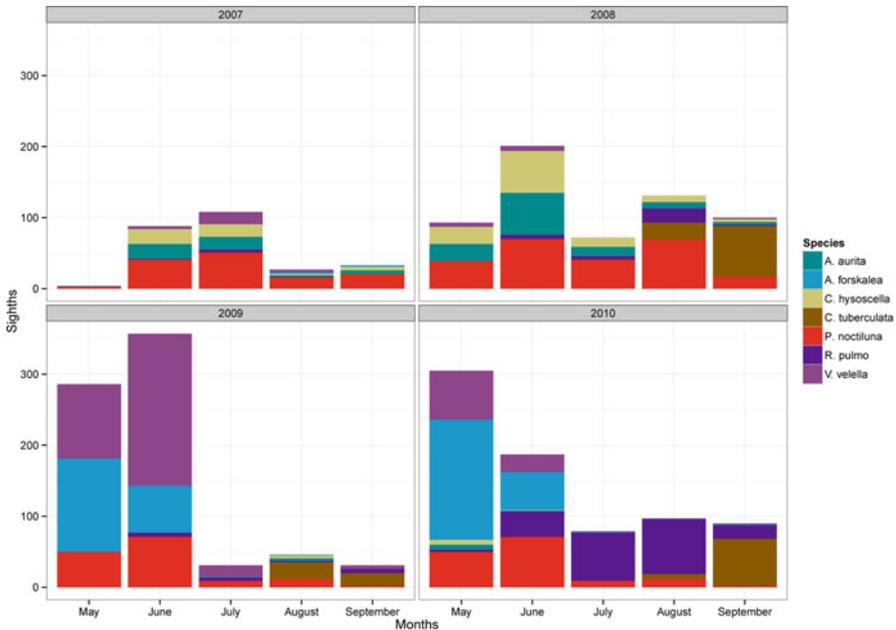


Fig. 11.3 Temporal variability of conspicuous jellyfish species stranded along the Catalan coasts, for the period 2007–2010. *Pelagia noctiluca* is shown in red at the base of the bars

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

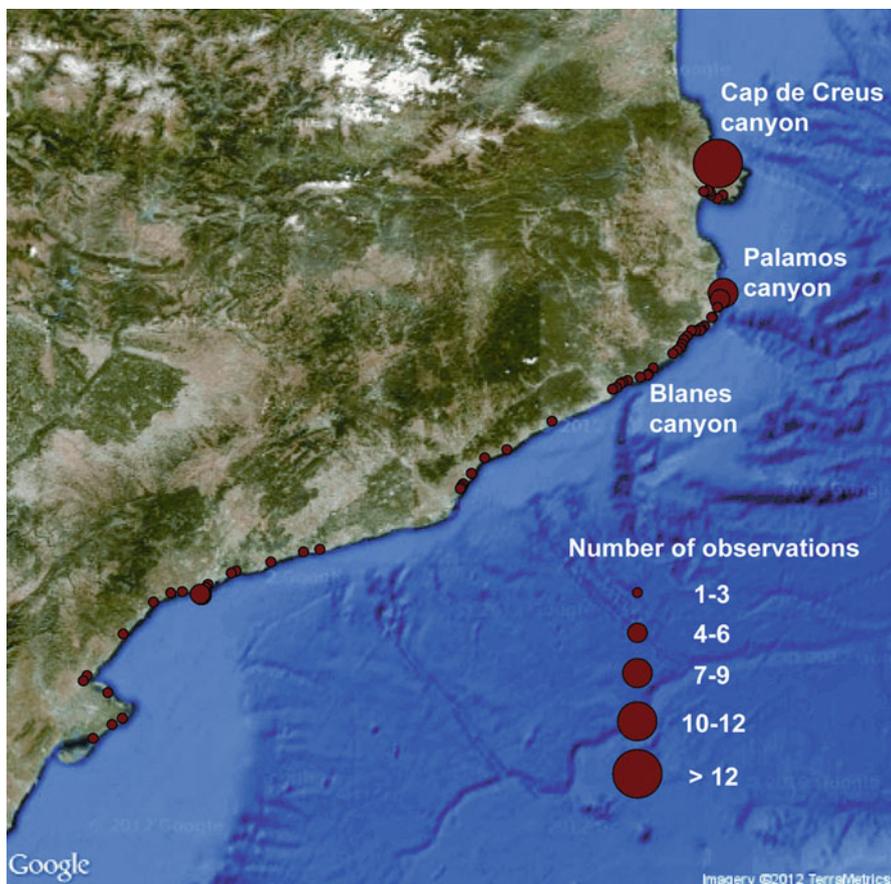


Fig. 11.4 Observations of stranded individuals of *Pelagia noctiluca* along the Catalan coast. Data represents mean annual values (2007–2010)

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

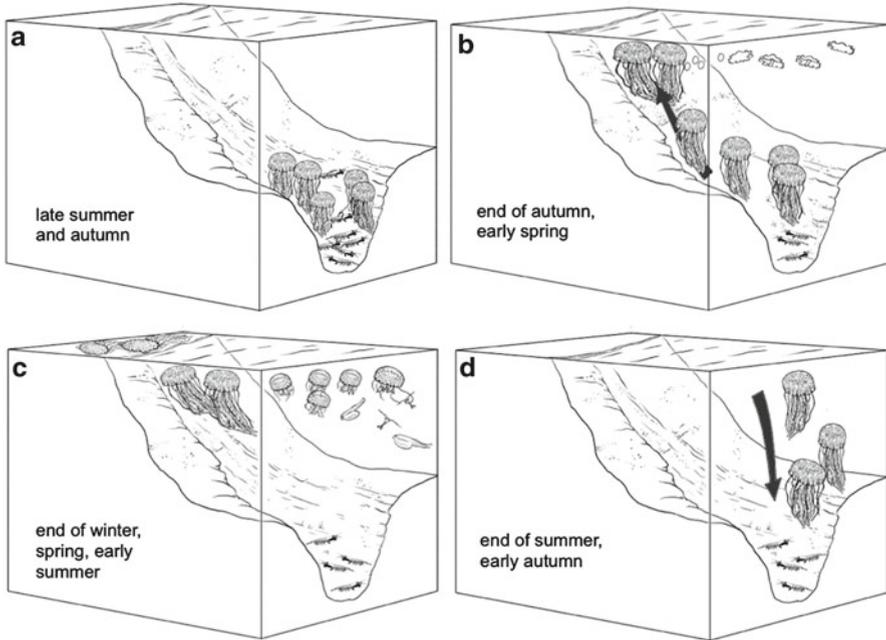


Fig. 11.5 (a–d) Hypothesis for seasonal vertical migration of *Pelagia noctiluca*. (a) Jellyfish overcome the warmer months at colder, mid-water levels; (b) by mid-autumn or early winter, jellyfish migrate upward for sexual reproduction; (c) throughout spring to early summer, at shallow levels jellyfish 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 Catalanian 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

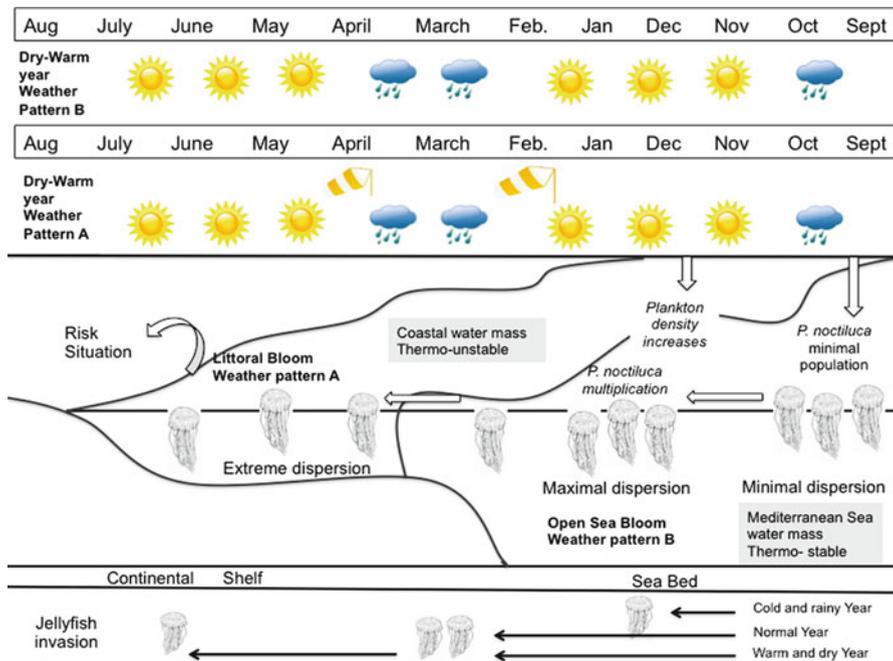


Fig. 11.7 Scheme of the proposed model by Rubio and Muñoz (1997), showing the different conditions leading a coastal bloom of *Pelagia noctiluca* (see text for interpretation)

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.

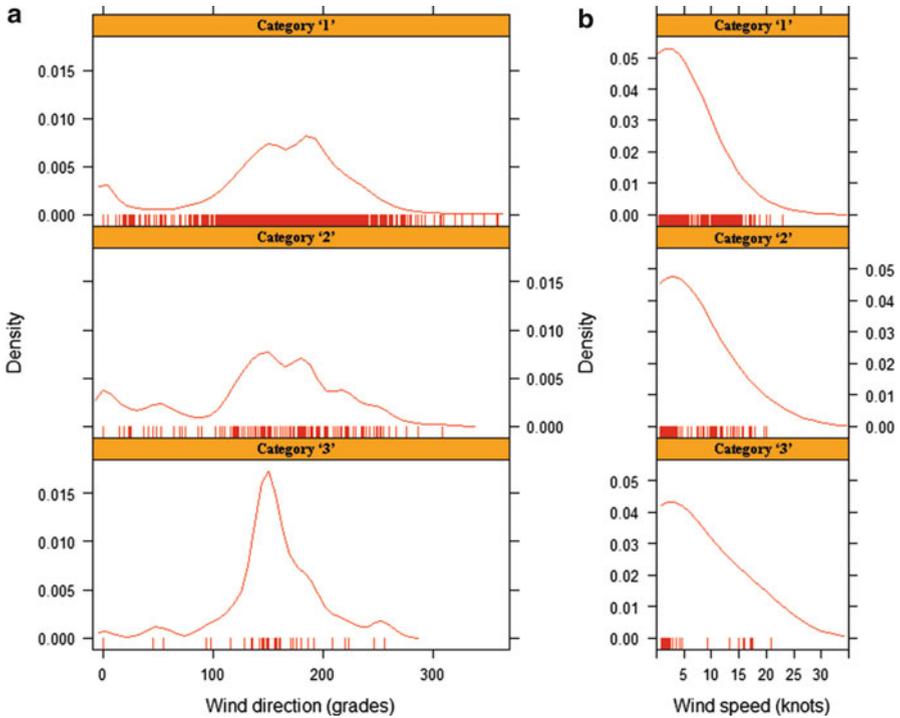


Fig. 11.8 (a–b) Relationship between stranded jellyfish species along the Catalan coast with (a) wind direction and (b) speed. Vertical lines above the x-axis represent the raw stranded data. Continuous line represents the kernel density function used to model the relationship between stranded individuals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

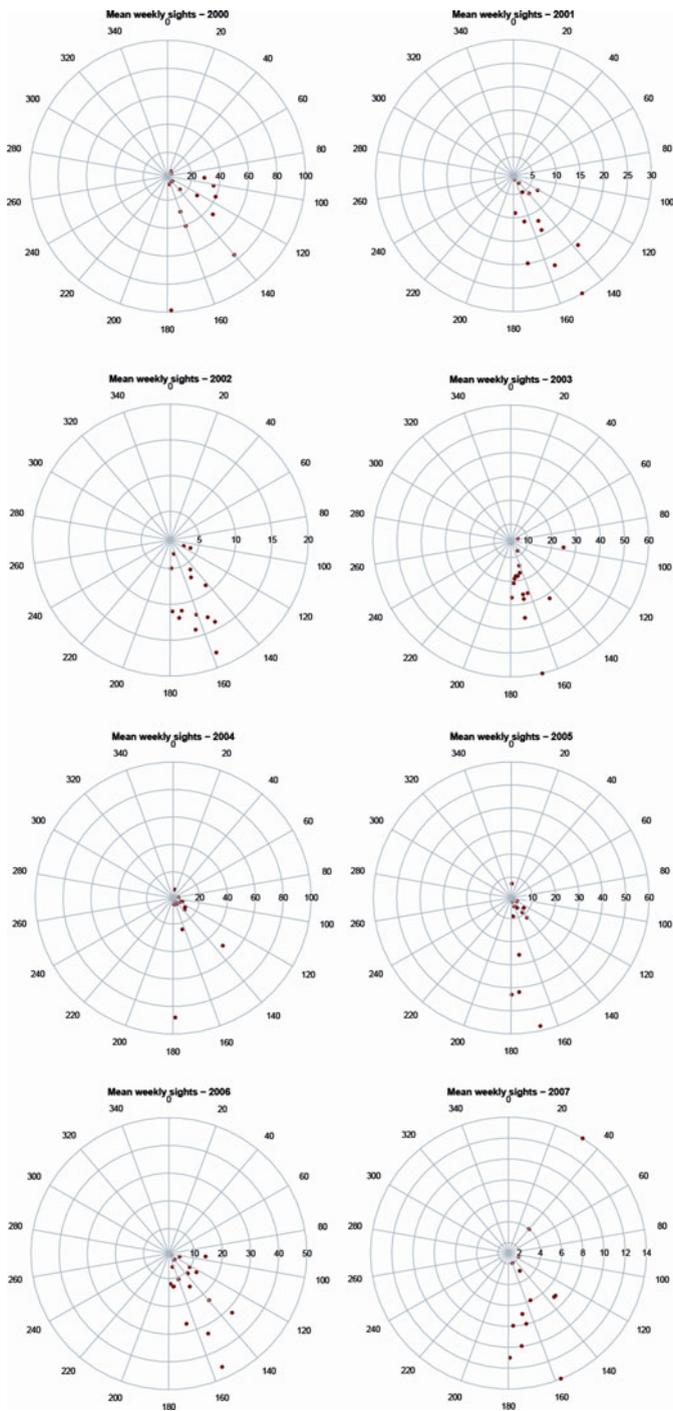


Fig. 11.9 Average weekly stranded jellyfish during May–Oct 2001–2007. *Degrees* represent compass directions, with north=0°. Different magnitude scales in each year reflects differences in the total records

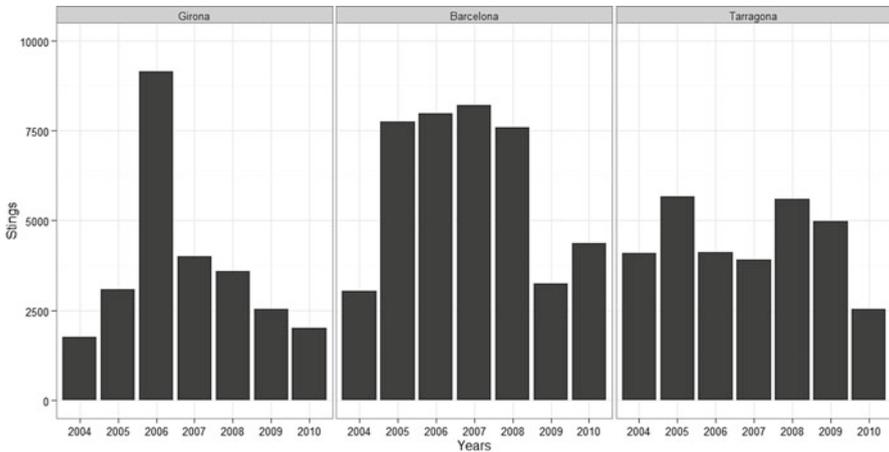


Fig. 11.10 Temporal distribution of people stung by jellyfish in the three provinces along the Catalan coast. Data showed the maximum number of assistances

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

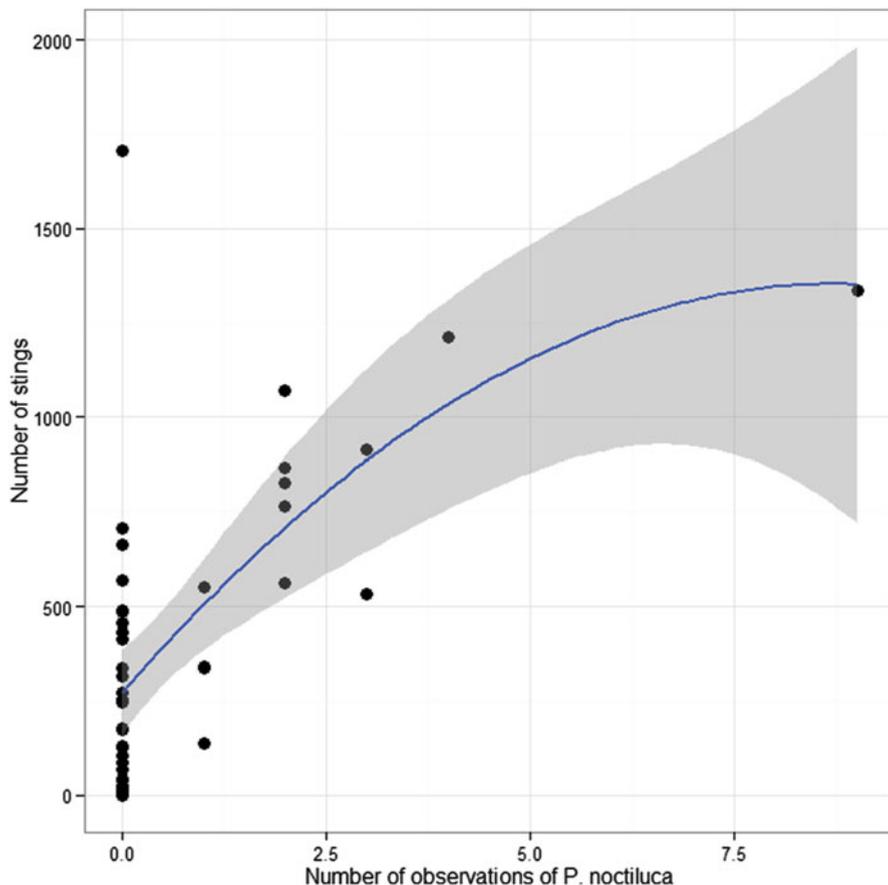


Fig. 11.11 Relationship between number of stings and strandings of *Pelagia noctiluca* along the coast of Barcelona (Catalonia)

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 4^a 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* (Forskål). 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, Bøgeberg 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 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* (Forsskal, 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, Berlina 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'Aigua, Generalitat de Catalunya, Barcelona
- Giorgi R, Avian M, De Olazabal S, Rottini-Sandrini L (1991) Feeding of *Pelagia noctiluca* in open sea. Jellyfish blooms in the Mediterranean. In: Proceedings of II workshop on jellyfish 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* swarms 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
- Leonart 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
- Marić 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
- Marić 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
- Moliner JC, Ibanez F, Nival P, Buecher E, Souissi S (2005) North Atlantic climate and northwestern Mediterranean plankton variability. *Limnol Oceanogr* 50:1213–1220
- Moliner 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, Semaestomae). *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, Martín J, Marcos M, Pascual A, Puig P, Gili J-M, Emelianov M, Monserrat S, Guillén J, Tintoré J, Segura M, Jordi A, Ruiz S, Basterretxea 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, Agnastaki 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, Smolaka 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: Semaestomeae): laboratory and open sea observations. *Mar Biol* 102:49–55
- Stebbing ARD (1980) Increase in gonozoid 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