

Mediterranean Marine Science

Vol 21, No 1 (2020)



Jelly surge in the Mediterranean Sea: threat or opportunity?

CINZIA GRAVILI

doi: [10.12681/mms.17966](https://doi.org/10.12681/mms.17966)

To cite this article:

GRAVILI, C. (2020). Jelly surge in the Mediterranean Sea: threat or opportunity?. *Mediterranean Marine Science*, 21(1), 11-21. <https://doi.org/10.12681/mms.17966>

Jelly surge in the Mediterranean Sea: threat or opportunity?

Cinzia GRAVILI

Laboratory of Zoology and Marine Biology, Di.S.Te.B.A, University of Salento, Lecce, Italy

Corresponding author: cinzia.gravili@unisalento.it

Handling Editor: Sultana ZERVOUDAKI

Received: 17 July 2018; Accepted: 18 October 2019; Published online: 28 March 2020

Abstract

The rise in water temperature in the Mediterranean Sea, and associated migrations of temperate marine biota, are occurring in the context of a global warming causing an expansion of the tropical jellyfish range, exacerbating jellyfish outbreaks linked to coastal development, nutrient loading, and overfishing. The gelatinous component of plankton is considered as ‘the dark side of ecology’ capable of appearing and disappearing at unpredictable times. In the last decade an increasingly high number of gelatinous plankton blooms are occurring and this makes us wonder if ‘a Mediterranean Sea full of jellyfish is a probable future’. The reasons for rising jellyfish blooms are, probably, manifold. Current studies are aimed to highlight how climatic change is interacting with the Mediterranean ecosystem favouring entrance, abundances and success of alien species and triggering ‘regime shifts’ such as from fish to jellyfish. Jellyfish damage the economic success of power plants, fish farms, tourism, and affect fisheries consuming larvae of commercial fish species. On the other hand, several studies were also taken into account on uses for jellyfish as biofuels and foods but more experimentation is needed to improve the first encouraging results.

Keywords: Jellyfish; threat; opportunity; climate change; alien species; Mediterranean Sea.

Introduction

The Fever of the Mediterranean Sea

Since the mid-1980s a pronounced warming trend has characterised the Mediterranean Sea temperature with extensive mass mortalities of organisms characterized by cold-water affinities whereas species well-adapted to high temperatures show a positive feedback (Rivetti *et al.*, 2014).

Shaltout and Omstedt (2014) analyzed data about Mediterranean Sea surface temperatures and their response to global change observing a significant annual warming. The basin represents, indeed, a ‘model basin’ for all oceans as it is characterized by several traits and a peculiar history (Templado, 2014) being much smaller than any ocean, almost closed, and with a high rate of endemism. For these reasons, it can be used as ‘a Climate Test Basin’ (Garrett, 1994) and is the subject of changes of its biota responding quickly to climate change (Bianchi, 2007; Boero & Bonsdorff, 2007; Lejeune *et al.*, 2010; Boero & Gravili, 2013; Gravili *et al.*, 2013; Boero, 2015). In addition, climate change may favour some jellyfish species through increased availability of flagellates, a jellyfish food source, in surface waters. Furthermore, temperature change can interact in many ways with

global biogeographic changes (Hughes, 2000; Gravili & Boero, 2014) inducing the ‘tropicalization’ of the Mediterranean basin, a phenomenon characterized by success and abundances of sub-tropical species in warm-temperate waters (Bianchi & Morri, 2004; Bianchi, 2007), and on global scale is forcing temperate marine biota towards the poles (Boero *et al.*, 2016). In addition, alien species invasion is closely linked to opportunities provided by anthropic activities such as shipping transport, the Suez Canal (opened in 1869 and, recently, double), and escape of tropical species from culturing grounds (Boero, 2002; Galil *et al.*, 2015).

Moreover, scientists are also concerned that warmer water could alter the system of global currents that regulates the Earth’s temperature changing gyres and ocean currents around the world (Anonymous, 2010b), forcing migrations and species extinctions (Hughes, 2000; Hoegh-Guldberg & Bruno, 2010; Boero & Gravili, 2013; Gravili & Boero, 2014; Gravili *et al.*, 2015).

Jellyfish Surge

In this paper, the term ‘jellyfish’, refers to gelatinous zooplankton that includes medusae of the taxa Hydrozoa, Scyphozoa, and Cubozoa. Jellyfish are a component of

marine ecosystems, relatively little studied but conspicuous that shows population fluctuation characterized by sudden outbursts (blooms) followed by crashes (Purcell, 2005). Jellyfish are a natural presence in natural ecosystems and have bloomed in the past too (Hagadorn *et al.*, 2002; Young & Hagadorn, 2010; Brotz *et al.*, 2012).

The first signs of a possible change in the frequency of jellyfish blooms worldwide were recognized by Mills (Mills, 1995, 2001) and numerous localized increases are reported by subsequent reviews of jellyfish populations in several world seas (Black Sea, Baltic Sea, the Northern Benguela Current off Namibia, Sea of Japan, East China and Yellow Seas), as well as in the Mediterranean Sea off the coasts of Spain and France and coastal Middle Eastern area (Purcell, 2005; Boero *et al.*, 2016; Brotz *et al.*, 2012; Mills, 2001; Brodeur *et al.*, 2002; Uye & Ueta, 2003, 2004; Kawahara *et al.*, 2006; Link & Ford, 2006; Purcell *et al.*, 2007; Chudnow, 2008; Cho, 2011; Boero, 2013; Pitt & Lucas, 2014).

In the Mediterranean Sea several scientists reported a surge in the number of jellyfish that threatens the biodiversity of the basin and also the health of thousands of tourists (Tremlett, 2013; De Donno *et al.*, 2014). Therefore, the Mediterranean biota is undergoing a process of 'jellyfication' (Roux *et al.*, 2013). Similar trends in jellyfish populations have been observed on a global scale too (Brotz *et al.*, 2012; Brotz & Pauly, 2012). Although many jellyfish populations fluctuate with oceanic climate (see Purcell, 2005, 2012), the proliferation of jellyfish appears in large part to be related to human impacts (global warming, eutrophication, habitat modification, overfishing, aquaculture, ocean acidification) on the marine environment. Gelatinous species, in fact, are adapted to develop large populations through asexual reproduction and being opportunistic are favoured against species that, on the contrary, require predictable environmental conditions (Boero *et al.*, 2016). In addition, sea warming influences species phenology: life cycle might be altered leading to changing of phenological relationships between species (Hughes, 2000). Warm-water scyphozoans are liable to lengthen the time-window of medusae production as answer to temperature increases leading to a probable expansion of the period of jellyfish growth and reproduction (Boero *et al.*, 2016). On the other hand, cold-water species could be negatively affected by temperature increases as reported by case studies about *Aurelia* and *Cyanea* species (Lynam *et al.*, 2004). In addition, climate change may improve winter survival of tropical species expanding to temperate waters, and broaden the mid-latitude jellyfish reproductive periods and, as a consequence, enhancing both native and alien outbreaks (Boero *et al.*, 2016). Furthermore, with the disappearance of predators, jellyfish blooms are increasing in frequency, intensity, and duration worldwide, as well as in the Mediterranean Sea (Hughes, 2000; Purcell & Uye, 2007; Boero *et al.*, 2008a; Richardson *et al.*, 2009; Boero, 2013; Duarte *et al.*, 2013; Guilford, 2013; Tremlett, 2013; Canepa *et al.*, 2014; Boero *et al.*, 2016). Overfishing, in fact, forced trophic networks causing the increase of jellyfish populations through elimination their predators and competi-

tors (Purcell *et al.*, 1999, 2001; CIESM, 2001; Daskalov, 2002; Parsons & Lalli, 2002; Bilio & Niermann, 2004; Lynam *et al.*, 2005; Purcell, 2005; Tatsuki, 2005; Xian *et al.*, 2005; Hay, 2006; Boero, 2013; Benedetti-Cecchi *et al.*, 2015) with a 'top-down control of marine food web' by gelatinous predators (Mills, 2001; Gershwin, 2013): short-lived invertebrates (such as jellyfish) and planktivorous fishes increase disfavoured large and long-lived predators (Pauly *et al.*, 1998). Moreover, jellyfish are favoured when forage fish (as herring and sardines) are harvested for aquaculture fishmeal as they have fewer competitors for zooplankton. For the above reasons, a challenge for researchers is to separate normal jellyfish fluctuations from those for which anthropic impacts may be responsible (Schrope, 2012; Boero, 2013; Boero *et al.*, 2016). Could jellyfish blooms be as a 'miner's canary' that bellwether of change when the ecosystem is disturbed?

To answer that, further studies are required to monitor jelly bloom phenomena: research on this topic is lacking, probably, for a number of reasons, among these several problems that the scientific community has to detect them. To eliminate the scarcity of gelatinous plankton long-term monitoring, a Citizen Science campaign began in 2009 (Boero, 2013), along the Mediterranean coasts, allowing the creation of a long-term database. There have been numerous Mediterranean records of jellyfish species: the tropical scyphozoan *Phyllorhiza punctata* Lendenfeld, 1884 (Boero *et al.*, 2009), the Atlantic species *Catostylus tagi* (Haeckel, 1869) (Boero, 2011), the new species *Pelagia benovici* Piraino, Aglieri, Scorrano & Boero, 2014 (Piraino *et al.*, 2014), *Cotylorhiza erythraea* Stiasny, 1920 (Galil *et al.*, 2016), and two *Aurelia* species (Scorrano *et al.*, 2016). However, alien species often characterize recurrent jellyfish outbreaks in the Eastern Mediterranean (Galil, 2008), whereas blooms phenomena consist of indigenous species in the Western-Central Mediterranean colonizing several unique habitats such as coralligenous assemblages, *Posidonia oceanica*, and vermetid reefs and exhibiting strong Atlantic affinities (Harmelin & d'Hont, 1993; Green & Short, 2003; Boudourisque, 2004; Sardà *et al.*, 2004; Ballesteros, 2006; Galil, 2008; Gravili *et al.*, 2013). Moreover, in recent years, numerous alien species, previously confined to the eastern basin, showed an expansion of their distribution area to the central-western basins of the Mediterranean due to the effects of climate changes (Richardson *et al.*, 2009; Occhipinti-Ambrogi & Galil, 2010; Zenetos *et al.*, 2012; Tsiamis *et al.*, 2018). Several studies reported the effects of alien species invasions on native populations, communities, and whole ecosystems, increasing in spread and in dominance through the success of a few invasive species that might be mediated by physical change (Galil, 2015; Galil *et al.*, 2015). On the other hand, while numerous species spread to new habitats, others are in decline or even in extinction due to overexploitation and loss of their habitats (Boero & Gravili, 2013; Gravili *et al.*, 2015).

Animal waste and agricultural often loads coastal waters with nutrients, which cause eutrophication where algal proliferation impoverishes the water of oxygen. Fur-

thermore, eutrophication provides more food for jellyfish polyps favouring both jellyfish and polyps more than fish because they are low oxygen levels tolerants (Cho, 2011). Waters around aquaculture, where fish waste produce eutrophication, support jellyfish blooms and their structures and pens often provide polyp habitats.

But how we can define the term increase of jellyfish?

Brotz *et al.* (2012) reported as the detection of jellyfish true trends could be influenced by several factors. First of all, the scarcity of historical information on jellyfish, because these organisms were usually damaged or not recorded during zooplankton surveys (Pugh, 1989; Hay, 2006) that, often, use methodologies that recommended their removal through plankton-gear designed to exclude jellyfish from samples (Dovel, 1964; Heinle, 1965).

Another factor is the extreme variability on both spatial and temporal scales, due to their ecology that contribute to why jellyfish tend to be understudied too (Brotz *et al.*, 2012).

Many hydrozoans and scyphozoans, and all cubozoans, have a life history consisting of a sessile polyp phase and a planktonic medusa phase. A few species have their polyps that may asexually bud more polyps or form dormant cysts capable of overcoming unfavourable environmental conditions and rapidly reproduce when conditions are favourable (Boero *et al.*, 2008a; Richardson *et al.*, 2009; Arai, 2009). On the other hand, studies on the dynamics of jellyfish populations are often based on records of the location, relative size, and blooms timing (Mills, 2001; Purcell, 2005; Boero *et al.*, 2008a; Dawson & Hamner, 2009; Brotz & Pauly, 2012) unlike researches about finfishes that use analytic models (Palomares & Pauly, 2009). In this complex framework, jellyfish have natural cycles of abundance and their pulses determine the cycling spatial and temporal diversity of plankton as ‘the dark side of ecology’ (Boero & Mills, 1997; Boero *et al.*, 2008a). This scenario could be explained by the benthopelagic cycles (Boero *et al.*, 2008a), typical of most jellyfish, where the presence of an asexually reproducing polyp stage in the life cycle could determine long time intervals characterized by absence of some jellyfish that might, then, reappear suddenly such as the endemic *Drymonema dalmatinum* Haeckel, 1880 in the Adriatic Sea and *Rhizostoma luteum* (Quoy & Gaimard, 1827) in the Gibraltar Strait (Bayha & Dawson, 2010; Prieto *et al.*, 2013). Moreover, for a long time researchers have considered the stages of polyps and medusae separately creating several classification systems for them. On the other hand, the reconstruction of their full life cycle is a pre-requisite essential for a unified classification (Boero *et al.*, 1997), and for a complete knowledge of the jellyfish ecology and their evolutionary patterns. Finally, but not less important, there are taxonomic concerns linked to the term ‘jellyfish’ may refer to different phyla such as Cnidaria, Ctenophora, and Chordata. The use of such a term that ignores taxonomy as such organisms are phylogenetically distant, without proper taxonomic resolution, prevents a knowledge of the mechanisms and consequences involved (Haddock, 2004; Brotz *et al.*, 2012). The latter problem is aggravated by the ‘loss of taxonom-

ic expertise’ characterized by the retirement of taxonomy experts replaced by new researchers in molecular biology or ecology (Boero, 2001; Gravili, 2017).

Global Threats

The jellyfish aggregations are becoming a serious problem: fisheries and nuclear power plants could undergo further losses. Jellyfish in large numbers can devastate power stations by clogging the cooling systems (Gershwin, 2013).

Further problems derived from nets full of jellyfish with consequent disruption of fisheries. The profit of the fishing industry is reduced due to delays in the fishing process because the net clogging, rips of fishing nets caused by the excessive weight of water-filled medusae (Moffett, 2007), and suffocation of desirable species essential to the fishing industry (Purcell *et al.*, 2000).

Jellyfish blooms are often negatively perceived because they may affect fishery through competition for food or direct predation resulting in reduction of fish stocks (Lynam *et al.*, 2006; Purcell *et al.*, 2015). Furthermore, jellyfish populations can cause mass mortality in caged fish aquaculture, produce negative impacts on coastal tourism and human health due to painful stings, and block cooling pipelines (Purcell *et al.*, 2007; O’Rourke, 2013; Bosch-Belmar *et al.*, 2016). In particular, blooms of gelatinous cnidarian stingers are associated to a wide range of neurotoxic, cytotoxic, and hemolytic effects on farmed fish, such as the case study of the species *Pelagia noctiluca* (Forsskål, 1775) (Fig. 1) that is a direct causative agent for several fish mortality events in Northern European and Mediterranean aquaculture farms (Bosch-Belmar *et al.*, 2016). Other potentially harmful species for aquaculture facilities are the hydromedusae *Phialella quadrata* (Forbes, 1848) and *Solmaris corona* (Keferstein & Ehlers, 1861) (Baxter *et al.*, 2011), and the siphonophore *Muggiaea atlantica* Cunningham, 1892 (Fosså *et al.*, 2003).

Moreover, swarms of jellyfish have disrupted power generation everywhere in the world: power plants out-

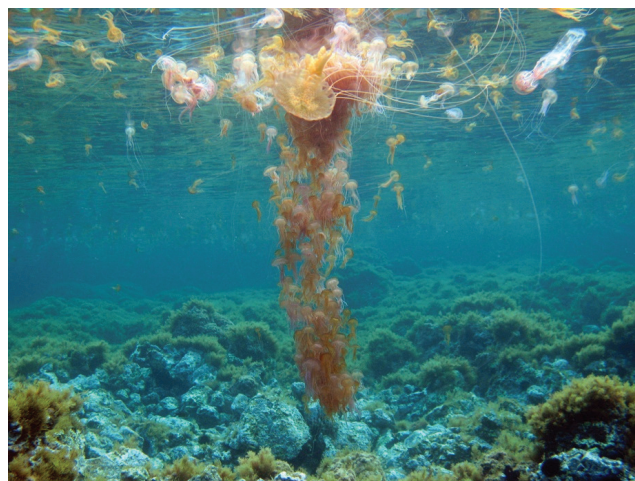


Fig. 1: *Pelagia noctiluca* (Photo credit: Francesco Di Trapani - MED-JELLYRISK project).

side (Scotland, Japan) and inside the Mediterranean Sea (Israel) were victims of the jellyfish threat causing power reductions or shutdowns (O'Rourke, 2013), and fish stocks were destroyed in Ireland and Tunisia by tearing nets and harming fish (Schrope, 2012). In the fishing business, the situation is worse with clogged trawl lines and burst nets. In addition, jellyfish reduce the population of the commercial fish by eating their eggs, larvae and juveniles, consuming the zooplankton they eat, and transmitting parasites on fish. Jellyfish have seemed to fill the empty niche in conjunction with fish species decline (Pauly *et al.*, 1998; Jackson, 2008) and their peculiar biology means that once their populations increase may be impossible to turn getting off the food network (Gershwin, 2013).

Brotz *et al.* (2012) examining 45 major marine ecosystems found that 62% saw an increase in blooms since 1950. Jellyfish have often invaded numerous beach holidays. Tourism is severely damaged by jellyfish blooms along the Mediterranean coastline shortening swimming season for tourists: about 150,000 people are treated for jellyfish stings in the Mediterranean each summer (Guilford, 2013). In addition, the "dead zones", created by what scientists call 'eutrophication', contribute to the jellyfish bloom (Gershwin, 2013). Farming pesticides and sewage pumped into rivers and poured into the seawater affects phytoplankton, forming algal blooms that float to the bottom, impoverishing the water of oxygen. This phenomenon, threatening the survival of most creatures, may favour the expansion of jellyfish colonies. Gershwin (2013) wrote as human impacts are helping jellyfish reproduction: their sessile stage (polyp) is the "key to their ability to bloom in such incredibly rapid fashion and shocking numbers." In fact, the proliferation of anthropic structures such as boats, platforms, offshore wind turbines, are some of the new surfaces where polyps can cling to and proliferate. Moreover, a number of invasive species of jellyfish are thriving in the Mediterranean basin impacting on fishing and other industries (Öztürk & İşinibilir, 2010).

As mentioned above, the main vector of introduction of alien species is shipping (Galil, 2009). In particular, benthic phase of most jellyfish have been transported on ship hulls, while hydromedusan and scyphozoan ephyrae are often found in ballast water. Numerous species can overcome adverse seasonal conditions in the form of encysted stages in ballast waters or attached as 'fouling' to the ships-hulls (Boero, 2002). On the other hand, the jellyfish *Pelagia noctiluca*, usually considered to be the most important jellyfish species in the Mediterranean Sea due to its widespread distribution and ecological role, can be considered 'invasive' when it spreads out from offshore to coastal waters with periodic occurrences of extraordinary abundances (Sabatés *et al.*, 2010; Canepa *et al.*, 2014). Climatic conditions, probably, also determine optimal conditions for this species both speed reproduction and extend the reproductive season with the appearance of more frequent blooms (high temperature and atmospheric pressure, low rainfall, mild winters) causing negative interaction on tourism (Molinero *et al.*,

2005; Purcell *et al.*, 2007; Anonymous, 2010c; Canepa *et al.*, 2014; Rivetti *et al.*, 2014). Goy *et al.* (1989) detected for *P. noctiluca*, through a long-term dataset, a cyclic trend of about 12 years in the western basin of the Mediterranean. In the late 1990s, persistent blooms occurred almost annually (Malej *et al.*, 2004; Anonymous, 2008; Mariottini *et al.*, 2008; Anonymous, 2010a; Daly Yahia *et al.*, 2010), and *P. noctiluca* records began more frequent also in areas such as the Adriatic Sea where this species was relatively rare until the last 1970s (Zavodnik, 1987).

Other jellyfish species appear to exhibit sustained increases in the Mediterranean Sea, such as the cosmopolitan species *Chrysaora hysoscella* (Linnaeus, 1767) that appears to be in expansion in the Aegean area in recent years (Öztürk & İşinibilir, 2010). Furthermore, in the Mediterranean Sea there are several examples of non-indigenous jellyfish species: two species of the *Cassiopea* genus *C. andromeda* (Forsskål, 1775) and *C. polyoides* Keller, 1883 (Brotz & Pauly, 2012; Schembri *et al.*, 2010); *Carybdea marsupialis* (Linnaeus, 1758), Mediterranean cubomedusa widely distributed in the tropical waters of the Atlantic (Boero & Minelli, 1986). More alien jellyfish species were recorded in the Mediterranean Sea: *Rhopilema nomadica* Galil, Spanier, and Ferguson, 1990 (Deidun *et al.*, 2011; Daly Yahia *et al.*, 2013), one of the most successful invasive species of jellyfish in the eastern Mediterranean that is causing significant economic losses; the tropical invasive scyphozoan *Phyllorhiza punctata* Lendenfeld, 1884 (Boero *et al.*, 2009; Galil *et al.*, 2009; Galil *et al.*, 2010; Çevik *et al.*, 2011; Gülşahin & Tarkan 2012); the scyphozoan *Marivagia stellata* Galil and Gershwin, 2010 (Galil *et al.*, 2010).

Change seen as opportunity

As seen above, in the Mediterranean Sea every year an increasing number of jellyfish blooms are recorded as a consequence of climatic and anthropic causes that are shaping changes in marine biodiversity and food sources (Leone & Piraino, 2015).

Big blooms may be the new normality but with new technologies we could turn them into an economic opportunity as valuable resources. Jellyfish create shelter for fish in their tentacles and in a few Countries provide an important source of food; their toxins, their tissues and the green fluorescent protein (responsible for their bioluminescence) are being studied for medical uses (Cho, 2011).

Recent researches suggest methods of turning proteins, carbohydrates and lipids into ethanol alcohol (Hsieh *et al.*, 2001). On the other hand, in order to obtaining ethanol production from jellyfish requires washing them in fresh water to remove most of the salt that could be marketed as jelly salt (Lee *et al.*, 2014). Finally, ethanol can be converted into a drink or used as fuel vehicles (Huo *et al.*, 2011).

In the Mediterranean Sea, nutraceutical value and antioxidant properties of a few of the most abundant and commonly recorded jellyfish species [*Aurelia* sp.1, *Coty-*

lorhiza tuberculata (Macri, 1778) and *Rhizostoma pulmo* (Macri, 1778)] (Figs 2, 3) were subject to investigation (Leone *et al.*, 2015). Marine organisms, in fact, still represent a largely unexplored reservoir of natural products (source of potential healthy food, bioactive compounds and, even, new drugs) due to the presence of secondary metabolites (Mayer *et al.*, 2013). For this reason, recent researches (Gates, 2010; Guérard *et al.*, 2010; Leone *et al.*, 2013; Mariottini & Pane, 2013; Mayer *et al.*, 2013) have focused on many bioactive molecules extracted from marine organisms with potential anti-inflammatory, antimicrobial, and anticancer properties. In particular, cnidarians are an important source of physiologically active compounds (Leone *et al.*, 2013; Mariottini & Pane, 2013). The collagen, the main structural protein in the jellyfish body mass (Hsieh & Rudloe, 1994; Addad *et al.*, 2011), is a structural protein family component of extracellular matrices in connective tissues (Aouacheria *et al.*, 2006; Ricard-Blum, 2011) characterized by low immunogenicity and high biocompatibility sharing several features with their human counterparts (Meena *et al.*, 1999; Esposito *et al.*, 2010). These marine invertebrates are becoming an engaging source for collagen better tolerated than that extracted from other organisms as porcine and bovine skins that is more and more rejected for religious reasons or disease risks.

Jellyfish are used in the cosmetics for the skin as well as in the pharmaceutical and biomedical industry for their therapeutic value in the treatment of hypertension, ulcers, arthritis, bone pain, digestion problems, as softening skin (Hsieh & Rudloe, 1994; Omori & Nakano, 2001; Leone *et al.*, 2015).

Projects such as ‘The EU-project ‘GoJelly project’ (see <https://www.geomar.de/en/service/kommunikation/singlepm/article/jellyfish-disgusting-useful/>) aims to change the perception that jellyfish are regarded as annoying and dangerous proposing their use as source to produce microplastic filter, fertilizer or fish feed. Another project such as The EcoJel project (see http://ec.europa.eu/regional_policy/en/projects/ireland/ecojel-assessing-jellyfish-increase-in-the-irish-sea), for example, is helping the EU to become a smart, sustainable and inclusive economy by 2020, as set out in the EU 2020 growth strategy, identifying and managing the threats and opportuni-

ties on sectors such as tourism, aquaculture and fisheries presented by the predicted increase in jellyfish blooms in the Irish Sea. Indeed, it is a priority to identify and manage threats and opportunities of jellyfish increase: jellyfish might lead to the closure of some beaches and at the same time can also present business opportunities around diving with jellyfish; blooms, cause of mass mortality in fish farms, could present a chance for harvesting jellyfish as food to export to Asian markets. In China and in Japan jellyfish are appreciated as food for their composition [high content in omega-3 and omega-6 fatty acids, low content in cholesterol, fat and salt decreasing incidence of coronary heart diseases (Hsieh & Rudloe, 1994; Hsieh *et al.*, 2001; Omori & Nakano, 2001)]. On the other hand, the cnidarian lipid composition may vary considerably depending on their diet or symbiotic association with unicellular algae (Papina *et al.*, 2003; De Souza *et al.*, 2007; Dunn *et al.*, 2012; Leone *et al.*, 2013). In this framework, there could be positive aspects to an sea full of jellyfish (called ‘Jellyfish Apocalypse’ by Lee *et al.*, 2014) as scientists have looked into using jellyfish in several ways: age reduction powers in one type of jellyfish (Rich, 2012) (life-cycle reversal in *Turritopsis dohrnii* (Weismann, 1883) medusa (Piraino *et al.*, 1996; Martell *et al.*, 2016), proteins used for disease control purposes (Hsieh *et al.*, 2001), and biomarkers used in medical diagnostics (Stepanenko *et al.*, 2008). On the other hand, jellyfish as new food sources must be fully characterised from nutritional, nutraceutical, biochemical, microbial and toxicological point of view. Furthermore, any potential risks for health must be carefully evaluated in order to increase consumer confidence. These new perspectives require the development of appropriate processing technologies for extraction of some bioactive compounds from jellyfish ensuring to avoid bio-accumulate chemical contaminants.

Several jellyfish species show nutritional and biological features resulting good candidates as feed sources and/or bioactive compounds. What we have therefore is, similarly to the Asiatic edible species, the potential possibility of Mediterranean jellyfish as natural biological resources for different food, industrial and pharmaceutical sectors (Leone & Piraino, 2015).

Humans could exploit the increase of jellyfish by de-



Fig. 2: *Cotylorhiza tuberculata* (Photo credit: Gianluca Romano).



Fig. 3: *Rhizostoma pulmo* (Photo credit: Gianluca Romano).

veloping new benefits. The ‘Jellyfish Apocalypse’, therefore, can be converted to an opportunity through their use as food, as it already happens in the eastern countries in Asia where business have already developed for jellyfish products, and biofuel (Lee *et al.*, 2014).

Future perspective

In the framework of a rapid changing of the Mediterranean pelagic ecosystem structure, from one dominated by fish to a gelatinous state, management actions are necessary to stop such trend through the coupling of tactical strategies and longer-term research managing the marine environment in a precautionary and holistic way (Brotz & Pauly, 2012; Coll *et al.*, 2012). On the other hand, jellyfish may be regarded, due to their high abundances-reproductive and regenerative potentials, as a new source of nutraceutical, pharmacologic and food/feed compounds, providing the opportunity of several potential use medicine, tissue engineering, and food industry (Boero *et al.*, 2002, 2008a; Piraino *et al.*, 2004; Boero, 2013; Doyle *et al.*, 2014; Lee *et al.*, 2014; Leone *et al.*, 2015). More research is necessary to perfect the technology, still at the experimental status, using yeasts and bacteria to turn jellyfish protein into alcohol: this plan must be taken into consideration for the future.

Finally, further studies are also needed to clarify aspects related to insufficient scientific knowledge, food safety assessment, and data access.

Conclusion

Jellyfish are ancient creatures that together to other organisms evolved into a balanced and calibrated ecological puzzle. Anthropogenic actions continue to disrupt these interdependent relationships seeing profound effects on our environment. Jellyfish blooms are, probably, the result of just one of countless habitats we have destroyed. On the other hand, adaptation strategies and management have been developed in order to prevent negative impacts (Matsushita *et al.*, 2005; Lucas *et al.*, 2014) as well as mitigation measures against jellyfish proliferation impacts in the context of research projects such as Med-JellyRisk (see www.jellyrisk.eu) (MED-JELLYRISK, 2015).

In conclusion, it is clear that our lifestyle is not compatible with a healthy ecosystem (Boero, 2015). Policy decisions made in the past continue to have profound impacts on ecosystems and global climate, not just for this century, but also for the next millennia (Clark *et al.*, 2016). According to Gershwin (2013), the future of the marine ecosystems is, probably, starting now by facing the problems created by past mistakes and being proactive in solving them.

Acknowledgements

I would like to thank Francesco Di Trapani and Gianluca Romano for pictures.

References

- Addad, S., Exposito, J.Y., Faye, C., Ricard-Blum, S., Lethias, C., 2011. Isolation, characterization and biological evaluation of jellyfish collagen for use in biomedical applications. *Marine Drugs*, 9, 967-983.
- Anonymous, 2008. *Jellyfish outbreaks a sign of nature out of sync*. Reefblue.net. 2008-06-27. <http://www.reefblue.net/en/news/3> (Accessed 1 March 2018).
- Anonymous, 2010a. *Blooming jellyfish in northeast Atlantic and Mediterranean: overfishing, warming waters to blame*. Science Daily, Rockville, Maryland, U.S.A. 2010-12-14. <https://www.sciencedaily.com/releases/2010/12/101213071115.htm> (Accessed 1 March 2018).
- Anonymous, 2010b. *Sea Temperature Rise*. *National Geographic*. <http://ocean.nationalgeographic.com/ocean/critical-issues-sea-temperature-rise/> (Accessed 1 March 2018).
- Anonymous, 2010c. *Tourists warned to be on guard for ‘mauve stinger’ after swarms of jellyfish invade Spain’s Costa Blanca*. Daily Mail, London, United Kingdom. 2010-08-03. http://www.dailymail.co.uk/travel/travel_news/article-1299851/Tourists-warned-guard-mauve-stinger-swarms-jellyfish-invade-Spains-Costa-Brava.html (Accessed 1 March 2018)
- Aouacheria, A., Geourjon, C., Aghajari, N., Navratil, V., Deléage, G. *et al.*, 2006. Insights into early extracellular matrix evolution: Spongin short chain collagen-related proteins are homologous to basement membrane type IV collagens and form a novel family widely distributed in invertebrates. *Molecular Biology and Evolution*, 23, 2288-2302.
- Arai, M.N., 2009. The potential importance of podocysts to the formation of scyphozoan blooms: a review. *Hydrobiologia*, 616, 241-246.
- Ballesteros, E., 2006. Mediterranean coralligenous assemblages: A synthesis of present knowledge. *Oceanography and Marine Biology - An Annual Review*, 44, 123-195.
- Baxter, E.J., Rodger, H.D., McAllen, R., Doyle, T.K., 2011. Gill disorders in marine-farmed salmon: investigating the role of hydrozoan jellyfish. *Aquaculture Environment Interactions*, 1, 245-257.
- Bayha, K.M., Dawson, M.N., 2010. New family of allomorphic jellyfishes, Drymonematidae (Scyphozoa, Discomedusae), emphasizes evolution in the functional morphology and trophic ecology of gelatinous zooplankton. *Biological Bulletin (Wood Hole, MA)*, 219, 249-267.
- Benedetti-Cecchi, L., Canepa, A., Fuentes, V., Tamburello, L., Purcell, J.E. *et al.*, 2015. Deterministic factors overwhelm stochastic environmental fluctuations as drivers of jellyfish outbreaks. *PLoS ONE*, 10, e0141060.
- Bianchi, C.N., 2007. Biodiversity issues for the forthcoming tropical Mediterranean Sea. *Hydrobiologia*, 580, 7-21.
- Bianchi, C.N., Morri C., 2004. Climate change and biological response in Mediterranean Sea ecosystems: a need for broad-scale and long-term research. *Ocean Challenge*, 13, 32-36.

- Bilio, M., Niermann, U., 2004. Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. *Marine Ecology Progress Series*, 269, 173-183.
- Boero, F., 2001. Light after dark: the partnership for enhancing expertise in taxonomy. *Trends in Ecology & Evolution*, 16, 266. <http://www.biomareweb.org/downloads/tree.pdf> (Accessed 2 March 2018)
- Boero, F., 2002. Ship-driven biological invasions in the Mediterranean Sea. p. 87-91. In: *Alien marine organisms introduced by ships, Istanbul, 6-9 November 2002. CIESM Workshop Monograph*, 20. <http://www.ciesm.org/publications/Istanbul02.pdf> (Accessed 1 March 2018).
- Boero, F., 2011. New species are welcome, but... what about the old ones? *Italian Journal of Zoology*, 78, 1-2.
- Boero, F., 2013. Review of jellyfish blooms in the Mediterranean and Black Sea. *General Fisheries Commission for the Mediterranean - Studies and Reviews*, 92, pp. i-vii, 1-53. <http://www.fao.org/docrep/017/i3169e/i3169e.pdf> (Accessed 1 March 2018).
- Boero, F., 2015. The future of the Mediterranean Sea ecosystem: towards a different tomorrow. *Rendiconti Lincei. Scienze Fisiche e Naturali*, 26, 3-12.
- Boero, F., Bonsdorff, E.A., 2007. Conceptual framework for marine biodiversity and ecosystem functioning. *Marine Ecology*, 28, 134-145.
- Boero, F., Gravili, C., 2013. The bio-ecology of marine extinctions, with a lesson from the Hydrozoa. p. 75-79. In: *Marine extinctions - patterns and processes*. Briand, F., (Ed.). CIESM Workshop Monograph n° 45, Valencia (Spain), 10-13 October 2012.
- Boero, F., Mills, C.E., 1997. Agricultural versus ethological oceanography. *Trends in Ecology & Evolution*, 12, 208-209. <https://faculty.washington.edu/cemills/TREE97.pdf> (Accessed 2 March 2018).
- Boero, F., Minelli, A., 1986. First record of *Carybdea marsupialis* from the Adriatic Sea. *Bollettino del Museo Civico di Storia Naturale di Venezia*, 35, 179-180.
- Boero, F., Bouillon, J., Piraino, S., Schmid, V., 1997. Diversity of hydromedusan life cycles: ecological implications and evolutionary patterns. p. 53-62. In: *Proceedings of the 6th International Conference on Coelenterate Biology, The Leeuwenhorst, Noordwijkerhout, The Netherlands, 16-21 July 1995*. den Hartog, J.C., van Ofwegen, L.P., van der Spoel, S. (Eds). Nationaal Natuurhistorisch Museum, Leiden.
- Boero, F., Bouillon, J., Piraino, S., Schmid, V., 2002. Asexual reproduction in the Hydrozoa (Cnidaria). p. 141-158. In: *Reproductive Biology of Invertebrates XI: Progress in Asexual Reproduction*. Hughes, R.N. (Ed.). Oxford & IBH Publishing Co., New Delhi, India.
- Boero, F., Bouillon, J., Gravili, C., Miglietta, M.P., Parsons, T. *et al.*, 2008a. Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series*, 356, 299-310.
- Boero, F., Féral, J.P., Azzurro, E., Cardin, V., Riedel, B. *et al.*, 2008a. Climate warming and related changes in Mediterranean marine biota. I. Executive Summary of Ciesm Workshop. p. 5-21. *Climate warming and related changes in Mediterranean marine biota*. 35, *Helgoland*, 27-31 May 2008. http://www.ciesm.org/online/monographs/download.php?file=Helgoland08_ExecSum.pdf (Accessed on 01 03 2018).
- Boero, F., Putti, M., Trainito, E., Prontera, E., Piraino, S. *et al.*, 2009. First records of *Mnemiopsis leidyi* (Ctenophora) from the Ligurian, Tyrrhenian and Ionian Seas (Western Mediterranean) and first record of *Phyllorhiza punctata* (Cnidaria) from the Western Mediterranean. *Aquatic Invasions*, 4, 675-680.
- Boero, F., Brotz, L., Gibbons, M.J., Piraino, S., Zampardi, S., 2016. Impacts and effects of ocean warming on jellyfish. p. 213-237. In: *Explaining Ocean Warming: Causes, scale, effects and consequences*. Lagiffoley, D., Baxter, J.M. (Eds). IUCN, Gland, Switzerland.
- Bosch-Belmar, M., M'Rabet, C., Dhaouadi, R., Chalhaf, M., Daly, Yahia M.N. *et al.*, 2016. Jellyfish stings trigger gill disorders and increased mortality in farmed *Sparus aurata* (Linnaeus, 1758) in the Mediterranean Sea. *PLoS ONE*, 11, e0154239.
- Boudouresque, C.F., 2004. Marine biodiversity in the Mediterranean: Status of species, populations and communities. Scientific Reports of Port-Cros National Park, France, 20, 97-146.
- Brodeur, R.D., Sugisaki, H., Hunt, G.L., 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series*, 233, 89-103.
- Brotz, L., Cheung, W.W.L., Kleisner, K., Pakhomov, E., Pauly, D., 2012. Increasing jellyfish populations: Trends in Large Marine Ecosystems. *Hydrobiologia*, 690, 3-20.
- Brotz, L., Pauly, D., 2012. Jellyfish populations in the Mediterranean Sea. *Acta Adriatica*, 53, 213-232. http://hrcaak.srce.hr/index.php?show=clanak&id_clanak_jezik=138945 (Accessed 1 March 2018).
- Canepa, A., Fuentes, V., Sabatés, A., Piraino, S., Boero, F. *et al.*, 2014. *Pelagia noctiluca* in the Mediterranean Sea. Chapter 11. p. 237-266. In: *Jellyfish Blooms*. Pitt, K.A., Lucas, C.H. (Eds). Springer, Dordrecht Heidelberg New York London.
- Çevik, C., Derici, O.B., Çevik, F., Cavas, L., 2011. First record of *Phyllorhiza punctata* von Lendendfeld, 1884 (Scyphozoa: Rhizostomeae: Mastigiidae) from Turkey. *Aquatic Invasions*, 6, S27-S28.
- Cho, R., 2011. *Giant jellyfish swarms – Are humans the cause?* State of the Planet. <http://blogs.ei.columbia.edu/2011/02/26/giant-jellyfish-swarms-are-humans-the-cause/> (Accessed 1 March 2018).
- Chudnow, R., 2008. *Are jellyfish populations increasing worldwide (and why)?* Honours Bachelor's Thesis. Dalhousie University, Halifax, 84 pp.
- CIESM. 2001. Gelatinous plankton outbreaks: theory and practice. *CIESM Workshop Series*, Monaco, 14, 90 pp. <http://www.unioviado.es/JLAcuna/papers/Acuna2001-Zooplankton%20outbreaks.PDF> (Accessed 1 March 2018).
- Clark, P.U., Shakun, J.D., Marcott, S.A., Mix, A.C., Eby, M. *et al.*, 2016. Consequences of twenty-first-century policy for multi-millennial climate and sea-level change. *Nature Climate Change*, 6, 360-369.
- Coll, M., Piroddi, C., Albouy, C., Lasram, F.B.R., Cheung, W.W.L. *et al.*, 2012. The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Global Ecology and Biogeography*, 21, 465-480.

- Daly Yahia, M.N., Batistić, M., Lučić, D., Fernández De Puellas, M.L., Licandro, P. *et al.*, 2010. Are the outbreaks of *Pelagia noctiluca* more frequent in the Mediterranean basin? *ICES Cooperative Research Report*, 300, 8-14. http://digital.csic.es/bitstream/10261/45787/1/Prieto_2010.pdf (Accessed 1 March 2018).
- Daly Yahia, M.N., Kéfi-Daly Yahia, O., Maïte Gueroun, S.K., Aissi, M., Deidun, A. *et al.*, 2013. The invasive tropical scyphozoan *Rhopilema nomadica* Galil, 1990 reaches the Tunisian coast of the Mediterranean Sea. *BioInvasions Records*, 2, 319-323.
- Daskalov, G.M., 2002. Overfishing drives a trophic cascade in the Black Sea. *Marine Ecology Progress Series*, 225, 53-63. <http://www.everythingconnects.org/uploads/7/0/3/5/7035190/m225p053.pdf> (Accessed 1 March 2018)
- Dawson, M.N., Hamner, W.M., 2009. A character-based analysis of the evolution of jellyfish blooms: adaptation and exaptation. *Hydrobiologia*, 616, 193-215.
- De Donno, A., Idolo, A., Bagordo, F., Grassi, T., Leomanni, A. *et al.*, 2014. Impact of stinging jellyfish proliferations along South Italian coasts: Human health hazards, treatment and social costs. *International Journal of Environmental Research and Public Health*, 11, 2488-2503.
- De Souza, L.M., Iacomini, M., Gorin, P.A.J., Sari, R.S., Haddad, M.A. *et al.*, 2007. Glyco- and sphingophosphonolipids from the medusa *Phyllorhiza punctata*: NMR and ESI-MS/MS fingerprints. *Chemistry and Physics of Lipids*, 145, 85-96.
- 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.
- Dovel, W.L., 1964. An approach to sampling estuarine macroplankton. *Chesapeake Science*, 5, 77-90.
- Doyle, T.K., Hays, G.C., Harrod, C., Houghton, J.D.R., 2014. Ecological and societal benefits of jellyfish. p. 105-127. In: *Jellyfish Blooms*. Pitt, K.A., Lucas, C.H. (Eds). Springer Science + Business Media, Dordrecht, The Netherlands.
- Duarte, C.M., Pitt, K.A., Lucas, C.H., Purcell, J.E., Uye, S. *et al.*, 2013. Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and Environment*, 11, 91-97.
- Dunn, S.R., Thomas, M.C., Nette, G.W., Dove, S.G. *et al.*, 2012. A lipidomic approach to understanding free fatty acid lipogenesis derived from dissolved inorganic carbon within cnidarian-dinoflagellate symbiosis. *PLoS ONE*, 7, e46801.
- Exposito, J.Y., Valcourt, U., Cluzel, C., Lethias, C., 2010. The fibrillar collagen family. *International Journal of Molecular Sciences*, 11, 407-426.
- Fosså, J., Flood, P., Olsen, A., Jensen, F., 2003. Småog usynlige, men plagsomme maneter av arten *Muggiaea atlantica* (Small and invisible, but troublesome jellyfish of the species *Muggiaea atlantica*). *Fisk og Havet (Fish Sea)*, 2, 99-103.
- Galil, B., Boero, B., Fraschetti, S., Piraino, S., Campbell, M. *et al.*, 2015. The enlargement of the Suez Canal and introduction of non-indigenous species to the Mediterranean Sea. *ASLO - letter to the editors*, 4 pp.
- Galil, B.S., 2008. Alien species in the Mediterranean Sea: which, when, where, why? *Hydrobiologia*, 606, 105-116.
- Galil, B.S., 2009. Taking stock: inventory of alien species in the Mediterranean Sea. *Biological Invasions*, 11, 359-372.
- Galil, B.S., 2015. The expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. p. 115. In: *Proceedings of the 76° Congresso Nazionale dell'Unione Zoologica Italiana, Viterbo, 15-18 Settembre 2015*. Zapparoli, M., Belardinelli, M.C. (Eds). Quaderni del Centro Studi Alpino, IV, Università degli Studi della Tuscia.
- Galil, B.S., Gershwin, L.-A., Douek, J., Rinkevich, B., 2010. *Marivagia stellata* gen. et sp. nov. (Scyphozoa: Rhizostomeae: Cepheidae), another alien jellyfish from the Mediterranean coast of Israel. *Aquatic Invasions*, 5, 331-340.
- Galil, B.S., Gershwin, L.-A., Zorea, M., Rahav, A., Rothman, S.B.-S. *et al.*, 2016. *Cotylorhiza erythraea* Stiasny, 1920 (Scyphozoa: Rhizostomeae: Cepheidae), yet another erythraean jellyfish from the Mediterranean coast of Israel. *Marine Biodiversity*, 47 (1), 229-235.
- Galil, B.S., Shoval, L., Goren, M., 2009. *Phyllorhiza punctata* von Lendenfeld, 1884 (Scyphozoa: Rhizostomeae: Mastigiidae) reappeared off the Mediterranean coast of Israel. *Aquatic Invasions*, 4, 481-483.
- Garrett, C., 1994. The Mediterranean Sea as a climate test basin. p. 227-237. *Ocean Processes in Climate Dynamics: Global and Mediterranean Examples* 419. Series NATO ASI Series. Publisher Springer, Netherlands.
- Gates, K.W., 2010. Marine products for healthcare: Functional and bioactive nutraceutical compounds from the Ocean, Vazhiyil Venugopal. *Journal of Aquatic Food Product Technology*, 19, 48-54.
- Gershwin, L.-A., 2013. *Stung! On jellyfish blooms and the future of the ocean*. The University of Chicago Press Books, Chicago.
- Goy, J., Morand, P., Etienne, M., 1989. Longterm fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. *Deep-Sea Research*, 36, 269-279. http://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_7/b_fdi_51-52/010019861.pdf (Accessed 1 March 2018)
- Gravili, C., 2017. Alien jellyfish in expansion: The contribution of taxonomy to ecology. Chapter 2. p. 27-49. In: *Jellyfish. Ecology, Distribution Patterns and Human Interactions*. Mariottini, G.L. (Ed.). Nova Publishers, New York. <https://lccn.loc.gov/2016028482> (Accessed 2 March 2018)
- Gravili, C., Bevilacqua, S., Terlizzi, A., Boero, F., 2015. Missing species among Mediterranean non-Siphonophoran Hydrozoa. *Biodiversity and Conservation*, 24, 1329-1357.
- Gravili, C., Boero, F.A., 2014. Bioregionalization of the genus *Halecium* (Hydrozoa: Haleciidae): sentinel taxon of the global warming? p. 128. In: *Proceedings of the 75th National Conference of the Unione Zoologica Italiana, Università degli Studi di Bari, 22-25 September 2014*. Thalassia Salentina (Suppl.), Università degli Studi di Bari Aldo Moro.
- Gravili, C., Di Camillo, C.G., Piraino, S., Boero, F., 2013. Hydrozoan species richness in the Mediterranean Sea: past and present. *Marine Ecology*, 34, 41-62.
- Green, E.P., Short, F.T., 2003. The world atlas of seagrasses. University of California Press, Berkeley, California, 336 pp.
- Guérard, F., Decourcelle, N., Sabourin, C., Floch-Laizet, C., le Grel, L. *et al.*, 2010. Recent developments of marine ingredients for food and nutraceutical applications: A review. *Journal Canadien des Sciences Halieutiques et Aquatiques*,

- 2, 21-27. <http://hal.univ-brest.fr/hal-00636874> (Accessed 1 March 2018)
- Guilford, G., 2013. *Jellyfish are taking over the seas, and it might be too late to stop them*. Quartz. <https://qz.com/133251/jellyfish-are-taking-over-the-seas-and-it-might-be-too-late-to-stop-them/> (Accessed 21 February 2018).
- Gülşahin, N., Tarkan, A.N., 2012. The first record of *Phyllorhiza punctata* von Lendenfeld, 1884 from the southern Aegean Coast of Turkey. *BioInvasions Records*, 1, 41-44.
- Haddock, S.H.D., 2004. A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia*, 530, 549-556. <https://pdfs.semanticscholar.org/cdbd/18b577f290381c225f9b690dfdb452509f0b.pdf> (Accessed 2 March 2018).
- Hagadorn, J.W., Dott, R.H., Damrow, D., 2002. Stranded on a late Cambrian shoreline: medusae from central Wisconsin. *Geology*, 30, 147-150.
- Harmelin, J.-G., d'Hont J.-L., 1993. Transfers of bryozoan species between the Atlantic Ocean and the Mediterranean Sea via the Strait of Gibraltar. *Oceanologica Acta*, 16, 63-72. <http://archimer.ifremer.fr/doc/00094/20531/> (Accessed 2 March 2018).
- Hay, S., 2006. Marine ecology: gelatinous bells may ring change in marine ecosystems. *Current Biology*, 16, R679-R682.
- Heinle, D.R., 1965. A screen for excluding jellyfish and ctenophores from Clarke-Bumpus plankton samples. *Chesapeake Science*, 6, 231-232.
- Hoegh-Guldberg, O., Bruno, J.F., 2010. The Impact of Climate Change on the World's Marine Ecosystems. *Science*, 328, 1523-1528.
- Hsieh, Y.-H., Leong, Fui-Ming, Rudloe, J., 2001. Jellyfish as food. *Hydrobiologia*, 451, 11-17.
- Hsieh, Y.H.P., Rudloe, J., 1994. Potential of utilizing jellyfish as food in Western countries. *Trends in Food Science & Technology*, 5, 225-229.
- Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution*, 15, 56-61.
- Huo, Y.-X., Cho, K.M., Lafontaine Rivera, J.G., Monte, E., Shen, C.R. *et al.*, 2011. Conversion of protein into biofuels by engineering nitrogen flux. *Nature Biotechnology*, 29, 346-351.
- Jackson, J.B.C., 2008. Ecological extinction and evolution in the brave new ocean. *Proceeding of the National Academy of Science of the United States of America*, 105, 11458-11465.
- Kawahara, M., Uye, S., Ohtsu, K., Iizumi, H., 2006. Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. *Marine Ecology Progress Series*, 307, 161-173.
- Lee, J.H., Christian, H., Looman, A., Bodnar, L., Medina, C., 2014. *Jellyfish Apocalypse: Problems, causes and opportunities*. Alaska Ocean Sciences Bowl high school competition. Kodiak High School. <https://seagrant.uaf.edu/nosb/papers/2014/kodiak-elusive-jellyfish.pdf> (Accessed 1 March 2018)
- Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudourisque, C.F., Perez, T., 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology & Evolution*, 4, 250-260.
- Leone, A., Lecci, R.M., Durante, M., Meli, F., Piraino, S., 2015. The bright side of gelatinous blooms: nutraceutical value and antioxidant properties of three Mediterranean jellyfish (Scyphozoa). *Marine Drugs, Special Issue "Marine Functional Food"*, 13, 4654-4681.
- Leone, A., Lecci, R.M., Durante, M., Piraino, S., 2013. Extract from the zooxanthellate jellyfish *Cotylorhiza tuberculata* modulates gap junction intercellular communication in human cell cultures. *Marine Drugs*, 11, 1728-1762.
- Leone, A., Piraino, S., 2015. Jellyfis: old Eastern food becomes the Western novel food. In: EFSA (European Food Safety Authority) 2015. Shaping the Future of Food Safety, Together. *Proceedings of the 2nd EFSA Scientific Conference, Milan, Italy, 14-16 October 2015. EFSA Journal*, 13, s1310.
- Link, J.S., Ford, M.D., 2006. Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. *Marine Ecology Progress Series*, 320, 153-159.
- Lucas, C.H., Gelcich, S., Uye, S.I., 2014. Living with jellyfish: Management and adaptation strategies. p. 129-150. In: *Jellyfish Blooms*. Pitt KA, Lucas CH (Eds). Springer, Dordrecht, The Netherlands.
- Lynam, C.P., Gibbons, M.J., Axelsen, B.E., Sparks, C.A.J., Coetzee, J. *et al.*, 2006. Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology*, 16, R492-R493.
- Lynam, C.P., Hay, S.J., Brierley, A.S., 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography*, 49, 637-643.
- Lynam, C.P., Heath, M.R., Hay, S.J., Brierley, A.S., 2005. Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series*, 298, 157-167.
- Malej, A., Malej, A.J., 2004. Invasion of the Jellyfish *Pelagia noctiluca* in the Northern Adriatic: a non-success story. p. 273-285. In: *Aquatic invasions in the Black, Caspian, and Mediterranean Seas: the ctenophores Mnemiopsis leidyi and Beroe in the Ponto-Caspian and other aquatic invasions*. Dumont, H., Shiganova, T.A., Niermann, U., (Eds). Nato Science Series: 4. Earth and Environmental Sciences. Springer, Netherlands.
- Mariottini, G.L., Giacco, E., Pane, L., 2008. The Mauve Stinger *Pelagia noctiluca* (Forsskål, 1775). Distribution, ecology, toxicity and epidemiology of stings. A review. *Marine Drugs*, 6, 496-513.
- Mariottini, G.L., Pane, L., 2013. Cytotoxic and cytolytic cnidarian venoms. A review on health implications and possible therapeutic applications. *Toxins (Basel)*, 6, 108-151.
- Martell, L., Piraino, S., Gravili, C., Boero, F., 2016. Life cycle, morphology and medusa ontogenesis of *Turritopsis dohrnii* (Cnidaria: Hydrozoa). *Italian Journal of Zoology*, 83, 390-399.
- Matsushita, Y., Honda, N., Kawamura, S., 2005. Design and tow trial of JET (Jellyfish Excluder for Towed fishing gear). *Nippon Suisan Gakkaishi*, 71, 965-967. <http://agris.fao.org/agris-search/search.do?recordID=JP2006005632> (Accessed 1 March 2018).
- Mayer, A.M.S., Rodríguez, A.D., Tagliatalata-Scafati, O., Fusetani, N., 2013. Marine pharmacology in 2009–2011: Marine compounds with antibacterial, antidiabetic, antifungal, anti-inflammatory, antiprotozoal, antituberculosis, and antiviral activities; affecting the immune and nervous

- systems, and other miscellaneous mechanisms of action. *Marine Drugs*, 11, 2510-2573.
- MED-JELLYRISK. 2015. *Enhancing management approach and mitigation measures against jellyfish proliferations impacts*. Project funded by the ENPI CBC MED (European Neighbourhood and Partnership Instrument Cross-Border Cooperation in the Mediterranean). <http://www.jellyrisk.eu> (Accessed 20 February 2017)
- Meena, C., Mengi, S.A., Deshpande, S.G., 1999. Biomedical and industrial applications of collagen. *Proceedings of the Indian Academy of Sciences Animal Sciences*, 111, 319-329.
- Mills, C.E., 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES Journal of Marine Science*, 52, 575-581.
- Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, 451, 55-68.
- Moffett, S., 2007. *Invasion of Jellyfish Envelops Japan In Ocean of Slime*. The Wall Street Journal. Nov. 27, 2007. <http://online.wsj.com/news/articles/SB119612452419404666> (Accessed 1 March 2018).
- Molinero, J.C., Ibanez, F., Nival, P., Buecher, E., Souissi, S., 2005. North Atlantic climate and northwestern Mediterranean plankton variability. *Limnology and Oceanography*, 50, 1213-1220.
- O'Rourke, M., 2013. The power of the jellyfish. Risk Management. <http://www.rmmagazine.com/2013/11/01/the-power-of-the-jellyfish/> (Accessed 1 March 2018).
- Occhipinti-Ambrogi, A., Galil, B., 2010. Marine alien species as an aspect of global change. *Advances in Oceanography and Limnology*, 1, 199-218.
- Omori, M., Nakano, E., 2001. Jellyfish fisheries in southeast Asia. *Hydrobiologia*, 451, 19-26.
- Öztürk, B., İşinbilir, M., 2010. An alien jellyfish *Rhopilema nomadica* and its impacts to the Eastern Mediterranean part of Turkey. *Journal of the Black Sea/Mediterranean Environment*, 16, 149-156. <http://dergipark.ulakbim.gov.tr/jbme/article/viewFile/5000144414/5000131915> (Accessed 2 March 2018).
- Palomares, M.L.D., Pauly, D., 2009. The growth of jellyfishes. *Hydrobiologia*, 616, 11-21.
- Papina, M., Meziane, T., van Woesik, R., 2003. Symbiotic zooxanthellae provide the host-coral *Montipora digitata* with polyunsaturated fatty acids. *Comparative Biochemistry and Physiology B Biochemistry and Molecular Biology*, 135, 533-537.
- Parsons, T.R., Lalli, C.M., 2002. Jellyfish population explosions: Revisiting a hypothesis of possible causes. *La Mer*, 40, 111-121. http://www.sfjo-lamer.org/la_mer/40-3/40-3-2.pdf (Accessed 2 March 2018)
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.Jr., 1998. Fishing down marine food webs. *Science*, 279, 860-863.
- Piraino, S., Aglieri, G., Martell, L., Mazzoldi, C., Melli, V. *et al.*, 2014. *Pelagia benovici* sp. nov. (Cnidaria, Scyphozoa): a new jellyfish in the Mediterranean. *Zootaxa*, 3794, 455-468.
- Piraino, S., Boero, F., Aeschbach, B., Schmid, V., 1996. Reversing the life cycle: medusae transforming into polyps and cell transdifferentiation in *Turritopsis nutricula* (Cnidaria, Hydrozoa). *Biological Bulletin*, 190, 302-312.
- Piraino, S., de Vito, D., Schmich, J., Bouillon, J., Boero, F., 2004. Reverse development in Cnidaria. *Canadian Journal of Zoology*, 82, 1748-1754.
- Pitt, K.A., Lucas, C.H. (Eds), 2014. *Jellyfish Blooms*. Springer, Dordrecht Heidelberg New York London, 304 pp.
- Prieto, L., Armani, A., Macias, D., 2013. Recent stranding of the giant jellyfish *Rhizostoma luteum* Quoy and Gaimard, 1827 (Cnidaria: Scyphozoa: Rhizostomeae) on the Atlantic and Mediterranean coasts. *Marine Biology*, 160, 3241-3247.
- Pugh, P.R., 1989. Gelatinous zooplankton – the forgotten fauna. *Progress in Underwater Science*, 14, 67-78.
- Purcell, J.E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of Marine Biological Association of the United Kingdom*, 85, 461-476.
- Purcell, J.E., 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annual Review of Marine Science*, 4, 209-235.
- Purcell, J.E., Brown, E.D., Stokesbury, K.D.E., Haldorson, L.H., Shirley, T.C., 2000. Aggregations of the jellyfish *Aurelia labiata*: abundance, distribution, association with age-0 walleye pollock, and behaviors promoting aggregations in Prince William Sound, Alaska, USA. *Marine Ecology Progress Series*, 195, 145-158. <http://www.int-res.com/articles/meps/195/m195p145.pdf> (Accessed 2 March 2018)
- Purcell, J.E., Graham, W.M., Dumont, H.J. (Eds). 2001. Jellyfish blooms: ecological and societal importance. *Developments in Hydrobiology*. 155. Kluwer Academic, Dordrecht, 334 pp.
- Purcell, J.E., 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*. *Coastal and Estuarine Studies*, 55, 241-263.
- Purcell, J.E., Milisenda, G., Rizzo, A., Carrion, S.A., Zampardi, S. *et al.*, 2015. Digestion and predation rates of zooplankton by the pleustonic hydrozoan *Veella veella* and widespread blooms in 2013 and 2014. *Journal of Plankton Research*, 0 (0), 1-12.
- Purcell, J.E., Uye, Sin-ichi, Lo, Wen-Tseng, 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, 350, 153-174.
- Ricard-Blum, S., 2011. The collagen family. *Cold Spring Harbor Perspective in Biology*, 3, a004978.
- Rich, N., 2012. *Can a jellyfish unlock the secret of immortality?* The New York Times. http://www.nytimes.com/2012/12/02/magazine/can-a-jellyfish-unlock-the-secret-of-immortality.html?ref=jellyfish&_r=0 (Accessed 4 May 2018)
- Richardson, A.J., Bakun, A., Hays, G., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution*, 24, 312-322.
- Rivetti, I., Fraschetti, S., Lionello, P., Zambianchi, E., Boero, F., 2014. Global warming and mass mortalities of benthic invertebrates in the Mediterranean Sea. *PLoS ONE*, 9, e115655.
- Roux, J.-P., van der Lingen, C.D., Gibbons, M.J., Moroff, N.E., Shannon, L.J. *et al.*, 2013. Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic

- fishes: lessons from the Benguela. *Bulletin of Marine Science*, 89, 249-284.
- Sabatés, A., Pagès, F., Atienza, D., Fuentes, V., Purcell, J.E., 2010. Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. *Hydrobiologia*, 645, 153-165.
- Sardà, F., Calafat, A., Flexas, M.M., Tselepidis, A., Canals, M. *et al.*, 2004. An introduction to Mediterranean deep-sea biology. *Scientia Marina*, 68, 7-38. <http://agris.fao.org/agris-search/search.do?recordID=ES2005000364> (Accessed 2 March 2018)
- Schembri, P.J., Deidun, A., Vella, P.J., 2010. First record of *Cassiopea andromeda* from the central Mediterranean Sea. *Marine Biodiversity Records*, 3, e6.
- Schrope, M., 2012. Attack of the blobs. *Nature*, 482, 20-21.
- Scorrano, S., Aglieri, G., Boero, F., Dawson, M.N., Piraino, S., 2016. Unmasking *Aurelia* species in the Mediterranean Sea: an integrative morphometric and molecular approach. *Zoological Journal of the Linnean Society*, 180 (2), 243-267.
- Shaltout, M., Omstedt, A., 2014. Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. *Oceanologia*, 56, 411-443.
- Stepanenko, O.V., Verkhusha, V.V., Kuzentsova, I.M., Uversky, V.N., Turoverov, K.K. *et al.*, 2008. Fluorescent proteins as biomarkers and biosensors: throwing color lights on molecular and cellular processes. *Current Protein & Peptide Science*, 9, 338-369.
- Tatsuki, N., 2005. Eutrophication and the increase of jellyfish population in the Seto Inland Sea. *Bulletin of the Plankton Society of Japan*, 52, 27-31. <http://agris.fao.org/agris-search/search.do?recordID=JP2006001910> (Accessed 2 March 2018)
- Templado, J. 2014. Future trends of Mediterranean biodiversity. p. 479-498. In: *The Mediterranean Sea: Its history and present challenges*. Goffredo, S., Dubinsky, Z. (Eds). Springer Science+Business Media, Dordrecht.
- Tremlett, G., 2013. *The Guardian*. <https://www.theguardian.com/environment/2013/jun/03/jellyfish-surge-mediterranean-environment-tourists> (Accessed 2 March 2018).
- Tsiamis, K., Zenetos A., Deriu I., Gervasini E., Cardoso A.C. *et al.*, 2018. The native distribution range of the European marine non-indigenous species. *Aquatic Invasions* 13 (2), 187-198.
- Uye, S., Ueta, Y., 2003. Recent increase of jellyfish in Hiroshima Bay based on the poll survey for fishermen. *Bulletin of the Japanese Society of Fisheries Oceanography*, 67, 271-273.
- Uye, S., Ueta, Y., 2004. Recent increase of jellyfish populations and their nuisance to fisheries in the Inland Sea of Japan. *Bulletin of the Japanese Society of Fisheries Oceanography*, 68, 9-19. <http://agris.fao.org/agris-search/search.do?recordID=JP2004007303> (Accessed 1 March 2018).
- Xian, W., Kang, B., Liu, R., 2005. Jellyfish blooms in the Yangtze estuary. *Science*, 307, 41.
- Young, G.A., Hagadorn, J.W., 2010. The fossil record of cnidarian medusae. *Palaeoworld*, 19, 212-221.
- Zavodnik, D., 1987. Spatial aggregations of the swarming jellyfish *Pelagia noctiluca*. *Marine Biology*, 94, 265-269.
- Zenetos, A., Gofas, S., Morri, C., Rosso, A., Violanti, D. *et al.*, 2012. Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science*, 13, 328-352.