

Chapter 12

Jellyfish Blooms and Their Impacts on Welfare Benefits: Recreation in the UK and Fisheries in Italy

Maria Giovanna Palmieri, Marije Schaafsma, Tiziana Luisetti, Alberto Barausse, Amii Harwood, Antara Sen, and R.K. Turner

12.1 Introduction

Jellyfish blooms may be regarded as an ecosystem shock, where the danger lies in the sudden outbreaks of jellyfish biomass, which may invoke changes and reactions in the ecosystem that are non-linear or affect multiple species (Daskalov et al. 2007). The main problem for a detailed assessment of the impacts of jellyfish outbreaks on ecosystem services provision is the paucity of jellyfish population datasets covering large temporal and spatial scales and the limited understanding of the role of jellyfish in ecosystems, the interaction with fish and other species

M.G. Palmieri (✉) • A. Harwood
Centre for Social and Economic Research on the Global Environment (CSERGE),
School of Environmental Sciences, University of East Anglia,
Norwich Research Park, Norwich NR4 7TJ, UK
e-mail: m.g.palmieri@uea.ac.uk

M. Schaafsma
Geography and Environment and Centre for Biological Sciences, University of Southampton,
University Road, Southampton SO17 1BJ, UK

T. Luisetti
Centre for Environment Fisheries & Aquaculture Science (CEFAS),
Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

A. Barausse
Environmental Systems Analysis Lab (LASA), University of Padova,
via Marzolo 9, 35131 Padova, Italy

A. Sen
Affiliate of the Centre for Social and Economic Research on the Global Environment
(CSERGE), School of Environmental Sciences, University of East Anglia,
Norwich Research Park, Norwich NR4 7TJ, UK

R.K. Turner
School of Environmental Sciences, University of East Anglia, Norwich, UK

populations, and the influence of human activities on the occurrence of blooms (Boero et al. 2008; Condon et al. 2012; Purcell et al. 2007). There is insufficient evidence to say under which conditions jellyfish blooms may cause irreversible ecosystem shifts, let alone to what extent these are caused by human pressures, as jellyfish also have a natural bloom-and-bust cycle following climatic patterns. The range of conditions at which ecosystems stay in a stable state is also unknown (see Fig. 2.4); shifts are usually unpredictable (Scheffer et al. 2001).

In the absence of scientific knowledge about the physical, chemical and biological components of the marine ecosystem, economic valuation of the impacts of jellyfish blooms can only be based on some simplifying rules and assumptions to assess changes in ecosystem services provision, in combination with the exploration of different scenarios – alternative stable states of the ecosystem with prior and post levels of ecosystem services provision (Crépin et al. 2012).

This chapter provides a review of the occurrence, causes, and impacts of jellyfish blooms throughout the world. It then presents two case studies of jellyfish impacts in Europe and provides estimates of the potential welfare losses stemming from impacts of blooms on recreation in the UK and fisheries in Italy.

12.2 Jellyfish Blooms: Occurrence, Causes, and Impacts

12.2.1 Is a “Jellification” of Global Seas Taking Place?

In the last decades extensive outbreaks of both indigenous and alien jellyfish have been recorded in several regions worldwide raising concern about a possible “jellification” of global seas (Jackson et al. 2001; Lynam et al. 2006; Attrill et al. 2007; Richardson et al. 2009). In the East China and Yellow Seas jellyfish blooms have become an annual event. Outbreaks of the giant jellyfish *Nemopilema nomurai* have taken place nearly each year since 2000 and blooms of other species, such as *Cyanea nozakii* and *Aurelia aurita*, have also increased during the same period (Dong et al. 2010). From Chinese waters jellyfish are carried northward into the Sea of Japan, where blooms of *Aurelia aurita* and *Nemopilema nomurai* also appear to have increased in the last decades (Uye 2008, 2010; Kawahara et al. 2006). In the Bering Sea the biomass of jellyfish, in particular the cnidarian *Chrysaora melanaster* (see Box 12.1), increased more than tenfold during the 1990s but declined after 2000 (Brodeur et al. 1999, 2002, 2008). The Northeast Atlantic has also recently witnessed an increasing trend in jellyfish abundance with outbreaks of a number of cnidarian species (Lilley et al. 2009; Licandro et al. 2010; Bastian et al. 2011; Lynam et al. 2011). In the southern North Sea and in Baltic waters the alien ctenophore *Mnemiopsis leidyi* has formed blooms along the coasts of the Netherlands, Belgium, and Denmark starting from 2006 (Faasse and Bayha 2006; Riisgård et al. 2012; Van Ginderdeuren et al. 2012). In the Mediterranean Sea outbreaks of this species have occurred in 2009 along the Mediterranean coasts of Italy, Spain, and Israel (Boero et al. 2009; Fuentes et al. 2010), while each summer since the

Box 12.1. Glossary

Jellyfish: Free-swimming gelatinous animals belonging to the phyla Ctenophora and Cnidaria.

Ctenophora: Invertebrate phylum, sometimes called comb jellies or sea gooseberries, which propel themselves through the sequential beating of their rows of cilia. They have colloblasts, which are cells that discharge a glue to ensnare preys. Ctenophores are holoplanktonic, lacking a benthic life stage and thus remaining in the plankton their entire life.

Cnidaria: Invertebrate phylum that contains animals, which vary in size from a few millimetres to a few metres. This phylum includes the “true jellyfish”, which all produce structures called nematocysts and generally have alternating polyp and medusa life stages.

Polyp: The benthic stage of cnidarians with a general body plan of a cylindrical body and a ring of tentacles surrounding an oral opening.

Medusa: The mobile, bell-shaped stage of cnidarians that actively swim through muscular contraction of their bells.

Nematocysts: Stinging cells that are concentrated in the tentacles and mouth appendages of cnidarians and are used to poison or stun preys.

Statoliths: Calcium carbonate structures in the margin of the swimming bell of medusae that are used to sense gravity and so help in maintaining orientation.

(Adapted from Richardson et al. 2009)

mid-1980s swarms of another alien, the cnidarian *Rhopilema nomadica*, have appeared along the Levantine coast (Galil 2008). In addition to alien jellyfish, record abundances of indigenous species, including *Pelagia noctiluca*, *Aurelia aurita*, *Chrysaora hysoscella*, *Cothyloriza tuberculata*, and *Rhizostoma pulmo*, have been documented in the last decades in Mediterranean waters (CIESM 2001; Kogovšek et al. 2010; Brotz and Pauly 2012). *Mnemiopsis leidyi* was accidentally introduced in the Black Sea in the early 1980s and from there spread to the adjacent seas of Azov, Marmara, the Aegean and the Caspian (Costello et al. 2012). By the late 1980s and for many years the pelagic ecosystem of the Black Sea became a dead-end gelatinous food-web (Shiganova et al. 2001). In the northern Benguela off Namibia reports of blooms of *Chrysaora hysoscella* and *Aequorea forskalea* have been increasing since the 1990s (Lynam et al. 2006). In the Gulf of Mexico *Aurelia aurita* and *Chrysaora quinquecirrha* increased both in distribution and abundance from the mid-1980s for over 10 years (Graham 2001), while the alien *Phyllorhiza punctata* formed its first bloom in 2000 (Graham et al. 2003).

Some scientists argue that not enough information is available yet to confirm increasing trends of jellyfish blooms. Condon et al. (2012) suggest that the perception that outbreaks are increasing globally is based on reports of increases in a few regions and on media reports, while recent blooms may be simply part of long-term

cycles in jellyfish populations. Condon et al. (2013) used all available long-term time series of annual jellyfish abundances in the global seas to test this latter hypothesis. The authors conclude that, although there has been a weak but significant overall increase in jellyfish abundance since the 1970s, the perceived global increase in jellyfish over the past decades coincides with the most recent rising phase of a pattern of decadal oscillations in jellyfish populations (i.e. natural bloom-and-bust cycles following climatic patterns). However, the results of the study also show that some coastal zones are experiencing enhanced jellyfish blooms, including the Sea of Japan, North Atlantic shelf regions, Barents Sea, Limfjorden (Denmark), and parts of the Mediterranean Sea, although jellyfish populations in these regions also exhibit decadal oscillations.

12.2.2 Environmental Perturbations Favouring Jellyfish Blooms

Jellyfish are provided with a suite of attributes that enable them to survive in disturbed marine ecosystems and to rebound rapidly as conditions improve (Richardson et al. 2009). These attributes include fast growth rates, the ability to shrink when starved, and the capacity to fragment and regenerate (Richardson et al. 2009). Jellyfish are efficient, gluttonous and non-selective predators (Arai 1997). They can mature and reproduce quickly, both sexually and a-sexually (Arai 1997). Jellyfish can withstand poor environments more easily than fish, and can survive in polluted and hypoxic conditions (Purcell et al. 2001; Grove and Breitburg 2005).

Direct evidence linking jellyfish blooms to anthropogenic perturbations is lacking in most cases, but correlative evidence suggests the existence of links (Purcell 2012). Potential causes of abnormal jellyfish mass occurrence include overfishing, global warming, eutrophication, chemical pollution, the increase of artificial hard substrates, and the transport of exotic species (reviewed in Mills 2001; Hay 2006; Purcell et al. 2007; Richardson et al. 2009; Purcell 2012). Often, these causes occur and are mutually reinforcing (Purcell 2012).

Due to overfishing and ocean pollution, the natural predators of jellyfish, such as tuna, sharks, and sea turtles, are disappearing (Pauly et al. 1998). At the same time, resources are increasingly available to jellyfish as the abundance of zooplanktivorous fish, which compete with jellyfish for food, decreases (Purcell and Arai 2001; Daskalov et al. 2007).

Jellyfish outbreaks have been associated with variations in water mass and high salinity, as well as warm temperature, which influence jellyfish life cycles and reproductive output (Purcell 2005). Climate change may further increase the probabilities of jellyfish blooms. It may increase the availability of flagellates (single celled organisms, eaten by small zooplankton, on which jellyfish feed), lengthen the reproduction and growth season, as well as extend the spatial distribution of jellyfish poleward due to water temperature increases and shift the population distributions into currently colder areas (Richardson et al. 2009; Purcell 2012). At the same time, decreased oceanic CO₂ levels, leading to sea acidification, could

impact on organisms that build shells or skeletons of calcium and thus favour the proliferation of gelatinous organisms (Attrill et al. 2007). Many jellyfish also have calcium statoliths for orientation, but it is unknown how acidification may impact on statoliths secretion (Purcell et al. 2007).

Eutrophication is another possible cause of jellyfish blooms. The high level of nutrients in eutrophied waters favours phytoplankton blooms and generally leads to greater biomass at all trophic levels, which implies more food for jellyfish polyps (Purcell et al. 2007). Eutrophication also causes complex changes in the food web, which can ultimately favour jellyfish outbreaks (Purcell et al. 2007). Another effect of eutrophication is the lowering of the oxygen levels, which jellyfish and polyps can sustain more easily than fish (Purcell et al. 2001; Grove and Breitbart 2005). Jellyfish can also better deal with turbidity and lower water clarity caused by eutrophication, as they do not need eyesight to hunt (Eiane et al. 1999).

Coastal and sea-shore development has created good places for jellyfish polyps to settle on, such as piers, marinas, aquaculture structures, oil platforms, and wind energy constructions (Duarte et al. 2013). Finally, alien jellyfish have invaded areas where they were transported to in ballast water or by hull fouling as polyps (Graham and Bayha 2007; Costello et al. 2012).

12.2.3 Impacts of Jellyfish Blooms on the Provision of Ecosystem Services

The environmental change process in marine ecosystems may enhance jellyfish populations and blooms in the future, increasing the likelihood of negative jellyfish impacts on human activities. Currently, jellyfish blooms have negative impacts in a number of ways (reviewed in Purcell et al. 2007) but only a few economic estimates of these impacts are available.

Impacts on fisheries are the most frequently reported. These impacts arise because of the biological impacts of jellyfish on food webs and because of interference with fishing operations. Biological impacts derive from resource competition with fish and predation on fish eggs and juveniles (reviewed in Purcell and Arai 2001). This has been the case with the alien ctenophore *Mnemiopsis leidyi*, which contributed to the collapse of the anchovy fisheries in the Black Sea because of predation of *Mnemiopsis leidyi* on anchovy eggs and competition with anchovy for zooplankton (Shiganova et al. 2001). The collapse of the fishery caused significant economic losses estimated at hundreds of millions of US dollars over several decades (Knowler 2005). A decrease in the biomass of commercial fish species in association with an increase in jellyfish populations has also been observed elsewhere in the world (Lynam et al. 2005, 2006; Dong et al. 2010) but estimates of economic losses are not available. Jellyfish have been reported to interfere with fishing operations in a number of ways, including reduction in fish catches, clogging and bursting nets, requiring more labour to remove jellyfish from nets, increasing fish mortality due to nematocyst venom, causing painful stings to fishermen, displacing hauls to areas more distant from landing ports, and preventing fishermen

from operating (Purcell et al. 2007 and references therein, Schiariti et al. 2008; Uye 2008; Nagata et al. 2009; Dong et al. 2010; Quiñones et al. 2013; Palmieri et al. 2014). In 2000 outbreaks of the alien *Phyllorhiza punctata* may have caused losses of up to USD 12 million¹ to the shrimp fishery of the northern Gulf of Mexico because of fouled fishing gear and harvest (Graham et al. 2003). In 2003 blooms of *Nemopilema nomurai* caused a loss in fishing revenue of approximately USD 18 million in just one of the 17 Japanese prefectures, where interferences of jellyfish with fishing operations were reported (Kawahara et al. 2006). Quiñones et al. (2013) estimated that in the austral summer 2008–2009 by-catch of *Chrysoara plocamia* caused losses of more than USD 200,000 to the Peruvian purse seiners of Ilo in only 35 days of fishing. Palmieri et al. (2014) estimated that economic losses due to reduced fish catches could amount to more than EUR eight million per year for the Italian Northern Adriatic trawling fleet if no additional fishing effort was made to mitigate losses.

Jellyfish blooms can also affect aquaculture. Jellyfish may damage shellfish and decapods (lobster, crab) culture and kill fish in cages through haemorrhage and suffocation (Purcell et al. 2007). A number of fish mass killings have taken place in the last years in salmon farms in Northern European countries. In 2002 almost one million salmon were lost at two farms in the Scottish Western Isles for a combined loss of around EUR three million.² In 2003 a jellyfish outbreak in Norway accounted for the death of over 600 t of farmed salmon (Heckmann 2004). In 2007 a jellyfish bloom in Northern Ireland caused a financial loss of a salmon farm stock of over EUR one million and a more recent bloom in 2013 caused other substantial losses.³

Jellyfish blooms have been reported to interfere with coastal power plant operations by clogging power plant intakes. In Israel the costs to remove the jellyfish from two power plants were estimated at almost USD 60,000 in just one summer (Galil 2008). In July 2008 over 4,000 t of *Aurelia aurita* were removed from the clogged intake screens of one power plant in China (Dong et al. 2010). In 2011 two nuclear reactors had to shut down for a few days at a Scottish power plant after an influx of jellyfish.⁴

Some jellyfish species interfere with recreational activities and have impacts on human health. Jellyfish stinging is a serious health problem along the coasts of some Asian and Indo-Pacific countries, where extremely venomous jellyfish are common and can cause death (Fenner and Williamson 1996; Burnett 2001). In other regions of the world, like the Mediterranean, stings from jellyfish are not lethal but may cause severe discomfort and pain and sometimes require medical treatment (Mariottini and Pane 2010; De Donno et al. 2009). In regions with popular touristic seaside resorts, stinging has sometimes occurred at epidemic levels. During the

¹The original value, as well as other values in this section, have been corrected for inflation and converted to 2011 prices.

²<http://news.bbc.co.uk/1/hi/scotland/2178959.stm>

³<http://www.irishtimes.com/news/ireland/irish-news/jellyfish-bloom-kills-thousands-of-farmed-salmon-off-co-mayo-1.1567468>

⁴<http://www.theguardian.com/environment/2011/jun/30/jellyfish-shut-nuclear-reactors-torness?uni=Article:in%20body%20link>

summers 2006–2007, for instance, tens of thousands of bathers were stung by jellyfish on Spanish and French beaches (Galil 2008). It is unknown to what extent beach recreation has declined as a result of jellyfish presence but many coastal towns have taken remediating actions to protect the tourism industry. Spain has set out nets to mark out bathing areas and reduce the number of jellyfish to a minimum. According to local newspapers, the community near Mar Menor, which experiences annual blooms of two jellyfish species, spends around EUR 600,000 per year^{5,6} to this effect. Similar systems have been deployed in Monaco and along the coasts of Cannes and Marseille (Galil 2008). It must be pointed out that the figures presented above on the costs of the investments to protect bathers from jellyfish are financial values and thus do not provide a complete picture of the economic welfare impact of jellyfish blooms on recreational activities (see Chap. 4). In addition to impairing swimming/bathing, jellyfish outbreaks can also impact on other recreational activities, like walking, when they lead to mass strandings and bad smell from decomposition on beaches.⁷

On the positive side, jellyfish provide some benefits to humans (reviewed in Purcell et al. 2007). Some species of jellyfish potentially enhance fisheries recruitment by providing shelter under their bells to fish juveniles, which feed on the prey and parasites of their hosts. Jellyfish are on the diet of many vertebrates, including commercially valuable fish species. Jellyfish are also used for human consumption. A number of jellyfish species have been historically fished in several Southeast Asian countries (Omori and Nakano 2001; Nishikawa et al. 2008; Kitamura and Omori 2010) and jellyfish fisheries have begun to be developed more recently in countries such as Australia, India, Turkey, Mexico, and the United States (Hsieh et al. 2001).

Jellyfish-derived products are being tested in the production of cosmetics and drugs. Jellyfish are believed to contain collagen, which moisturise the skin, and to cure rheumatoid arthritis and bronchitis (Hay 2006; Sugahara et al. 2006). They provide Aequorin and Obelin, which are green fluorescent proteins that are for instance used as biomarkers in biomedical research.

Among the potential benefits of jellyfish is carbon uptake from the atmosphere. According to Condon et al. (2011), who looked at *Mnemiopsis leidyi*, jellyfish may be net up-takers of oceanic carbon. Evidence, however, is scarce and not conclusive (Brotz et al. 2011).

Finally, jellyfish have a recreational and educational value. There is a small niche for jellyfish recreation, where diving for luminescent jellyfish is possible or where the species do not sting, as for example in the Jellyfish Lake in the Palau Archipelago (Dawson et al. 2001). Jellyfish are also a popular attraction in many marine aquaria worldwide.

⁵ http://murciatoday.com/300-tons-of-jellyfish-extracted-from-the-mar-menor-in-the-last-8-days_12646-a.html

⁶ http://murciatoday.com/jellyfish-nets-ready-and-waiting-in-the-mar-menor_17156-a.html

⁷ <http://iltirreno.gelocal.it/pisa/cronaca/2012/04/24/news/colpa-delle-meduse-i-cattivi-odori-apparsi-sul-litorale-1.4416394>

12.3 Case Study in the UK: Recreation

12.3.1 Introduction

In the first case study, we discuss the potential impacts on tourism of jellyfish blooms along the English coastline. The abundance of jellyfish appears to have increased in the last two decades in the seas surrounding the UK due to climate variation and possibly to changes in food web structure (Attrill et al. 2007; Gibbons and Richardson 2009; Lynam et al. 2011). Climate change is expected to contribute to a further increase in jellyfish frequency over the next century (Attrill et al. 2007) and the occurrence of warm water species, such as *Pelagia noctiluca*, might become more frequent (Licandro et al. 2010). Moreover, human activities, such as maritime transport, may favour the introduction of alien species.

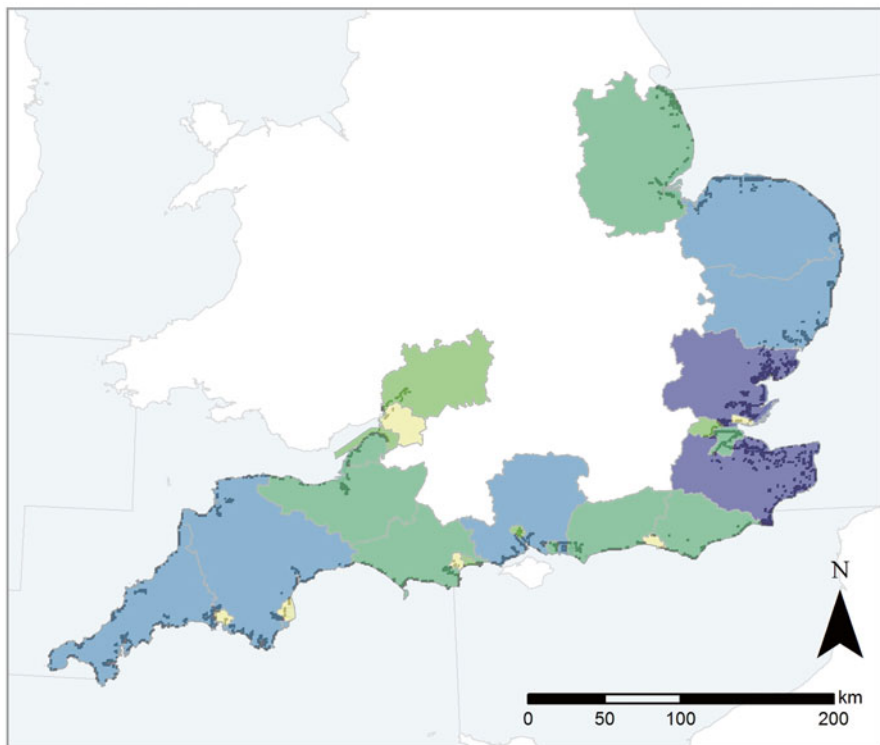
Along the English coast, beach recreation is an important activity for local, national and international visitors (Sen et al. 2011). Jellyfish outbreaks could therefore have a wide impact. Little information is available regarding the number of tourists that visit beaches along the English coast, and there are no studies that estimate the direct effect of jellyfish blooms on recreation along the English coastline.

12.3.2 Data and Methodology

To approximate the economic damage cost that jellyfish blooms may have in the future, we use the analysis produced for the UK National Ecosystem Assessment (NEA) on recreation (UK-NEA 2011). The spatially explicit approach of the UK-NEA is described in detail in Sen et al. (2014), who modelled the non-market value of open-air recreation throughout England. The model is based on a large survey about recreational behaviour among households in England (Natural England 2010). The model predicting annual visitor numbers takes into account a wide range of spatial characteristics, including habitats, population and accessibility. One of the findings of this model is that the number of trips to coastal areas is higher than for most other types of land cover, including grasslands, mountains, or woodlands. The model is combined with a meta-analysis on the value per recreational trip across different types of habitats. By multiplying the estimated number of visits by the value per trip, an estimate of the total annual value of visits to sites is obtained. The analysis is performed using GIS at a 1 km² scale.

We focus our analysis on the English part of the ICES fishing areas: zones VIIf, VIIe, VIIId and IVc.⁸ From the predicted visitor numbers to all 1 km² cells in the UK,

⁸ICES areas VIIe and VIIf include Cornwall and Isles of Scilly, Devon, Dorset, Gloucestershire, North Somerset, Plymouth, Poole, Somerset, South Gloucester, and Torbay. VIIId includes Bournemouth, Brighton and Hove, Bristol, East Sussex, Hampshire, Portsmouth, Southampton



Visits to coasts per year ('000s)

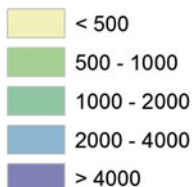


Fig. 12.1 Annual number of visits to coastal areas

we select the cells in the 26 counties in our study area (England), which contain some coastal land cover or sea according to the NEA definition of habitat types, within a 10 km distance from the coastline.

Figure 12.1 presents a map of the estimated annual number of visits to coastal locations. The map shows that Cornwall, Devon, Hampshire, Norfolk, Essex and Kent generate high visitor numbers. They will therefore generate higher benefits, representing the value that English households attach to recreation at coastal loca-

and West Sussex. IVC includes Essex, Kent, Lincolnshire, Medway, Norfolk, Southend-on-Sea, Suffolk and Thurrock.

tions. It does not reflect the financial value of the tourism sector, and excludes any values that international visitors may attach to these coastal areas.

Next, we adjust the visitor numbers by the percentage of coastal land cover and sea in each of the selected 1 km² cells. The average percentage of land cover is around 20 % and, because the NEA land cover map excludes some coastal areas, our estimate may be an underestimate. Finally, we multiply the estimated value per trip to a coastal location of EUR 4.67 (Sen et al. 2011)⁹ by the modified number of visits to coastal areas to get an estimate of the total value of recreational trips to coastal areas.

Since jellyfish blooms have a spatial and temporal dimension, we would ideally combine the estimates of annual value of coastal visits with spatial and temporal information about the probability of jellyfish blooms to assess the losses of recreational value due to blooms. In the absence of monitoring data on the temporal and spatial distribution of jellyfish outbreaks, we use public reports of mass jellyfish strandings along the UK coastline. These reports suggest that such mass strandings occur mostly between May and August, coinciding with warmer weather and higher visitor numbers, and last for a period of around 2 weeks. Most reports come from West-England (from Dorset all along to Gloucestershire), where long stretches of coastline are affected.

The MENE dataset (Natural England 2010) only includes annual visitor numbers, but does not provide information about the distribution of visits across months. To take account of the higher number of coastal visitors in the warmer summer months, we use the estimates from a study by Coombes et al. (2009) about visitor numbers along the coastline of East Anglia. The monthly percentage of visitors is higher for the summer months. We assume that visitors in other areas have a similar distribution across the year.

To assess the economic loss of jellyfish blooms in the absence of a map of the probability of the spread and timing of such events, we make the following additional assumptions:

- Jellyfish blooms affect coastal visits through mass beach strandings;
- Mass jellyfish strandings create such a stink that the trip creates no net benefit to the visitor, who may also consider health risks, i.e. the value per trip is set equal to zero;
- A typical mass jellyfish stranding lasts 2 weeks;
- Mass jellyfish strandings affect large areas. Therefore, we combine 26 different counties into three areas roughly according to the ICES fishing areas IVc, VIId, and VIIe and VIIf (England only);
- All sea and coastal land cover cells are equally and simultaneously affected, i.e. within the ICES areas we assume that all beaches are equally affected.

⁹Note that this is a fixed value per trip and does not account for variation in values due to seasonality.

Table 12.1 Recreational benefits lost to 2-week mass jellyfish strandings along the English coastline (EUR*1000, 2011 prices)

ICES area	May	June	July	August
VIIe + VIIf	527	717	965	1,060
VIIId	414	563	757	832
IVc	761	1,036	1,392	1,529
<i>Total</i>	1,703	2,317	2,903	3,421

12.3.3 Results

The recreational benefits lost across different ICES areas for different summer months based on these assumptions are summarised in Table 12.1. The table shows that, under these assumptions, a jellyfish swarm affecting all English coastal waters in August would imply a loss of recreational values of over EUR 3.4 million (2011 prices). However, such large scale swarms have not been registered in the past, which needs to be taken into account when interpreting the figures in Table 12.1.

For a widespread 2-week jellyfish outbreak, the loss of recreational values in the IVc area, which borders the North Sea, would be highest, varying between EUR 0.8 and 1.5 million. The VIIe and VIIf areas, bordering the Bristol Channel, Celtic Sea, and eastern part of the English Channel, would incur lower value losses, and the smallest zone VIIId reflecting the western part of the English Channel would see lowest value losses, according to these estimates. Note, however, that we cannot account for the probability of jellyfish blooms and these estimates do not reflect expected values, but historical records suggest that jellyfish are more likely to be found in ICES areas VIIe and VIIf than in the other two ICES areas.

In summary, this section presents a methodological approach that can be used when stated preference surveys are not applicable to get a first order-of-magnitude estimate of potential losses in social welfare related to the impacts of jellyfish abundance on recreational benefits along the English shoreline. It could be improved when more spatial information is available about the scale and spatial and temporal distribution of jellyfish blooms and visitation rates, as well as information to support and refine the assumptions of visitor reactions to these blooms.

12.4 Case study in Italy: Fisheries

12.4.1 Introduction

The Northern Adriatic (NA) Sea is one of the most exploited Mediterranean fishing grounds (Barausse et al. 2009), although the high primary productivity of the ecosystem has clearly decreased since the late 1990s (Mozetic et al. 2010). Starting from the end of the 1980s, plankton, fish and invertebrate communities in the NA

underwent abrupt changes, which were collectively identified as a regime shift in the ecosystem, probably driven by the interaction of different pressures, such as climate change, which caused variations in water temperature and circulation; reduced nutrient inputs from river catchments; anoxic phenomena; overexploitation of fishery resources; the crash of the stock of anchovy, a species which plays a key role in the food web; and the 10-year long bloom of the jellyfish *Pelagia noctiluca* (Barausse et al. 2011). This species competed with small pelagics for zooplankton and predated upon fish eggs, larvae and even adults, possibly stimulating the aforementioned anchovy population collapse and altering ecosystem functioning (Boero and Bonsdorff 2007; Conversi et al. 2010; Kogovšek et al. 2010; Barausse et al. 2011). Apart from the *Pelagia's* massive bloom, from the early 1980s the NA has experienced blooms of a number of other jellyfish species, whose occurrence appears to have increased in recent decades (Kogovšek et al. 2010). In this case study we discuss the links between welfare benefits (i.e. fishery landings), jellyfish blooms, and anthropogenic pressures in the NA ecosystem.

12.4.2 Data and Methodology

We use the Ecopath with Ecosim (EwE) modelling suite (see Chap. 3) to investigate the links between fishery landings, jellyfish blooms, and anthropogenic pressures, such as nutrient enrichment, in the NA ecosystem.

Scenarios of jellyfish outbreaks are modeled using an Ecosim simulation (Christensen and Walters 2004) based on the Ecopath trophic network model of the NA Sea described in Barausse et al. (2009). Ecosim can simulate the variation in the biomass of food web compartments over time based on processes such as changes in system productivity, fishing mortality, predator-prey interactions, migration fluxes, and biological invasions. Here, Ecosim (version 5.1) is used to assess how the NA ecosystem and particularly fisheries respond to sudden jellyfish blooms or invasions triggered by non-trophic causes (e.g. some unknown factor such as climate), which are simulated by forcing jellyfish abundance in the model. The parameter values of the Ecosim model, such as vulnerabilities, were previously calibrated by fitting the model to time series over the period 1996–2006 (Alberto Barausse, University of Padova, unpublished data). Four scenarios (S1–4) are run, all depicting the effects of an abrupt increase in jellyfish biomass (which is forced in the model to simulate a sudden bloom or invasion, as explained above):

- S1: 3-year jellyfish bloom, constant primary production
- S2: 3-year jellyfish bloom, 10 % decrease in primary production from 2006 to 2020
- S3: 10-year jellyfish bloom, constant primary production
- S4: 10-year jellyfish bloom, 10 % decrease in primary production from 2006 to 2020

Blooms are started at the end of the fitting period, i.e. 2007, and are assumed to last 3 years (scenarios S1 and S2), based on what has recently happened in the NA Sea for *Pelagia noctiluca* during the 2000s, or, alternatively, 10 years (scenarios S3 and S4), based on the intense outbreak of the same species which took place in the ecosystem in the period 1977–1986 (Kogovsek et al. 2010). *Pelagia noctiluca* is one of the most ecologically important jellyfish species in the ecosystem; it eats zooplankton, fish eggs, larvae and juveniles and can even kill adult fishes (Fernando Boero, Università del Salento, pers. comm.). Based on data in Malej and Malej (2004), Barausse et al. (2009) and Kogovsek et al. (2010), jellyfish biomass during the bloom is assumed to be twelve times as high as the biomass in the baseline Ecopath model; in the fourth (S1, S2) or the eleventh (S3, S4) year after the start of the bloom, jellyfish biomass is forced back to the baseline Ecopath value to simulate the end of the outbreak. Such bloom magnitude is likely to be conservative and to underestimate the real impact of gelatinous plankton outbreaks because reported estimates of jellyfish biomass in the NA Sea mostly refer to bloom conditions and the actual increase in jellyfish biomass during blooms should be, therefore, much higher.

To evaluate the ecological impact of the jellyfish bloom on fish landings, the model is run until 2020, the year when a Good Environmental Status should be achieved in Europe's seas according to the Marine Strategy Framework Directive (2008/56/EC). In the modelling scenarios S1 and S3, fishing effort, fishing mortalities and primary productivity in the ecosystem are kept equal to the 2006 values over 2007–2020, while in the scenarios S2 and S4 a 10 % linear decrease in phytoplanktonic primary productivity from 2006 to 2020 is simulated to mirror the current oligotrophication of the system (Mozetic et al. 2010), which is expected to affect the NA fisheries (Barausse et al. 2011). The impact of jellyfish on landings is evaluated in each scenario by comparing landings in 2020 with the landings predicted in that same year by a “reference” scenario which is identical from a modelling point of view (e.g. same changes in primary production and fishing pressure), except that no jellyfish outbreak is simulated.

To assess the welfare impact of the bloom on the NA Italian fisheries, we estimate the change in revenue based on the variation in landings. As the data in the model refer to five Italian fisheries sorted according to the fishing gear and one pooled Slovenian-Croatian fishery (as described in Barausse et al. 2009), we extract the data pertaining to the Italian landings. After collecting data on the 2011 prices of landings by fishing fleet in the three Italian regions of the NA (Veneto, Emilia Romagna, and Friuli Venezia Giulia), we calculate the mean prices of landings weighted on the basis of the quantities landed (IREPA 2012). The impact of the jellyfish bloom in terms of lost revenue is estimated by multiplying the price per kg per fishing fleet by the variation in landings in relation to the four scenarios.

12.4.3 Results

Table 12.2 reports the percentage change in landings in 2020 in the different scenarios, with respect to reference scenarios where no jellyfish bloom takes place. Interestingly, the results suggest that jellyfish blooms always have overall negative impacts on fisheries, since in all scenarios the blooms cause a decrease in total landings in 2020 with respect to the reference scenarios, a decrease of about 0.5 % in the case of the 3-year blooms and of about 2.3 % in the case of the 10-year blooms. These figures show that the response of fisheries to jellyfish blooms is disproportionately more negative in the case of the longer-lasting blooms, as such blooms (which are 3.3 times longer than the shorter-lasting ones) cause a decrease in landings which is 4.6 times stronger than the one caused by the shorter-lasting blooms. The model responses are not particularly sensitive to simulated changes in primary

Table 12.2 Changes in fishery landings (%) in 2020 due to the jellyfish bloom, for each model scenario. Changes were calculated with respect to the landings simulated in 2020 with the same trends in all other forcing functions (fishing mortality, primary productivity) as the given scenario except that no jellyfish bloom was simulated. Variations in landings are reported according to the fished group and to total fishery landings in the basin

	Scenario			
	S1	S2	S3	S4
Food web group	(%)	(%)	(%)	(%)
Sharks	0.3	0.3	1.9	1.2
Rays	0.0	0.0	1.8	2.0
European hake	0.0	0.0	2.0	-0.2
Zoobenthivorous fish – hard bottom	0.0	0.0	-1.7	-1.3
Zoobenthivorous fish – soft bottom	0.0	0.0	-0.7	-0.6
Mackerel	1.2	1.3	9.6	6.6
Horse mackerel	1.0	1.0	7.4	5.3
Other small pelagics	0.0	0.0	-0.6	0.5
Anchovies	0.5	0.5	1.6	1.2
Sardines	-6.4	-6.5	-29.5	-29.7
Nectobenthic zooplanktivorous fish	-0.1	-0.2	1.8	2.5
Omnivorous fish	-1.6	-1.6	-7.6	-5.7
Benthic piscivorous fish	-0.3	-0.3	4.7	2.5
Flatfishes	-0.5	-0.6	-2.5	-1.9
Squids	-2.8	-3.0	-7.0	-10.0
Benthic cephalopods	-0.2	-0.2	-1.2	-0.5
Macro-crustaceans	0.0	0.0	-0.1	0.0
Mantis shrimp	0.0	0.0	-0.3	-0.4
Commercial bivalves	0.0	0.0	-0.1	0.0
Gastropods	0.0	0.0	-0.2	-0.1
Filter feeding invertebrates	0.0	0.0	0.7	0.8
<i>Total landings</i>	<i>-0.5</i>	<i>-0.5</i>	<i>-2.3</i>	<i>-2.4</i>

production. Only few differences can be appreciated between total landings in scenarios S1 and S2, and in scenarios S3 and S4 (but some exceptions can be observed for single groups in S3 and S4), suggesting that in general a reduction in system primary productivity does not act synergistically with jellyfish outbreaks in reducing landings.

For all modelled food web groups, the response to jellyfish blooms is (often much) weaker in the case of the scenarios simulating the shorter-lasting jellyfish bloom. However, even a 3-year bloom causes a decrease of about 6.5 % in the landings of sardine, which is a key commercial species in the NA and also plays an important trophic role in the ecosystem (Barausse et al. 2009). In the case of the 10-year bloom, sardine fisheries are impacted heavily with decreases in landings of about 30 %. Instead, anchovy, another commercially and ecologically important species, gains some benefits from the jellyfish outbreaks, probably due to reduced competition for zooplankton with sardine, and its landings show a slight increase in all scenarios. In general, responses to jellyfish blooms vary across groups in a complex manner, with landings of medium-low trophic level groups feeding on or a few trophic connections away from zooplankton (by far the main food of jellyfish) being most strongly affected. For example, landings of mackerel and horse mackerel increase, since these two groups mostly feed on zooplankton and small pelagic fish such as anchovy, while squid catches decrease possibly due to food competition for small pelagics. Interestingly, landings in benthic piscivorous fish decrease slightly in the presence of a short jellyfish bloom, but increase markedly when a 10-year bloom is simulated, and moreover the decrease rate depends clearly on the simulated trend in primary production, suggesting that complex food web interactions define their response.

Looking at the response of different fleets to the jellyfish bloom, landings from all fleets decrease (data not shown). The Italian fleets account for around 60–70 % of the total reduction in catches landed in the NA region across the four scenarios.

Table 12.3 reports the changes in Italian landings and revenues (undiscounted and in 2011 prices) due to the jellyfish bloom for each model scenario. The strongest response is observed for the mid-water trawling fleet. The reduction in catches by this fleet accounts for around 90 % of the total reduction in landings across scenarios. However, the revenue losses account for only around 50–60 % of the total. This is because the mid-water trawling fleet catches large amounts of a limited number of low value species (Gramitto et al. 2010), some of which are heavily impacted by the jellyfish bloom, such as sardine and common mullets (omnivorous fish group). The other trawling fleets catch smaller quantities of a higher number of species, many of which of high commercial value (Gramitto et al. 2010), and the different magnitude of their losses may depend on the diversification of their catches. While the otter trawling fleet targets some high value species heavily impacted by the bloom, such as squids and soles (flatfishes group), the beam trawling fleet, in addition to impacted species, also targets some that are marginally impacted, such as gastropods and bivalves. The latter is the main target of hydraulic dredges, which appear to be impacted negligibly. Heavy losses are registered for the

Table 12.3 Changes in Italian NA fishery landings (t) and revenues (€, 2011 prices) in 2020 due to the jellyfish bloom, for each model scenario. Changes were calculated with respect to the landings simulated in 2020 with the same trends in all other forcing functions (fishing mortality, primary productivity) as the given scenario except that no jellyfish bloom was simulated. Changes are reported by fishing fleet and according to total landings by all Italian NA fleets. Revenue values are undiscounted. Values reported in parentheses are percentage changes

	Scenario							
	S1		S2		S3		S4	
	(t)	(€)	(t)	(€)	(t)	(€)	(t)	(€)
Fishing fleet								
Hydraulic dredges	-0.1	-410 (0.0)	-0.2	-614 (0.0)	-4.8	-15,462 (-0.1)	1.5	4,915 (0.0)
Beam trawling	-4.9	-31,046 (-0.1)	-5.0	-31,248 (-0.1)	-30.8	-193,738 (-0.5)	-18.4	-115,718 (-0.3)
Otter trawling	-14.3	-89,914 (-0.2)	-14.0	-88,301 (-0.2)	-49.6	-312,682 (-0.6)	-43.6	-274,378 (-0.6)
Mid water trawling	-220.5	-198,432 (-0.4)	-199.4	-179,482 (-0.4)	-1,232.6	-1,109,376 (-2.1)	-1,294.0	-1,164,643 (-2.5)
Other and artisanal fisheries	-11.6	-86,880 (-0.5)	-11.9	-89,520 (-0.5)	-57.5	-431,280 (-2.3)	-41.5	-311,520 (-1.7)
<i>Total landings</i>	<i>-251.4</i> <i>(-0.3)</i>	<i>-406,682</i> <i>(-0.2)</i>	<i>-230.5</i> <i>(-0.3)</i>	<i>-389,165</i> <i>(-0.2)</i>	<i>-1,375.3</i> <i>(-1.7)</i>	<i>-2,062,538</i> <i>(-1.1)</i>	<i>-1,396.0</i> <i>(-1.9)</i>	<i>-1,861,344</i> <i>(-1.1)</i>

small scale fisheries, which target heavily impacted species of high value, such as soles (Gramitto et al. 2010).

If we look at the overall reduction in the Italian NA landings, we can see that a 10-year bloom could cause a decrease in landings of around 2 %. This may have repercussions at the national level in terms of decreased seafood supply, especially in the case of the heavily impacted sardine, as around 40 % of the national production of this species originates from the Adriatic basin (Mulazzani et al. 2012), but it is also the case for other species, such as soles, which are more abundant in the NA region compared to other Mediterranean fishing grounds (Grati et al. 2013).

In terms of revenues, a 10-year bloom could entail revenue reductions to the Italian NA fisheries of around EUR two million (undiscounted and in 2011 prices). Decreasing revenues, such as those we describe here, could put pressure on the financial viability of fishing enterprises and affect the ability of the fishing industry to support, through employment and incomes, the economy and community cohesion of the small coastal communities of the region.

12.5 Conclusions

The case studies described in this chapter show that jellyfish blooms can have marked effects on recreation and fisheries, entailing considerable losses of welfare benefits. This result confirms the evidence collected in the literature on the negative impacts of jellyfish outbreaks, which include not only impacts on recreation and fisheries but also on other benefits, such as other production activities (e.g. aquaculture, energy production) and human health.

These results warrant a consideration of increased efforts towards the monitoring and control of jellyfish blooms. To this end, it is necessary to improve the scientific knowledge about trends in jellyfish populations through long-term monitoring programmes, which could provide indicators of jellyfish outbreaks (Condon et al. 2012), as in the case of the invasion of alien species (Stohlgren and Schnase 2006). It will be necessary to improve the understanding of the role that jellyfish play in ecosystems, as there is a lack of knowledge of the biology and ecology of these organisms (Boero et al. 2008). Furthermore, it would be good to investigate the influence of human activities on the occurrence of blooms through the development of models including system stressors (e.g. fishing, eutrophication, global warming) to assess their relative importance and explore ecosystem resilience (Richardson et al. 2009).

Until a higher level of understanding of jellyfish blooms is gained, we need to deal with their impacts based on current information. As long as there is uncertainty about what constitutes ecological threshold points, careful management that keeps ecological changes within some safe minimum standards should be advocated unless the social costs are unacceptable (Crowards 1998; Perrings 2001). Harmful algal blooms (HABs) may provide a model for the management of jellyfish blooms. Past controversies on HABs trends have been overcome through pragmatic discussions of the management of their impacts and more resources are now dedicated to the monitoring of HABs and to their control (Brotz and Pauly 2012).

References

- Arai, M. N. (1997). *A functional biology of scyphozoa*. London: Chapman & Hall.
- Attrill, M. J., Wright, J., & Edwards, M. (2007). Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography*, *52*, 480–485.
- Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y., & Palmeri, L. (2009). Trophic network model of the Northern Adriatic Sea: Analysis of an exploited and eutrophic ecosystem. *Estuarine, Coastal and Shelf Science*, *83*(4), 577–590.
- Barausse, A., Michieli, A., Riginella, E., Palmeri, L., & Mazzoldi, C. (2011). Long-term changes in community composition and life-history traits in a highly exploited basin (northern Adriatic Sea): The role of environment and anthropogenic pressures. *Journal of Fish Biology*, *79*, 1453–1486.
- Bastian, T., Stokes, D., Kelleher, J. E., Hays, G. C., Davenport, J., & Doyle, T. (2011). Fisheries bycatch data provide insights into the distribution of the mauve stinger (*Pelagia noctiluca*) around Ireland. *ICES Journal of Marine Science*, *68*(3), 436–443.
- Boero, F., & Bonsdorff, E. (2007). A conceptual framework for marine biodiversity and ecosystem functioning. *Marine Ecology*, *28*, 134–145.
- Boero, F., Bouillon, J., Gravili, C., Miglietta, M. P., Parsons, T., & Piraino, S. (2008). Gelatinous plankton: Irregularities rule the world (sometimes). *Marine Ecology Progress Series*, *356*, 299–310.
- Boero, F., Putti, M., Trainito, E., Prontera, E., Piraino, S., & Shiganova, T. A. (2009). First records of *Mnemiopsis leidyi* (Ctenophora) from the Ligurian, Thyrrenian and Ionian Seas (Western Mediterranean) and first record of *Phyllorhiza punctata* (Cnidaria) from the Western Mediterranean. *Aquatic Invasions*, *4*(4), 675–680.
- Brodeur, R. D., Mills, C. E., Overland, J. E., Walters, G. E., & Schumacher, J. D. (1999). Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fisheries Oceanography*, *8*, 296–306.
- Brodeur, R. D., Sugisaki, H., & Hunt, G. L., Jr. (2002). Increases in jellyfish biomass in the Bering Sea: Implications for the ecosystem. *Marine Ecology Progress Series*, *233*, 89–103.
- Brodeur, R. D., Decker, M. B., Cianelli, L., Purcell, J. E., Bond, N. A., Stabeno, P. J., Acuna, E., & Hunt, G. L., Jr. (2008). Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. *Progress in Oceanography*, *77*, 103–111.
- Brotz, L., & Pauly, D. (2012). Jellyfish populations in the Mediterranean Sea. *Acta Adriatica*, *53*(2), 213–232.
- Brotz, L., Lebrato, M., Robinson, K. L., Sexton, M., Sweetman, A. K., Pitt, K., & Condon, R. (2011). Implications of increased carbon supply for the global expansion of jellyfish blooms. *Limnology & Oceanography Bulletin*, *20*, 38–39.
- Burnett, J. W. (2001). Medical aspects of jellyfish envenomation: Pathogenesis, case reporting and therapy. *Hydrobiologia*, *451*, 1–9.
- Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: Methods, capabilities and limitations. *Ecological Modelling*, *172*, 109–139.
- CIESM. (2001). *Gelatinous plankton outbreaks: Theory and practice*. CIESM Workshop Series 14. Monaco: CIESM, 112pp.
- Condon, R. H., Steinberg, D. K., Del Giorgio, P. A., Bouvier, T. C., Bronk, D. A., Graham, W. M., & Ducklow, H. W. (2011). Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(25), 10225–10230.
- Condon, R. H., Graham, W. M., Duarte, C. M., Pitt, K. A., Lucas, C. H., Haddock, S. H., Sutherland, K. R., Robinson, K. L., Dawson, M. N., Decker, M. B., Mills, C. E., Purcell, J. E., Malej, A., Mianzan, H., Uye, S.-i., Gelcich, S., & Madin, L. P. (2012). Questioning the rise of gelatinous zooplankton in the world's oceans. *Bioscience*, *62*(2), 160–169.

- Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R., Mianzan, H., Borgeberg, M., Purcell, J. E., Decker, M. B., Uye, S. I., Madin, L. P., Brodeur, R. D., Haddock, S. H., Malej, A., Parry, G. D., Eriksen, E., Quinones, J., Acha, M., Harvey, M., Arthur, J. M., & Graham, W. M. (2013). Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(3), 1000–1005.
- Conversi, A., Fonda Umani, S., Peluso, T., Molinero, J. C., Santojanni, A., & Edwards, M. (2010). The Mediterranean sea regime shift at the end of the 1980s, and intriguing parallels with other European basins. *PLoS One*, *5*(5), e10633.
- Coombes, E. G., Jones, A. P., & Sutherland, W. J. (2009). The implications of climate change on coastal visitor numbers: A regional analysis. *Journal of Coastal Research*, *25*(4), 981–990.
- Costello, J. H., Bayha, K. M., Mianzan, H. W., Shiganova, T. A., & Purcell, J. E. (2012). Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: A review. *Hydrobiologia*, *690*, 21–46.
- Crépin, A.-S., Biggs, R., Polasky, S., Troell, M., & de Zeeuw, A. (2012). Regime shifts and management. *Ecological Economics*, *84*, 15–22.
- Crowards, T. M. (1998). Safe minimum standards: costs and opportunities. *Ecological Economics*, *25*(3), 303–314.
- Daskalov, G. M., Grishin, A. N., Rodionov, S., & Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(25), 10518–10523.
- Dawson, M. N., Martin, L. E., & Penland, L. K. (2001). Jellyfish swarms, tourists, and the Christ-child. *Hydrobiologia*, *451*, 131–144.
- De Donno, A., Idolo, A., & Bagordo, F. (2009). Epidemiology of jellyfish stings reported to summer health centres in the Salento peninsula (Italy). *Contact Dermatitis*, *60*(6), 330–335.
- Dong, Z., Liu, D., & Keesing, J. K. (2010). Jellyfish blooms in China: Dominant species, causes and consequences. *Marine Pollution Bulletin*, *60*(7), 954–963.
- Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S. I., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R., Malej, A., Madin, L., Mianzan, H., Gili, J. M., Fuentes, V., Atienza, D., Pages, F., Breitburg, D., Malek, J., Graham, W. M., & Condon, R. H. (2013). Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment*, *11*(2), 91–97.
- Eiane, K., Aksnes, D. L., Bagøien, E., & Kaartvedt, S. (1999). Fish or jellies – A question of visibility? *Limnology and Oceanography*, *44*(5), 1352–1357.
- Faasse, M. A., & Bayha, K. M. (2006). The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: An unrecognized invasion? *Aquatic Invasions*, *1*(4), 270–277.
- Fenner, P. J., & Williamson, J. A. (1996). Worldwide deaths and severe envenomation from jellyfish stings. *Medical Journal of Australia*, *165*, 658–661.
- Fuentes, V. L., Angel, D. L., Bayha, K. M., Atienza, D., Edelist, D., Bordehore, C., Gili, J. M., & Purcell, J. E. (2010). Blooms of the invasive ctenophore *Mnemiopsis leidyi* span the Mediterranean Sea in 2009. *Hydrobiologia*, *645*, 23–37.
- Galiil, B.S. (2008). The price of change: The economic impacts of alien species and jellyfish outbreaks in the Mediterranean Sea. In: *Economic valuation of natural coastal and marine ecosystems*. CIESM Workshop Monographs, No. 37. Monaco: CIESM, 112 pp.
- Gibbons, M. J., & Richardson, A. J. (2009). Patterns of pelagic cnidarian abundance in the North Atlantic. *Hydrobiologia*, *616*, 51–65.
- Graham, W. M. (2001). Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linné) (Cnidaria: Scyphozoa) in the northern Gulf of Mexico. *Hydrobiologia*, *451*, 97–111.
- Graham, W. M., & Bayha, K. M. (2007). Biological invasions by marine jellyfish. *Ecological Studies*, *193*(5), 239–255.

- Graham, W. M., Martin, D. L., Felder, D. L., Asper, D. L., & Perry, H. M. (2003). Ecological and economic implications of a tropical jellyfish invader in the Gulf of Mexico. *Biological Invasions*, 5, 53–69.
- Gramitto, M. E., Lucchetti, A., & Colarossi, M. (2010). *Guida pratica all'attività di ispezione e controllo nella pesca marittima*. CNR-ISMAR Technical Report, Ancona, 178pp.
- Grati, F., Scarcella, G., Polidori, P., Domenichetti, F., Bolognini, L., Gramolini, R., Vasapollo, C., Giovanardi, O., Raicevich, S., Celic, I., Vrgoc, N., Isajlovic, I., Jenic, A., Marceta, B., & Fabi, G. (2013). Multi-annual investigation of the spatial distributions of juvenile and adult sole (*Solea solea* L.) in the Adriatic Sea (northern Mediterranean). *Journal of Sea Research*, 89, 12–22.
- Grove, M., & Breitburg, D. L. (2005). Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. *Marine Ecology Progress Series*, 301, 185–198.
- Hay, S. (2006). Marine ecology: Gelatinous bells may ring change in marine ecosystems. *Current Biology*, 16(17), R679–R682.
- Heckmann, R. (2004). What else can happen? Other problems for fish production. *Aquaculture Magazine*, Mar/Apr, 1–8.
- Hsieh, Y.-H. P., Leong, F.-M., & Rudloe, J. (2001). Jellyfish as food. *Hydrobiologia*, 451, 11–17.
- IREPA. (2012). *Osservatorio economico sulle strutture produttive della pesca marittima in Italia 2011*. Napoli: Edizioni Scientifiche Italiane, 252pp. <http://www.irepa.org/attachments/articolo/320/Osservatorio%20Nazionale%202011.pdf>
- Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlanson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J., & Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–637.
- 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.
- Kitamura, M., & Omori, M. (2010). Synopsis of edible jellyfishes collected from Southeast Asia, with notes on jellyfish fisheries. *Plankton and Benthos Research*, 5(3), 106–118.
- Knowler, D. (2005). Reassessing the costs of biological invasion: *Mnemiopsis leidyi* in the Black Sea. *Ecological Economics*, 52(2), 187–199.
- Kogovšek, T., Bogunović, B., & Malej, A. (2010). Recurrence of bloom-forming scyphomedusae: Wavelet analysis of a 200-year time series. *Hydrobiologia*, 645, 81–96.
- Licandro, P., Conway, D. V. P., Daly Yahia, M. N., Fernandez De Puelles, M. L., Gasparini, S., Hecq, J. H., Tranter, P., & Kirby, R. R. (2010). A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters*, 6(5), 688–691.
- Lilley, M. K. S., Houghton, J. D. R., & Hays, G. C. (2009). Distribution, extent of inter-annual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. *Journal of the Marine Biological Association of the United Kingdom*, 89(1), 39–48.
- 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.
- Lynam, C. P., Gibbons, M. J., Axelsen, B. E., Sparks, C. A., Coetzee, J., Heywood, B. G., & Brierley, A. S. (2006). Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology*, 16(13), R492–R493.
- Lynam, C. P., Lilley, M. K. S., Bastian, T., Doyle, T. K., Beggs, S. E., & Hays, G. C. (2011). Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology*, 17, 767–782.
- Malej, A., & Malej, A., Jr. (2004). Invasion of the jellyfish *Pelagia noctiluca* in the Northern Adriatic: A non-success story. Chapter 16. In H. Dumont, T. A. Shiganova, & U. Niermann (Eds.), *Aquatic invasions in the Black, Caspian and Mediterranean Seas* (pp. 273–285). Dordrecht: Kluwer.

- Mariottini, G. L., & Pane, L. (2010). Mediterranean jellyfish venoms: A review on scyphomedusae. *Marine Drugs*, 8(4), 1122–1152.
- Mills, C. E. (2001). Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, 451(1–3), 55–68.
- Mozetic, P., Solidoro, C., Cossarini, G., et al. (2010). Recent trends towards oligotrophication of the northern Adriatic: Evidence from chlorophyll a time series. *Estuaries and Coasts*, 33, 362–375.
- Mulazzani, L., Camanzi, L., & Malorgio, G. (2012). Price formation and geographic market integration: An empirical investigation of Adriatic small pelagic species. *Fisheries Research*, 119–120, 99–107.
- Nagata, R. M., Haddad, M. A., & Nogueira, M. J. R. (2009). The nuisance of medusae (Cnidaria, Medusozoa) to shrimp trawls in central part of southern Brazilian Bight from the perspective of artisanal fishermen. *Pan-American Journal of Aquatic Sciences*, 4(3), 312–325.
- Natural England. (2010). *Monitor of engagement with the natural environment: The national survey on people and the natural environment* (Tech. Rep. NECR050). Sheffield: Natural England.
- Nishikawa, J., Thi Thu, N., Ha, T. M., & The Thu, P. (2008). Jellyfish fisheries in Northern Vietnam. *Plankton and Benthos Research*, 3(4), 227–234.
- Omori, M., & Nakano, E. (2001). Jellyfish fisheries in southeast Asia. *Hydrobiologia*, 451, 19–26.
- Palmieri, M. G., Barausse, A., Luisetti, T., & Turner, R. K. (2014). Jellyfish blooms in the Northern Adriatic Sea: Fishermen's perceptions and economic impacts on fisheries. *Fisheries Research*, 155, 51–58.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing down marine food webs. *Science*, 279, 860–863.
- Perrings, C. (2001). The economics of biological invasions. *Land Use and Water Resources Research*, 1(3), 1–9.
- Purcell, J. E. (2005). Climate effects on formation of jellyfish and ctenophore blooms: A review. *Journal of the Marine Biological Association of the United Kingdom*, 85(3), 461–476.
- 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., & Arai, M. N. (2001). Interactions of pelagic cnidarians and ctenophores with fishes: A review. *Hydrobiologia*, 451, 27–44.
- Purcell, J. E., Breitburg, D. L., Decker, M. B., Graham, W. M., Youngbluth, M. J., & Raskoff, K. A. (2001). Pelagic cnidarians and ctenophores in low dissolved oxygen environments: A review. In N. N. Rabalais & R. E. Turner (Eds.), *Coastal hypoxia: Consequences for living resources and ecosystems* (Coastal and estuarine studies, Vol. 58, pp. 77–100). Washington, DC: American Geophysical Union.
- Purcell, J. E., Uye, S., & Lo, W.-T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: A review. *Marine Ecology Progress Series*, 350, 153–174.
- Quiñones, J., Monroy, A., Acha, E. M., & Mianzan, H. (2013). Jellyfish bycatch diminishes profit in an anchovy fishery off Peru. *Fisheries Research*, 139, 47–50.
- Richardson, A., Bakun, J. A., Hays, G. C., & Gibbons, M. J. (2009). The jellyfish joyride: Causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution*, 24(6), 312–322.
- Riisgård, H. U., Madsen, C. V., Barth-Jensen, C., & Purcell, J. E. (2012). Population dynamics and zooplankton-predation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark). *Aquatic Invasions*, 7(2), 147–162.
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856), 591–596.
- Schiariti, A., Kawahara, M., Uye, S., & Mianzan, H. (2008). Life cycle of the jellyfish *Lychnorhiza lucerna* (Scyphozoa: Rhizostomeae). *Marine Biology*, 156(1), 1–12.
- Sen, A., Harwood, A. R., Bateman, I. J., Munday, P., Crowe, A., Brander, L., Raychaudhuri, J., Lovett, A., Provins, A., & Foden, J. (2011). Economic assessment of the recreational value of

- ecosystems in Great Britain. In: *UK national ecosystem assessment technical report*. Cambridge: UK National Ecosystem Assessment, UNEP-WCMC.
- Sen, A., Harwood, A. R., Bateman, I. J., Munday, P., Crowe, A., Brander, L., Raychaudhuri, J., Lovett, A., Provins, A., & Foden, J. (2014). Economic assessment of the recreational value of ecosystem: Methodological development and national and local application. *Environmental and Resource Economics*, 57, 233–249.
- Shiganova, T., Mirzoyan, Z., Studenikina, E., Volovik, S., Siokou-Frangou, I., Zervoudaki, S., Christou, E., Skirta, A., & Dumont, H. (2001). Population development of the invader ctenophore *Mnemiopsis leidyi* in the Black Sea and in other seas of the Mediterranean basin. *Marine Biology*, 139, 431–445.
- Stohlgren, T. J., & Schnase, J. L. (2006). Risk analysis for biological hazards: What we need to know about invasive species. *Risk Analysis*, 26(1), 163–173.
- Sugahara, T., Ueno, M., Goto, Y., Shiraishi, R., Doi, M., Akiuama, K., & Yamauchi, S. (2006). Immunostimulation effect of jellyfish collagen. *Bioscience, Biotechnology, and Biochemistry*, 70, 2131–2137.
- UK National Ecosystem Assessment. (2011). *The UK national ecosystem assessment: Synthesis of the key findings*. Cambridge: UNEP-WCMC.
- Uye, S. (2008). Blooms of the giant jellyfish *Nemopilema nomurai*: A threat to the fisheries sustainability of the East Asian Marginal Seas. *Plankton Benthos Research*, 3, 125–131.
- Uye, S. (2010). Human forcing of the copepod-fish-jellyfish triangular trophic relationship. *Hydrobiologia*, 666, 71–83.
- Van Ginderdeuren, K., Hostens, K., Hoffman, S., Vansteenbrugge, L., Soenen, K., De Blauwe, H., Robbens, J., & Vincx, M. (2012). Distribution of the invasive ctenophore *Mnemiopsis leidyi* in the Belgian part of the North Sea. *Aquatic Invasions*, 7(2), 163–169.