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THE BROAD-SCALE DISTRIBUTION AND ABUNDANCE OF SCYPHOMEDUSAE IN IRISH WATERS

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A thesis presented to the National University of Ireland, Cork
in candidature for the degree of Doctor of Philosophy

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Contents

Declaration.....	iv
Funding Information.....	iv
Acknowledgements.....	v
General Abstract.....	vi
List of Figures.....	viii
List of Tables.....	x
Chapter 1.....	1
General Introduction.....	1
1. Definitions.....	2
2. Jellyfish stings, humans, and the economy.....	3
3. Jellyfish within marine ecosystems.....	5
4. A critical need for broad-scale data.....	8
5. Scyphomedusae in Irish waters.....	9
6. Objectives of the present work.....	11
Chapter 2.....	13
Fisheries bycatch data provide insights into the distribution of <i>Pelagia noctiluca</i> around Ireland.....	13
Abstract.....	14
1. Introduction.....	14
2. Methods.....	16
3. Results.....	19
4. Discussion.....	24
Chapter 3.....	28
Inter-annual and inter-regional distributions and abundances of <i>Aurelia aurita</i> and <i>Cyanea</i> spp. across the Irish Sea.....	28
Abstract.....	29
1. Introduction.....	29
2. Methods.....	31
2.1. Data collection.....	31
2.2. Environmental parameters.....	33

2.3. Statistical analysis	34
3. Results.....	35
3.1. Catch summary	35
3.2. Inter-annual variations of abundances and distributions of scyphomedusae across the study area	36
3.3. Inter-regional variations of jellyfish abundance.....	37
3.4. Environmental context	42
3.5. Jellyfish condition	42
4. Discussion	47
Chapter 4.....	51
Monitoring of the seasonal dynamics of scyphomedusae in the Irish Sea.....	51
Abstract	52
1. Introduction.....	52
2. Methods.....	54
2.1. Study area.....	54
2.2. Data collection	55
2.3. Seasonal trend	57
2.4. Distribution patterns.....	57
2.5. Environmental data	58
2.6. Camera trial.....	58
2.7. Net tow trials.....	59
3. Results.....	60
3.1. Surveys along ferry-route A.....	60
3.2. Seasonal abundance of <i>Aurelia aurita</i>	61
3.3. Seasonal abundance of <i>Cyanea capillata</i>	61
3.4. Spatial patterns and seasonal changes in the distributions of <i>Aurelia aurita</i> and <i>Cyanea capillata</i>	62
3.5. Environmental conditions along ferry-route A	64
3.6. Distribution patterns along ferry-route B in relation to environmental parameters.....	65
3.7. Camera trial.....	67
3.8. Net tow trials.....	68
4. Discussion	69

Chapter 5.....	76
Acoustic tracking of <i>Cyanea capillata</i>	76
Abstract.....	77
1. Introduction.....	77
2. Methods.....	79
2.1. Device attachment.....	79
2.2. Horizontal movements	80
2.3. Vertical movements	81
3. Results.....	83
3.1. Horizontal movements	83
3.2. Vertical movements	86
4. Discussion.....	86
Chapter 6.....	92
General Discussion	92
References.....	99
APPENDIX A.....	110
Statistic tables relative to Chapter 3.....	110
APPENDIX B	117
Lynam et al. (2011) Have Jellyfish in the Irish Sea benefited from climate change and overfishing?.....	117

Declaration

The thesis submitted here is my own work and has not been submitted for another degree, either at University College Cork or elsewhere.

Thomas Bastian

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General Abstract

Scyphomedusae are receiving increasing recognition as key components of marine ecosystems. However, information on their distributions and abundance beyond coastal waters is generally lacking. These data are required to identify the risks of detrimental impacts of jellyfish blooms on human activities. The present work looked at the opportunity to access new information on the distribution and abundance of scyphomedusae around Ireland by using existing infrastructures and sampling programmes.

During the annual Irish groundfish survey of 2009, the jellyfish bycatch obtained was documented. With 140 sampling stations distributed over an area >160 000 km², this new dataset provided original insights into the distribution of *Pelagia noctiluca* in Irish shelf waters at scale never reached before in a region of the Northeast Atlantic. The distribution of this species was marked by a high level of both intra- and inter-regional variations, with highest catch occurring off the Northwest of Ireland.

Similarly, data collected during the Irish Sea juvenile gadoid fish survey in early June 2007, 2008, 2009, and 2010, provided the first available quantitative, spatially explicit, information on the abundance of *Aurelia aurita* and *Cyanea* spp. (*Cyanea capillata* and *Cyanea lamarckii*) throughout the Irish Sea. Overall, scyphomedusae were present at 98% of the sampling stations ($N = 200$ sampling). The overall mean (\pm SD) abundance of *A. aurita* was 1.3 ± 3.9 g m⁻³ or 1.0 ± 3.0 ind. 100 m⁻³; for *C. capillata* it was 0.3 ± 0.7 g m⁻³ or 1.2 ± 4.2 ind. 100 m⁻³. However, the distributions and abundances of the different species exhibited spatial and inter-annual variability which differed in different regions of the basin. In addition, the analysis of CTD data revealed that the average size of *A. aurita* (as indicated by an individual condition index) varied between different hydrographical regions with larger individuals being found in stratified waters. It is suggested that these differences are linked to the differences in the timing and yields of the seasonal primary and secondary productions in the different regions of the Irish Sea.

Furthermore, a seasonal monitoring of the abundance of scyphomedusae in the Irish Sea was implemented using ships of opportunities. The surface abundance of scyphomedusae was surveyed along a >100 km long ferry route between Dublin (Ireland) and Holyhead (Wales, UK) as well as three additional surveys conducted along the >200 km-long transect between Dublin and Liverpool. A total of 37 surveys were conducted between April and September in 2009 ($N = 17$) and 2010 ($N = 20$). The first formal description of

the seasonal occurrence of *A. aurita* and *C. capillata* in a region of the Irish Sea is provided, and seasonal variations in the distribution of the species along the transect are described. In addition some of the jellyfish aggregations observed during the surveys were successfully linked with oceanographic features (i.e. fronts) indicated by automatic water sampling devices present on the survey-ship (FerryBox). The quality of surveys from ships of opportunity as a cost-effective tool to develop local knowledge on scyphomedusae and monitor their abundance across extended areas is discussed.

Finally, in order to inform the movements of *C. capillata* in an area where many negative interactions with bathers occur, the horizontal and vertical movements of 5 individual *C. capillata* were investigated through acoustic tracking. Duration of tracking trials ranged from 2.7 to 7.7 h with horizontal distances travelled by the tracked jellyfish ranging from 1.6 to 5.9 km. The horizontal movements of the 5 tracked individuals broadly followed the main currents (tidal flow). Each individual exhibited a variety of vertical movements, ranging from actively swimming up and down the water column to staying within a limited range of depth for several minutes. Results from this study demonstrated that the deployment of electronic devices on this highly venomous species is possible.

List of Figures

Figure 1.1. Life-cycle of a Scyphozoa.	2
Figure 1.2. Main scyphozoan species present in Irish waters.	10
Figure 2.1. Sampling stations during the Irish groundfish survey (IGFS) 2009.	17
Figure 2.2. Distribution of gelatinous bycatch during the IGFS 2009.	20
Figure 2.3. Distribution of <i>P. noctiluca</i> in the North subregion.	23
Figure 2.4. Environmental context in which <i>P. noctiluca</i> occurred in the North subregion.	23
Figure 2.5. Size distribution of <i>P. noctiluca</i> caught during the IGFS in 2009.	24
Figure 3.1. Sampling stations in the Irish Sea.	32
Figure 3.2. Inter-annual variations of biomass of <i>A. aurita</i> and <i>Cyanea</i> spp.	37
Figure 3.3. Volume standardised biomass (g m^{-3}) of <i>A. aurita</i> and <i>Cyanea</i> spp. in the Irish Sea in early June 2007-2010.	40
Figure 3.4. Densities ($\text{ind. } 100 \text{ m}^{-3}$) of <i>A. aurita</i> and <i>Cyanea</i> spp. in the Irish Sea in early June 2007-2010.	41
Figure 3.5. Near surface temperature and salinity, and stratification index in the Irish Sea in early June 2008-2010.	43
Figure 3.6. Inter-annual and inter-regional variations of the condition index (g ind^{-1}) of <i>A. aurita</i> and <i>Cyanea</i> spp.	45
Figure 3.7. Variations in the condition index of <i>A. aurita</i> and <i>Cyanea</i> spp. in different water types.	46
Figure 4.1. Study area for visual enumeration of scyphomedusae in the Irish Sea in 2009 and 2010.	54
Figure 4.2. Using ships of opportunity to monitor the surface abundance of scyphomedusae.	55
Figure 4.3. Seasonal occurrence of <i>A. aurita</i> and <i>C. capillata</i> between Dublin and Holyhead in 2009 and 2010.	62
Figure 4.4. Spatial patterns and season changes in the distribution of <i>A. aurita</i> and <i>C. capillata</i> between Dublin and Holyhead in 2009 and 2010.	63
Figure 4.5. Mean daily temperature and salinity between Dublin and Holyhead.	65
Figure 4.6. Distributions of <i>A. aurita</i> , <i>C. capillata</i> , and variation of environmental parameters between Dublin and Liverpool.	66
Figure 4.7. Comparison of surface counts of jellyfish by two observers with numbers derived from image analysis.	68

Figure 4.8. Comparison of densities of <i>A. aurita</i> from oblique net tows with surface densities from visual counts.....	69
Figure 4.9. Seasonality of different components of the ecosystem of the Irish Sea.	73
Figure 5.1. Images of <i>C. capillata</i> in and out of the water, and the acoustic tag.	79
Figure 5.2. Acoustic tracking of five <i>C. capillata</i> in July 2010.....	84
Figure 5.3. Speed of travel of jellyfish and drogues during tracking trials.....	85
Figure 5.4. Dive records of the five <i>C. capillata</i> tracked in July 2010.....	87

List of Tables

Table 2.1. Division of the study area of the IGFS 2009 into subregions.	18
Table 2.2. Gelatinous bycatch experienced during the IGFS 2009.....	21
Table 3.1. Sampling effort in the Irish Sea between 2007 and 2010.	33
Table 3.2. Catches of <i>A. aurita</i> and <i>Cyanea</i> spp. in the Irish Sea between 2007 and 2010.....	39
Table 3.3. Correlations between scyphomedusae abundance and condition index with environmental parameters.	44
Table 4.1. Dates of ferry surveys across the Irish Sea in 2009 and 2010.	56
Table 4.2. Numbers of individual <i>R. octopus</i> , <i>C. lamarckii</i> , and <i>C. hysoscella</i> observed during ferry surveys in 2009 and 2010.	60
Table 5.1. Acoustic tracking of <i>C. capillata</i> in July 2010.	82
Table 5.2. Measures of drift between the trajectories of jellyfish and drogues.	83
Table 5.3. Vertical swimming speed of different scyphozoan species.	91
Table A.1. Inter-annual variations of abundance of <i>Cyanea</i> spp. across the entire Irish Sea.	111
Table A.2. Inter-annual variations of abundance of <i>A. aurita</i> across the entire Irish Sea.....	111
Table A.3. Inter-annual variations in the distribution of <i>Cyanea</i> spp. in the Irish Sea. ..	112
Table A.4. Inter-annual variations in the distribution of <i>A. aurita</i> in the Irish Sea.	112
Table A.5. Correlations between the annual abundance of <i>Cyanea</i> spp. and <i>A. aurita</i> . ..	113
Table A.6. Comparison of annual distribution patterns of <i>Cyanea</i> spp. and <i>A. aurita</i> . ..	113
Table A.7. Inter-regional differences in the annual abundance of <i>Cyanea</i> spp.	114
Table A.8. Inter-regional differences in the annual abundance of <i>A. aurita</i>	114
Table A.9. Inter-annual variations of <i>A. aurita</i> biomass (g m^{-3}) in each region of the Irish Sea.	115
Table A.10. Inter-annual variations of <i>A. aurita</i> densities (ind.100 m^{-3}) in each region of the Irish Sea.	115
Table A.11. Inter-annual variations of <i>Cyanea</i> spp. biomass (g m^{-3}) in each region of the Irish Sea.	116
Table A.12. Inter-annual variations of <i>Cyanea</i> spp. densities (ind. 100m^{-3}) in each region of the Irish Sea.	116

Chapter 1

General Introduction

Chapter 1 – General Introduction

1. Definitions

Scyphomedusae are the sexually reproductive stage in the life cycle of Scyphozoa (Phylum Cnidaria). They produce haploid gametes (sperm or oocytes) which fuse with gametes of the opposite sex during fertilisation to form a new diploid zygote. This zygote develops into a planula larva, which settles on the sea bed and develops into a polyp. This sessile polyp stage, called a scyphistoma, will then grow, develop, and eventually strobilate to asexually produce ephyrae. These ephyrae will then be released in the water column and develop into medusae, therefore initializing a new cycle (Figure 1.1). However, the life-cycle of many scyphozoan species is more complex and plastic than this ‘typical’ picture. In particular, depending on the conditions, the scyphistoma can bud to asexually produce more polyps before undergoing strobilation; and in some cases, the planula can directly develop into an ephyra without producing a polyp (Arai, 1997; Lucas, 2001).

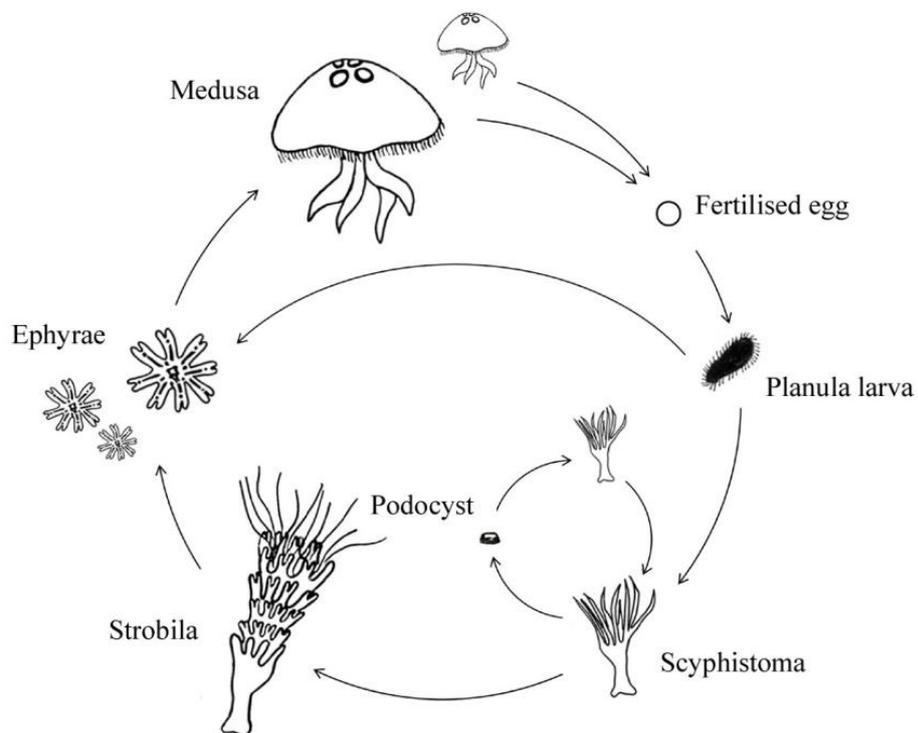


Figure 1.1. Life-cycle of a Scyphozoa.

In many scyphozoan species the planula larvae are released in the water column by females after internal fertilization. Figure adapted from Dr. E. J. Baxter original drawings.

The present work focuses only on the medusa stage, which is the most readily observed stage and which causes many socio-economic impacts (Purcell et al., 2007). Because a medusa stage is also present in the life cycle of some Hydrozoa and in all Cubozoa, the word ‘scyphomedusae’ will be used here to refer specifically to the medusae of Scyphozoa. Similarly, in the present work, the use of the word ‘jellyfish’ will be restricted to scyphomedusae; although in common language it often encompasses medusae of all taxa, as well as many other organisms characterized by a gelatinous body (e.g. siphonophores, ctenophores, salps).

Scyphomedusae are arguably the most conspicuous members of the planktonic community, especially because of their size (few cm to 1-2 m) and the tendency of some species to occur in large and dense aggregations. These high densities of scyphomedusae are often referred to as ‘jellyfish swarms’ or ‘jellyfish blooms’. In fact, at times, these ‘blooms’ can be so dense that descriptions of the sea looking “as if converted into a solid mass of jellyfish” (Cole, 1952; cited in Russell, 1970) are not uncommon. Because of their venomous nature (i.e. they sting), jellyfish are considered as pests by humans, and in recent years, more and more attention have been given to their potential direct and indirect impacts on various aspects of human activities (see next section).

2. Jellyfish stings, humans, and the economy

Jellyfish stings are caused by stinging capsules (the nematocysts) localised in a particular type of cells called cnidocytes, specific to Cnidarians. These cells are present in high densities on the tentacles of the medusae but are also present on the bell and oral arms. The nematocysts are composed of a coiled filament that is fired in response to a mechanical or chemical stimulus (Arai, 1997). It is through these filaments that the venom of the jellyfish is injected to any prey, predator, or unfortunate bather that happens to come in contact with the animal.

In most cases, the sting of scyphozoan jellyfish does not have as severe a consequence as the sting of the infamous gelatinous ‘stingers’ such as cubozoan jellyfish (also known as ‘box jellyfish’) and some siphonophores (e.g. *Physalia physalis*, the Portuguese man-of-war); it is nonetheless a source of concern. For example, in some years, high densities of the mauve stinger *Pelagia noctiluca* occur during summer months in the Mediterranean Sea (UNEP, 1984). Considering that millions of people converge toward this area for vacations every summer, blooms of *P. noctiluca* represent a serious health and safety issue, as much as a source of nuisance for the tourism industry (Mariottini et al., 2008).

Although epidemiological studies are scarce, Maretic et al. (1991) showed that, over the summer 1978, in Pula (Croatia), 52% of bathers were stung by a jellyfish, suggesting that “the total number of bathers stung every year along the Adriatic coasts amounts not to hundreds but to millions”. Most cases of stings by *P. noctiluca* are usually benign, however, in some cases bathers can have a worse reaction and require medical attention (Mariottini et al., 2008). At higher latitudes, the lion’s mane jellyfish *Cyanea capillata* can inflict even more severe stings than *P. noctiluca*. There are reported cases where, when stung by a lion’s mane jellyfish, people have experienced difficult and painful breathing, tachycardia and muscle spasms. Back stiffness and spasms are also reported symptoms, and anaphylactoid reactions have sometimes been observed (Lord and Wilks, 1918; Jellyfish Action Advisory Group, 2010). In the Irish Sea, open water swimmers have described experiencing “excruciating pain” after being stung by a lion’s mane jellyfish. One of them, a mother of three children described the pain as worse than child birth (T.K. Doyle, *pers. comm.*).

Given the risk linked to the presence of jellyfish in the water (or stranded on the beach), high abundances of jellyfish sometimes lead to beach closures. This was the case on the east coast of Ireland, in 2005, after mass strandings of lion’s mane jellyfish (T.K. Doyle, *pers. comm.*). In the Mediterranean Sea, closures due to swarms of *P. noctiluca* are not uncommon (V. Fuentes, *pers. comm.*). Beach closures are often a source of significant economic loss for coastal communities (e.g. Wiley et al., 2006) and even in cases where beaches are not officially closed, the discomfort caused by the presence of jellyfish can be enough to turn people away from infested areas (Galil, 2008). The specific cost related to these jellyfish related-events is currently under study, but considering the important mitigation measures taken by French and Spanish authorities in tourist areas (e.g. beach cleaning, installation of fixed nets, jellyfish ‘hoovering’ boats), they must be significant (ECOS, 2004).

Other economic sectors can be affected by jellyfish outbreaks, starting with coastal industrial facilities that depend on sea water intake for their functioning. There are several reported cases of dense aggregations of medusae obstructing the cooling water intakes of coastal power plants, forcing production at the installation to be temporarily stopped (Purcell et al., 2007). Some of the most recent cases concerned a power plant in Scotland and another one in Israel in July 2011 (BBC, 2011a; b). Aquaculture is another economic sector for which jellyfish are a source of serious concerns. Although most documented fish kills involving gelatinous plankton were due to small (< 5 mm) hydrozoan species, some were due to scyphomedusae (Merceron et al., 1995; Hay and Murray, 2008; Baxter,

2011). For example, in 2007 *Pelagia noctiluca* was responsible for a major fish kill in Northern Ireland, causing > €1M of damage (Doyle et al., 2008). Furthermore, recent studies have demonstrated that even the common jellyfish, *Aurelia* sp., generally regarded as innocuous as it cannot sting humans, can seriously affect farmed fish (Helmholz et al., 2010; Baxter et al., 2011). Considering the occurrence of this species in large numbers throughout Europe, these findings raise serious concerns for the aquaculture industry.

Finally, blooms of scyphomedusae are a substantial problem for the fishing industry (Purcell et al., 2007). Indeed, jellyfish rapidly clog fishing nets, and the tentacles entangled on the ropes and nets are a hazard for fishermen. Furthermore, the incidental catch of jellyfish also causes increased labour and downtime costs due to the necessity to separate jellyfish from the rest of the catch and to clean the nets. In extreme cases, the catch of a large amount of jellyfish can even represent a risk of capsizing for the smallest fishing vessels (e.g. Ryall, 2009). However, the main fisheries' concerns about jellyfish are related to the indirect effects that they can have on fish stocks through their position within the marine food-web.

3. Jellyfish within marine ecosystems

The role of jellyfish within marine ecosystems has been much clarified in recent decades. Like all organisms, scyphomedusae contribute to energy fluxes within the food web. Typically, they prey on micro and meso-zooplankton (mostly copepods and cladocerans) and other gelatinous organisms, and are preyed upon by a variety of predators (e.g. fish, turtles, birds) (Purcell, 1997; Arai, 2005). However, there is a persuasive argument that jellyfish differ from the other organisms present in the water column in that their life cycle presents the 'boom and bust' aspect typical of many small planktonic species, but is coupled with a biomass greater by orders of magnitude, reaching tonnes km⁻² (Pitt et al., 2009b). Moreover, in many cases, jellyfish blooms do not occur every year. Therefore, from a human point of view, the sudden development of such biomass is often seen as a temporary and anomalous perturbation, that can induce considerable qualitative and quantitative changes in the planktonic community and the rest of the system (Hay, 2006; Boero et al., 2008).

For example, studies suggest that dense aggregations of jellyfish can at times consume a significant part of the zooplankton standing stocks and therefore, enter into competition with other zooplanktivores for food (e.g. Purcell, 1997). However, the impact of jellyfish predation is not the same among all members of the planktonic community. For example,

in the Prince William Sound in Alaska (USA), jellyfish seem to have a limited effect on the standing stocks of copepods ($0.3\% \text{ d}^{-1}$), but significant effects on larvaceans (8.3% of standing stock d^{-1}) (Purcell, 2003). Similarly, off Oregon (USA), high densities of *Chrysaora fuscescens* have been showed to remove $>32\% \text{ d}^{-1}$ of the standing stock of euphausiid eggs, but $<1\% \text{ d}^{-1}$ of copepod standing stock (Suchman et al., 2008). Such differential predation pressure on the different members of the planktonic community is most likely due to the difference in the concentration of the potential prey (encounter rate) and/or their escape capability (Purcell, 1997; Suchman, 2000). Consequently, it has been suggested that, by removing a significant percentage of the standing stocks of key zooplankton groups, jellyfish exert competition pressure upon fish species feeding preferentially on these same groups (Brodeur et al., 2008b; Suchman et al., 2008).

In fact, this competition for food between jellyfish and fish could be an important structuring force in some ecosystems. For example, in the Benguela up-welling ecosystem and in Japan, jellyfish outbreaks have been observed to occur quickly after the anthropogenically-forced collapse of the zooplanktivorous fish populations. In these systems, jellyfish are thought to have benefited from the ecological niche left vacant by the removal of the planktivorous fish by fisheries (Richardson et al., 2009). In fact, acoustic surveys have revealed that the biomass of jellyfish is now higher than the biomass of fish in the Benguela ecosystem (Brierley et al., 2005; Lynam et al., 2006). With fish eggs and larvae also being part of the diet of some scyphomedusae (Purcell and Arai, 2001), such outbreaks have raised concerns that jellyfish may hamper the recovery of these fish stocks, even if mitigation measures are taken (Sommer et al., 2002).

Additional concern about jellyfish outbreaks affecting ecosystem services comes from the perception that scyphomedusae are ‘trophic dead ends’ (Lynam et al., 2006). This notion implies that, because they have only few predators, jellyfish block the ‘natural’ energy transfer between secondary producers (zooplankton) and higher trophic levels, therefore jeopardising the productivity of the ecosystem and ultimately the resources people derive from it (i.e. mostly fish harvesting). However, despite their nutritional value compared to other food items being low (Doyle et al., 2007b), jellyfish do have many predators and the number of identified ‘jelly-eaters’ is rapidly increasing: a recent review identified at least 69 fish species feeding on pelagic coelenterates (Arai, 2005); a number raised to 124 by another review published only four years later (Pauly et al., 2009). Even in the Benguela ecosystem, which is often presented as a case-study of an ecosystem that has already shifted to a jellyfish dominated state (Lynam et al., 2006; Richardson et al., 2009), a recent study discovered that the three bearded goby (*Sufflogobius bibarbatus*)

feeds extensively on jellyfish. This small fish, which is in turn preyed upon by fish and birds occupying higher trophic levels, actually contributes to maintaining the productivity of the system at a certain level (Utne-Palm et al., 2010). The word ‘trophic dead-end’ seems therefore inappropriate. Nonetheless, it is true that jellyfish are likely to reduce the efficiency of energetic flows towards higher trophic levels (Brodeur et al., 2011).

Scyphomedusae also directly and indirectly affect the lower trophic levels, and, in particular, they can alter the composition of microbial communities. Indeed, through sloppy-feeding and the production of mucus and exudates, jellyfish make available large quantities of organic and inorganic matter for these lower trophic levels (Pitt et al., 2009b). For example, studies in the York River Estuary have shown that the ctenophore *Mnemiopsis leydii* and the scyphozoa *Chrysaora quinquecirrha* are important sources of dissolved inorganic nitrogen and phosphorus in that system (Condon et al., 2010). However, these recycled nutrients contribute only a limited fraction of the daily primary production of the system. Instead, because of the large quantities of dissolved organic matter (DOM) they produce, jellyfish blooms could give a competitive advantage to bacteria over phytoplankton for the intake of these inorganic nutrients (Condon et al., 2010). In fact, recent incubation experiments with living animals have demonstrated that DOM produced by the scyphomedusa *Chrysaora quinquecirrha* is rapidly metabolised by heterotrophic bacteria. However, this consumed DOM is mostly used by bacteria for respiration rather than production. In other words, this organic matter is mostly metabolized into CO₂ rather than biomass, and therefore only a small fraction of it can be channelled toward higher trophic levels through flagellates and other bacteria grazers (Condon et al., 2011). In addition to jellyfish exudates, dead jellyfish also represent organic matter that can fuel the bacterial community. In the Adriatic Sea, increased bacterial abundance, production, and changes of community composition have been observed when jellyfish homogenates from *Aurelia* sp. were added to natural communities in incubation experiments (Tinta et al., 2010). In Norway, the microbial community around dead *Peryphilla peryphilla* exhibited contrasting responses: while some species used jellyfish as a substrate, others were inhibited (Titelman et al., 2006). Such observations highlight how thousands of jellyfish can potentially cause large community changes at the bottom of the pelagic food web and raise questions regarding the consequences of these changes for the rest of the system (Condon et al., 2011).

Furthermore, dead jellyfish can also play a role in benthopelagic coupling. Indeed, although a fast break-down and degradation of dead jellyfish can occur in the water column (Titelman et al. 2006), for some species (in particular Rhizostomeae) entire

individuals sink to the sea bed, and as such, constitute a flux of organic matter toward the benthos (Yamamoto et al., 2008). For example, in the Arabian Sea, depositions of the Rhizostomea *Crambionella orsini* were observed to depths of 3,300 m. Some patches were several centimetres thick and some metres wide, with the local standing stock of carbon estimated to be one order of magnitude higher than the annual carbon flux measured by sediment traps (Billett et al., 2006). Such inputs of organic material benefit not only the bacterial community present in the sediment (West et al., 2009), but also many scavengers (Yamamoto et al., 2008). Indeed, just like for fish, our knowledge of the number of identified benthic invertebrates feeding on jellyfish is expanding greatly. For example, within a year, interviews and consultation with recreational divers around Ireland led to the identification of 10 previously undocumented interactions between medusae and benthic scavengers (Doyle et al. in prep.). The recent application of molecular investigation methods such as stable isotope analysis, to jellyfish, has also revealed previously unsuspected roles (albeit indirect) of jellyfish in benthic-pelagic coupling through predation (Pitt et al., 2008).

4. A critical need for broad-scale data

As conceptual models of how jellyfish affect the pathways of energy in marine systems are emerging, one important challenge still lies ahead: the quantification of all of these ecological processes. Indeed, even qualitative evaluation of the part played by jellyfish in the functioning of the ecosystems remains limited by a lack of data on their abundance and broad-scale distributions (Pauly et al., 2009; Purcell, 2009). Furthermore, without reliable biomass estimates, it is difficult to extrapolate findings from laboratory or mesocosm experiments, and to reliably integrate jellyfish into numerical ecosystem models (Pauly et al., 2009). In addition, without knowledge of when and where jellyfish occur, and how widespread they are distributed, it is impossible to identify the other species that they truly interact with. For example, the seasonal patterns of occurrence of the common jellyfish *Aurelia aurita* exhibit huge variability in different places around the world (Lucas, 2001). Consequently, if gut contents analysis of *A. aurita* from a Swedish fjord show that the species can feed on fish larvae (Möller, 1984), there is no certainty that blooms of *A. aurita* actually do likewise in the Irish Sea. Developing knowledge of the broad-scale distributions and abundances of scyphomedusae is therefore critical to address such issues.

Over the past years, in addition to the classical sampling using net-tows, different techniques have been proposed to collect such broad-scale data (e.g. acoustic surveys or use of video profilers, but see review by Purcell, 2009). However, in many cases, the organisation of dedicated surveys is impossible due to logistical and resource limitations. Nevertheless, some alternatives exist. The main one consists in collaborating with fisheries agencies organising annual fish surveys. These surveys provide indeed the opportunity to access invaluable shiptime and to collect data across extended spatial scales (Hay et al., 1990; Brodeur et al., 1999; Graham, 2001). This is the approach used in the present work to collect data on the distribution of scyphomedusae in Irish waters.

5. Scyphomedusae in Irish waters

There are six species of Scyphozoa commonly found in the coastal waters around Ireland (Figure 1.2). Five species belong to the order Semaestomae: the common jellyfish *Aurelia aurita* (up to ~ 25 cm in bell diameter), the blue jellyfish *Cyanea lamarckii* (up to ~ 30 cm), the lion's mane jellyfish *Cyanea capillata* (up to ~ 50 cm), the compass jellyfish *Chrysaora hysoscella* (up to ~30 cm), and the mauve stinger *Pelagia noctiluca* (up to ~ 15 cm). The last species, *Rhizostoma octopus* (up to > 50 cm in bell diameter), belongs to the order Rhizostomeae. Some deep water species of the order Coronatae (e.g. *Periphylla periphylla*) can be found in more offshore waters (Russell, 1970).

Prior and subsequent to the pioneering studies conducted in the late 19th – early 20th century by Maud Delap on specimens from Valentia Harbour (Co. Kerry) (e.g. Delap, 1901; 1924), gelatinous species around Ireland had been the subject of little attention (Boyd et al., 1973). McGrath (1985; 1994) documented the occurrence of the siphonopore *Velella velella* in Irish waters, and Ballard and Myers (1997; 2000) studied the gelatinous plankton of Lough Hyne (Co. Cork) but it is only recently (2000s onwards) that broad-scale research on scyphomedusae in Irish waters was established as researchers with a primary interest in sea turtles started mapping the distribution and availability of jellyfish as a food source (Doyle, 2006; Houghton et al., 2006c). Jellyfish stranding events were then documented through extended beach surveys around Ireland and Wales, and provided solid evidence for the existence of differences in the distribution of the different species of scyphomedusae in the region (Doyle et al., 2007a). While *Aurelia aurita* was found all around Ireland and Wales, *C. hysoscella* was more frequent off the South and West coast of Ireland. On the other hand, *C. capillata* was only found in numbers on the



Figure 1.2. Main scyphozoan species present in Irish waters.

On the left, top to bottom: *Aurelia aurita*, *Chrysaora hysoscella*, and *Rhizostoma octopus*. On the right, top to bottom: *Pelagia noctiluca*, *Cyanea capillata*, and *Cyanea lamarckii*. Photos by Michelle Cronin, Oliver Buckley, Luke Harman, Anonymous, Damien Haberlin and Oliver Buckley, respectively.

coasts of the Irish Sea, while blooms of *R. octopus* consistently occurred in only three specific shallow bays (Doyle et al., 2007a; Houghton et al., 2007).

In 2007, with a large fish kill caused by *Pelagia noctiluca* in Northern Ireland (see previous section and Doyle et al., 2008), and beach closures following the mass stranding of highly venomous lion's mane jellyfish off Dublin, the question of the risk for further detrimental impact of jellyfish on human activities in Ireland was raised. Most of the jellyfish species present around Ireland had then already been subject to studies in other regions of the world (e.g. Grondahl, 1988; Brewer, 1989; Hay et al., 1990), and the findings of possible impact of *A. aurita*, *C. capillata* and *C. lamarckii* on the recruitment of juvenile fish in the North Sea (Lynam et al., 2005b) highlighted the need for an audit of the situation around Ireland and in the Irish Sea in particular. In addition, with suggestions that, in temperate zones, jellyfish populations may benefit from warming seas (Purcell, 2005), and evidence of an increasing trend in sea surface temperature around Ireland (McMahon and Hays, 2006; Cannaby and Hüsrevoğlu, 2009), the need to develop our knowledge on the ecology of jellyfish in Irish waters was made even more evident.

6. Objectives of the present work

The primary objective of the present work was to document the spatio-temporal at-sea distributions of scyphomedusae around Ireland, with the aim of providing a starting point to identify risks of detrimental impacts for human activities.

The specific objectives were to:

- Extend the current knowledge of the broad-scale distributions of scyphomedusae in Irish Waters to offshore waters (Chapters 2, 3 and 4).
- Describe spatial and seasonal variations of scyphomedusae abundance in the Irish Sea (Chapters 3 and 4).
- Investigate the trajectories and dive behaviour of individual jellyfish, to inform our understanding of the movement of jellyfish blooms (Chapter 5).

More specifically, Chapter 2 reveals how investigation of bycatch data from non-dedicated surveys can provide insights into the distribution of *P. noctiluca* around Ireland at a scale never accomplished before. Chapter 3 presents basin-wide inter-annual variations of the early-summer distributions and abundances of *A. aurita* and *Cyanea* spp. in the Irish Sea. Chapter 4 shows the results of two years of seasonal monitoring of jellyfish abundance along a >100 km-long transect across the Irish Sea and provide the first formal description of the seasonal dynamics (abundance and distribution) of *A.*

aurita and *C. capillata* in that region. Finally, results from the first-ever acoustic tracking of *C. capillata* are presented in Chapter 5, providing information on the horizontal and vertical movements of this species in an area where the risks of negative interactions with humans are high.

Although they represent locally important biomass, aggregations of large barrel jellyfish (*R. octopus*) were not a subject of focus in the current work as they have been recently documented by others (Houghton et al., 2006c; Lilley et al., 2009). However, occasional sightings or catches of *R. octopus* and of other scyphozoan species are reported in Chapter 2, 3 and 4.

Chapter 2

Fisheries bycatch data provide insights into the distribution of *Pelagia noctiluca* around Ireland

Chapter 2 – Fisheries bycatch data provide insights into the distribution of *Pelagia noctiluca* around Ireland

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TB, DS and JEK collected data. TB performed data analysis and wrote manuscript with contributions from all others.

Abstract

There is concern that jellyfish populations are proliferating in the Northeast Atlantic and that their socio-economic impacts will increase. Using information from the Irish Groundfish Survey, data are presented on the distribution of the mauve stinger, *Pelagia noctiluca*, over an area >160,000 km² around Ireland and the United Kingdom in 2009. The species accounted for 93% of the overall catch of gelatinous organisms, with an average catch biomass of 0.26 ± 2.3 kg ha⁻¹. The study area was divided into four subregions (North, West, Southwest, and South), and the distribution and abundance of *P. noctiluca* displayed both inter- and intraregional variations. Individual bell diameters ranged from 1 cm to 13.5 cm (median 4.5 cm, SD 1.2 cm), and the size distribution also varied spatially. It is the first time that such detailed information has been made available for *P. noctiluca* in a part of the Northeast Atlantic where its impact on the salmon aquaculture industry can be considerable. Finally, the possibility of using annual datasets from this type of fisheries survey to develop time-series that, in the future, will allow investigation of relationships between long-term variations of *P. noctiluca* populations and climatic factors in the area is addressed.

1. Introduction

Concern about the role and place of jellyfish within marine ecosystems has increased during recent decades as an increasing number of cases of negative interactions with human activities have been reported (see review by Purcell et al., 2007). It has been suggested that, in different places, jellyfish abundance may have increased in response to eutrophication, overfishing, and/or climate change (Arai, 2001; Mills, 2001; Purcell, 2005; Richardson et al., 2009). However, a global increase of jellyfish populations has

not yet been formally proven (Purcell et al., 2007; Boero et al., 2008; Haddock, 2008). It is also important to realize that some of the recent reports of the detrimental impacts of jellyfish may simply result from interactions between relatively new, quickly expanding coastal activities (e.g. aquaculture) and possible natural cycles in the outbreaks of some gelatinous organisms (Boero et al., 2008).

In Irish and UK waters, the mauve stinger *Pelagia noctiluca* (Scyphozoa, Semaestomeae, Pelagiidae) became a serious concern when it caused a major fish kill (~250,000 fish) in November 2007 in Northern Ireland's only salmon farm, resulting in an economic loss in excess of €1 million (Boero et al., 2008; Doyle et al., 2008). The species also caused fish loss off Scotland in the same year (Hay and Murray, 2008), and its involvement in other fish kills in the past has been established (Merceron et al., 1995). Such catastrophic fish kills are relatively rare, but it is likely that *P. noctiluca* has also been responsible for some of the chronic zooplankton-related mortalities experienced by finfish farms annually (Hay and Murray, 2008).

Pelagia noctiluca is a holoplanktonic oceanic species, found from the warm waters of the Gulf of Mexico and the Mediterranean Sea to the temperate waters of the North Sea (Russell, 1970; Graham et al., 2003; Licandro et al., 2010). A study of plankton samples collected around Scotland indicated that the abundance of oceanic species, including *P. noctiluca*, peaks in autumn off the north coast of Ireland (Fraser, 1968). However, apart from that work, our knowledge of *P. noctiluca* around Ireland and the UK remains mostly limited to reports of anecdotal sightings and stranding events (Russell, 1970; Doyle et al., 2008). These historical records show that the species has been frequently (but irregularly) observed around Irish and UK coasts at least since the 19th century, but are too scarce to investigate reliably the broad-scale distribution of the species or the potential factors driving interannual variability in the records, as has been done for other areas (Goy et al., 1989; Kogovsek et al., 2010).

In contrast, the species has been studied extensively in the Mediterranean Sea, where critical outbreaks and related economic detrimental impacts stimulated international research programmes during the 1980s (UNEP, 1984; 1991). There, the species appears to follow cycles of “years with *Pelagia*” followed by “several years without *Pelagia*”, the length and frequency of which differ in the various basins, and can be related to hydroclimatological and other environmental factors (Goy et al., 1989; Axiak and Civili, 1991; Kogovsek et al., 2010). However, even in the Mediterranean where the impacts of *P. noctiluca* on public health and tourism are critical (CIESM, 2008; Mariottini et al.,

2008), detailed information on its ecology, and in particular on its broad-scale distribution, is generally lacking.

The paucity of broad-scale data is a common issue in jellyfish studies (Purcell, 2009), mainly because of limited opportunities to access expensive ship time. In the case of *P. noctiluca*, the irregular nature of the species' outbreaks mentioned above is an additional obstacle to organizing access to such resources. As a result, most studies on the species have been restricted to nearshore areas (see examples in UNEP, 1991), and only a few basin-wide studies have been conducted (in the Adriatic and Ligurian Seas, see Goy et al., 1991; and Piccinetti and Piccinetti-Manfrin, 1991). Yet, considering the potential effect of the species on marine ecosystems, (e.g. competition with planktivorous fish and predation on fish eggs and larvae, see Sabatès et al., 2010; Malej, 1989; Giorgi et al., 1991) and aquaculture (previous paragraphs in this section), it is critical to access information on its widespread distribution.

Here we show how bycatch data from non-dedicated surveys such as the Irish Groundfish Survey (IGFS) can provide original insights into the distribution of *P. noctiluca* over extended spatial scales around Ireland and the UK. To our knowledge, it is the first time that such detailed information is available for the species in an area of the Northeast Atlantic on a scale equal to or larger than any known study from the Mediterranean Sea. We also discuss the possibility of using the annual dataset from the IGFS to develop a time-series that will, in future, allow investigation of relationships between long-term variations of *P. noctiluca* populations and climatic and other environmental factors, as has been done successfully for other species, in other parts of the world (Hay et al., 1990; Brodeur et al., 1999; 2008a; Graham, 2001; Lynam et al., 2005a).

2. Methods

The Irish Groundfish Survey (IGFS) is an annual demersal trawl survey conducted in autumn/winter by the Fisheries Science Services of the Irish Marine Institute, on the Irish continental shelf (Figure 2.1), using the RV “Celtic Explorer”. Its primary aim is to collect data on juvenile recruitment patterns for commercially exploited stocks of demersal fish. However, the IGFS encounters a certain level of bycatch of non-targeted species that provides the opportunity to collect additional information. The survey uses a semi-random, depth-stratified survey sampling design that yields about 170 fishing hauls. Each haul is carried out during daylight over a six-week period and is part of an

internationally coordinated survey effort under the International Bottom Trawl Working Group (IBTSWG) of ICES (see IBTSWG reports at www.ices.dk).

Sampling is by a high headline, 4-panel demersal trawl (mesh size 200 mm at wings, 20 mm at cod end) towed over the seabed for 30 min at a speed of ~4 knots (for more details see Anon., 1999). SCANMAR sensors monitor doors, wings, and headline opening throughout the operation, and the average value for each station, as well as the GPS positions of the start and the end of the transect, are recorded. Information on bottom depth is provided by vessel echosounder.

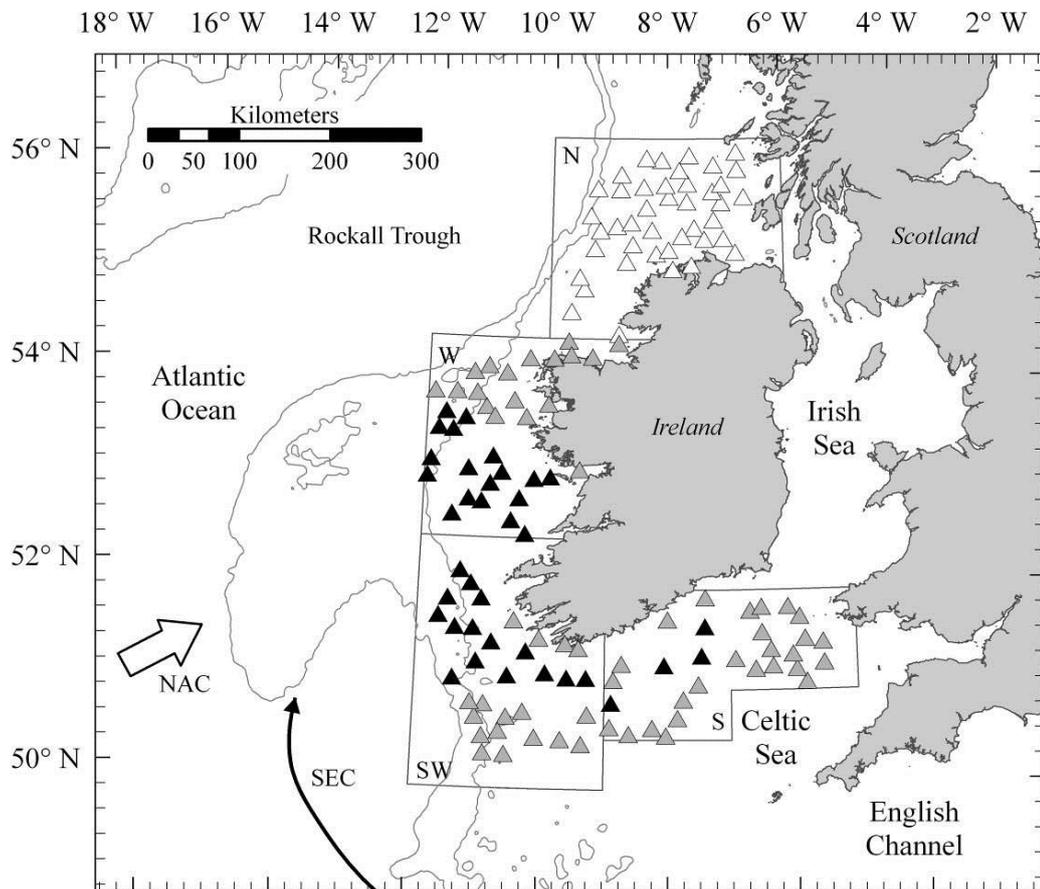


Figure 2.1. Sampling stations during the Irish groundfish survey (IGFS) 2009.

Sampling stations are represented by triangles, different shading depicting the temporal organization of the survey: first leg 26/09/2009 to 5/10/2009 (white), second leg 29/10/2009 to 13/11/2009 (grey), third leg 14–30/11/2009 (black). The study area has been subdivided into four subregions referred to herein as N, W, SW, and S and based on the ICES Divisions VIa VIIb, VIIj2, and VIIg (see Table 1). The grey lines represent the 200 m and 1000 m isobaths, and the general directions of the Shelf Edge Current (SEC) and North Atlantic Current (NAC) are shown as labelled arrows. The system of projection used is the Irish National Grid.

Table 2.1. Division of the study area of the IGFS 2009 into subregions.

Characteristics of each subregion of the study area presented in Figure 2.1, where N is the number of valid sampling stations (i.e. stations retained for analysis) within each subregion during the Irish Groundfish Survey of 2009. The surface area of each subregion was calculated after projection in the Irish National Grid coordinates system.

Subregion	ICES Division	Surface area (km ²)	N
North (N)	VIa	42,829	42
West (W)	VIIb	35,634	36
Southwest (SW)	VIIj2	50,444	32
South (S)	VIIg	35,713	30

In 2009, for the first time, scyphozoan jellyfish bycatch was systematically identified to the level of species for each sampling station. The IGFS 2009 was organized in three legs, the first from 26 September to 5 October, the second from 29 October to 13 November, and the third from 14 to 30 November. Four subregions were defined within the study area: North (N), West (W), Southwest (SW) and South (S), each based, respectively, on ICES Divisions VIa, VIIb, VIIj2, and VIIg (cf. <http://www.ices.dk/aboutus/icesareas.asp>), but restricted to the extent of the sampling stations (Table 2.1 and Figure 2.1).

Scyphozoan jellyfish were sorted by species, and the corresponding wet weight was measured using motion-compensated scales (POLs marine scales ± 2 g). Individual bell diameters were measured to the nearest 0.5 cm using a measuring board and the jellyfish placed with the external surface of the bell facing up. Large catches were subsampled by measuring only the first 150 individuals after successive equal divisions. This was done by placing two empty boxes under the box containing the jellyfish and tipping out the jellyfish sample into the two boxes, essentially splitting the sample into two with reasonable randomization. Measurements were completed within 2 h of the catch being brought on board.

Following the method described by Brodeur *et al.* (1999), a standardized catch (kg ha⁻¹) of each jellyfish species was calculated for each station by dividing the recorded wet weight of medusae by the width of the net multiplied by the distance towed (average per tow calculated from net-sensor records). When wing-spread information was missing as a result of sensor failure ($N = 27$), the average value of 20.97 m calculated from all other available data was used ($SD = 1.59$, $N = 113$). Distance covered was established using GPS coordinates of the start point, i.e. the point at which the trawl is on the seabed and stable, and the coordinates of the endpoint, i.e. 30 min thereafter.

The bottom trawl used on the IGFS is not ideal for sampling jellyfish effectively, because they are likely to be distributed throughout the water column, or located in dense surface aggregations, although dead jellyfish can potentially be aggregated on the seabed (Billett et al., 2006; Yamamoto et al., 2008). However, because deployment and recovery is standardized as part of an international survey programme, i.e. it did not vary throughout the survey, the quantity of jellyfish sampled can be used as an index to reveal spatial and temporal patterns (Brodeur et al., 1999). The significance of the differences in catch-biomass between the subregions was tested using Wilcoxon rank-sum tests.

During the survey, an external temperature sensor and thermosalinograph (SEABIRD SBE38 and SBE21) continuously recorded temperature and salinity from 3 m below the surface (water intake on the hull). These data were used to describe the environmental context of each catch. Unfortunately, the sensors were only working well during the first leg of the cruise.

3. Results

In all, 140 valid hauls were conducted. The mean (\pm SD) distance travelled was 3.67 ± 0.25 km. The mean (\pm SD) spread of the net wings was 20.97 ± 1.59 m, and the mean (\pm SD) height of the headline was 4.09 ± 0.29 m. Sampling depths ranged from 21 to 436 m (Figure 2.1). A total of 283.5 kg of gelatinous organisms was caught (mean per haul 2.0 ± 16.5 kg). Overall, *Pelagia noctiluca* was the most abundant species recorded; it was present in 62.9% of the hauls, representing 92.9% of the overall wet weight of gelatinous species recorded during the survey. Other scyphozoan species were *Aurelia aurita* (present at 27.1% of the stations; 3.2% of overall wet weight), *Rhizostoma octopus* (four individuals present at four stations in the S subregion) and *Periphylla periphylla* (a single individual weighing 0.11 kg, in the SW subregion $51^{\circ}36'N$ $11^{\circ}06'W$). All *A. aurita* were in poor condition and were likely dead or decaying animals, whereas *R. octopus* individuals were in excellent condition, with bright blue colouration around the bell (bell diameter 17–31 cm, wet weight 1.15–2.04 kg). Unidentified salps (Phylum Urochordata) were present in 22.1% of the hauls, contributing another 1.8% to overall gelatinous wet weight. Unidentified pieces of gelatinous material (most likely pieces of torn medusa bells) accounted for <1% of the overall wet weight recorded. The spatial and quantitative distributions of the catch of the overall gelatinous material, *P. noctiluca*, *A. aurita*, and salps are presented in Figure 2.2 and Table 2.2.

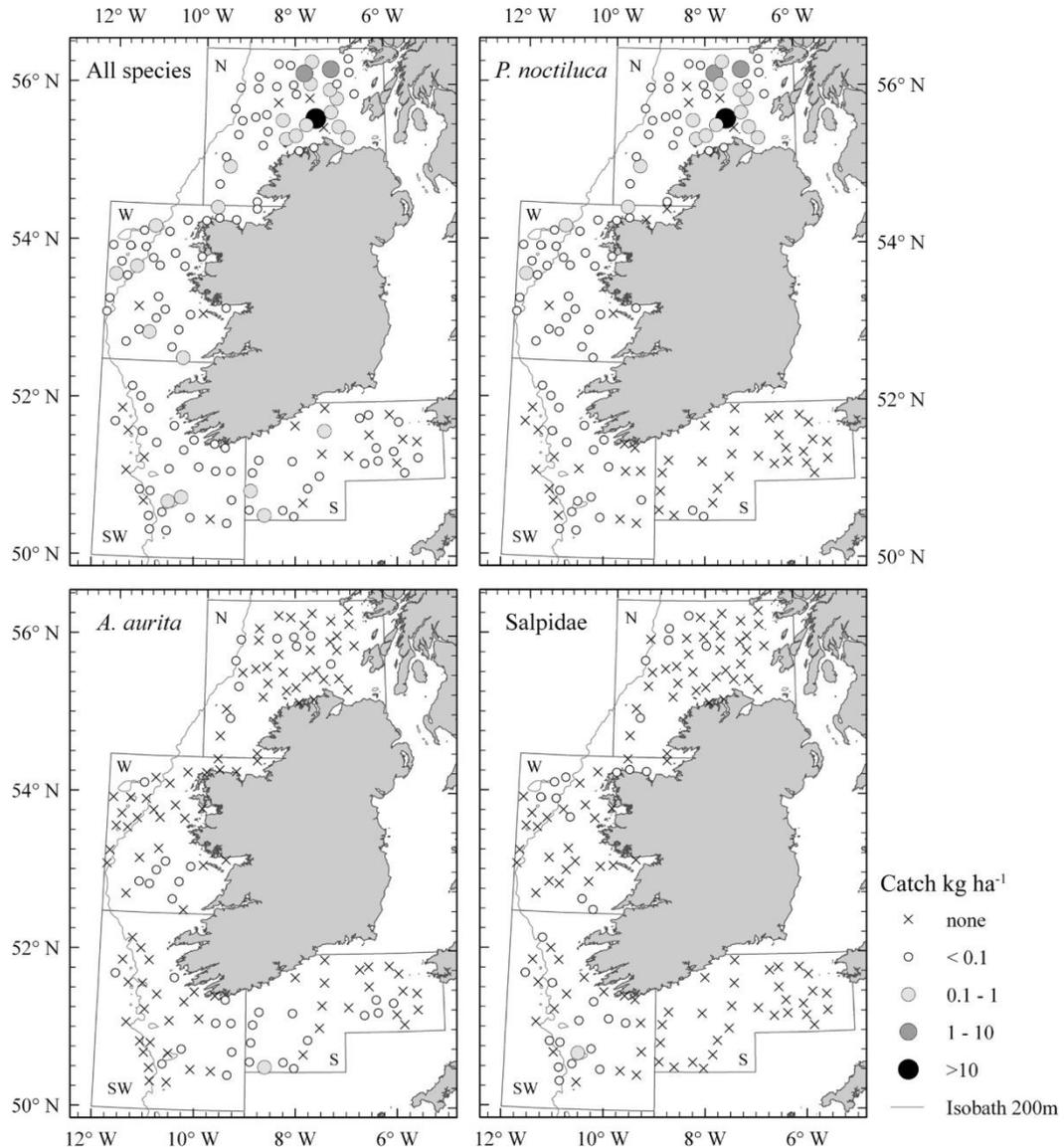


Figure 2.2. Distribution of gelatinous bycatch during the IGFS 2009.

A close-up of the *P. noctiluca* bycatch data in the N subregion is presented in Figure 2.3. The 200m isobaths is represented by a solid grey line.

The distribution of *P. noctiluca* was heterogeneous, with an apparent North–South gradient in density (Spearman’s rank correlation on density and latitude $r_s = 0.62$, $p < 0.001$). The N subregion yielded the highest biomass overall (mean catch rate 0.82 kg ha^{-1} , $\text{SD} = 4.2$), with *P. noctiluca* present at 90.4% of the stations. The same species was present at 88.9% of the stations of the W subregion and at 53.1% of the stations in the SW. Just five individuals were caught in the S. Table 2.2 summarizes *P. noctiluca* catches for each subregion. The catches in the N were significantly higher than those in the SW (Wilcoxon rank-sum $W = 934$, $p < 0.01$), but the difference between the N and W subregions was not significant ($W = 813$, $p = 0.57$). The difference between the W and

Table 2.2. Gelatinous bycatch experienced during the IGFS 2009.

Summary statistics based on standardised catch data (kg ha^{-1}) for each subregions of the study area. *N* is the number of stations per subregion, Frequency refers to the frequency of occurrence of each species, and % catch is the contribution of each species to the overall catch of gelatinous organisms in each subregion. Mean, median and SD are calculated over all stations, including zero stations. Statistics for the N subregion are presented (a) with and (b) without the single large catch of 196 kg (27.1 kg ha^{-1}) of *P. noctiluca* taken into account. Details for unidentified and rarely caught species (*R. octopus*) are not presented.

Taxon and parameter	Overall (<i>N</i> = 140)	North (a) (<i>N</i> = 42)	North (b) (<i>N</i> = 41)	West (<i>N</i> = 36)	Southwest (<i>N</i> = 32)	South (<i>N</i> = 30)
<i>Pelagia noctiluca</i>						
Frequency	0.64	0.90	0.90	0.89	0.53	0.07
% catch	93%	>99%	98%	72%	19%	0.5%
Mean	0.26	0.82	0.18	0.039	6.4×10^{-4}	1.7×10^{-4}
Median	0.0067	0.027	0.026	0.022	4.5×10^{-4}	0
SD	2.3	4.2	0.37	0.054	0.014	8.3×10^{-4}
Maximum	27.1	27.1	1.7	0.3	0.065	0.0045
<i>Aurelia aurita</i>						
Frequency	0.27	0.21	0.22	0.22	0.28	0.4
% catch	3%	0.5%	2%	10%	22%	60%
Mean	0.0084	0.0035	0.0036	0.0054	0.0072	0.020
Median	0	0	0	0	0	0
SD	0.024	0.0087	0.0088	0.014	0.019	0.044
Maximum	0.23	0.043	0.043	0.058	0.096	0.23
<i>Salpa</i> spp.						
Frequency	0.22	0.14	0.15	0.28	0.47	0
% catch	1.8%	<0.1%	0.1%	6.9%	51%	0
Mean	0.0049	1.8×10^{-4}	1.9×10^{-4}	0.0037	0.017	0
Median	0	0	0	0	0	0
SD	0.027	5.2×10^{-4}	5.3×10^{-4}	0.013	0.053	0
Maximum	0.30	0.0025	0.0025	0.073	0.30	0
Total catch						
Mean	0.28	0.83	0.18	0.054	0.033	0.034
Median	0.024	0.033	0.032	0.038	0.016	0.0095
SD	2.3	4.2	0.36	0.052	0.057	0.058
Maximum	27.1	27.1	1.7	0.31	0.30	0.23

SW subregions was significant ($W = 805$, $p < 0.01$). It is of note too that space and time were highly correlated, so any North–South gradient could also be the results of delays in

sampling (Spearman's rank correlation run on latitude and day of year, $r_s = 0.62$, $p < 0.001$).

Variation in abundance between stations was great within the N subregion, with catches of *P. noctiluca* ranging from zero to an exceptional 195 kg (27.1 kg ha^{-1}) between two stations located 17 km apart (Figure 2.3). Based on the wet weight of a random sample of 150 individuals (wet weight 1.27 kg), we estimated that this catch from ~30 km off the north coast of Ireland ($55^{\circ}37'N$ $07^{\circ}32'W$) contained >23,000 animals. Within the W and SW subregions, differences between stations were less pronounced and biomass was less (Table 2.2). The species was present over the full ranges of temperature ($11.4\text{--}14.7^{\circ}\text{C}$) and salinity ($34.13\text{--}35.58$ psu) experienced during the survey (Figure 2.4). An overall positive correlation was found between *P. noctiluca* catches and subsurface temperature ($r_s = 0.34$, $p = 0.002$) and salinity ($r_s = 0.22$, $p = 0.01$). However, there were no consistent pattern across individual subregions, but low sample size caused by sensor failure during the second and third legs rendered reliable analysis impossible. *P. noctiluca* catch rate (kg ha^{-1}) was not correlated with depth ($r_s = -0.02$, $p = 0.80$; alternative values if the catch of 27 kg ha^{-1} is excluded, $r_s = -0.005$, $p = 0.96$).

The bell diameter of individual *P. noctiluca* varied from 1 cm to 13.5 cm, with a median of 4.5 cm (SD = 1.2, $N = 4,116$; Figure 2.5). Small individuals (<4.5 cm) had a very thin/fragile/flexible yellowish or transparent bell, sometimes with triangular yellow/brown coloured markings. Large individuals (>5 cm) were usually characterized by having a thicker transparent bell with clear warts on top, and dark mauve gonads. Samples in the N had significantly larger median bell diameters than samples from the other subregions (Wilcoxon rank-sum test: N–W $W = 840$, $p < 0.01$; N–SW $W = 524$, $p < 0.001$; W–SW $W = 397$, $p < 0.01$), with an overall median bell diameter of 5.0 cm for the N ($N = 2,644$), 4.0 cm for the W ($N = 1,278$), and 3.5 for the SW ($N = 211$). Median bell diameter was not correlated to sample size in any subregion (Spearman's rank correlation: N $r_s = 6421.1$, $p = 0.1545$; W $r_s = 5605.5$, $p = 0.8817$; SW $r_s = 776.9$, $p = 0.855$). However, because of the significant correlation between time and space mentioned above, it was not possible to determine whether the interregional variation in size was attributable to an evolution of population with time or to different sizes being associated with different areas.

Based on the total wet weight of *P. noctiluca* at each station, divided by the number of individuals at each station, we calculated a mean (\pm SD) individual wet weight of 7.9 ± 5.9 g for the overall survey.

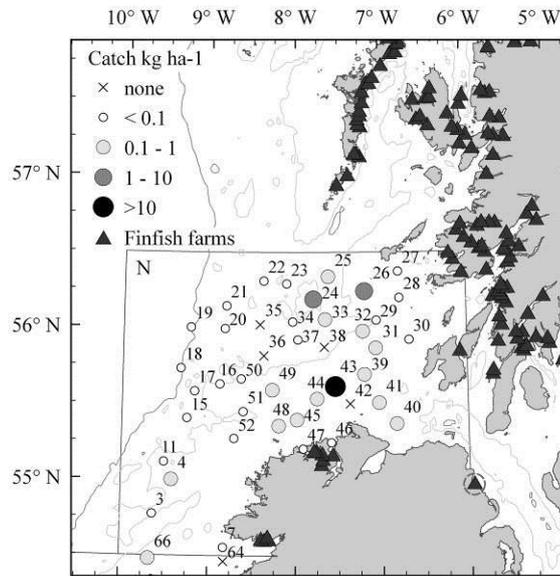


Figure 2.3. Distribution of *P. noctiluca* in the North subregion.

Jellyfish bycatch (kg ha^{-1}) is represented by plain circles (see legend), sampling stations with no jellyfish bycatch are figured by crosses. Dark triangles represent the position of fin fish farms, and a dashed grey circle identifies the Northern Irish farm where a massive fish kill happened in November 2007. Sampling station number is indicated to facilitate comparison with Figure 2.4. Solid grey lines are the 100 m (light grey) and 200 m (dark grey) isobaths.

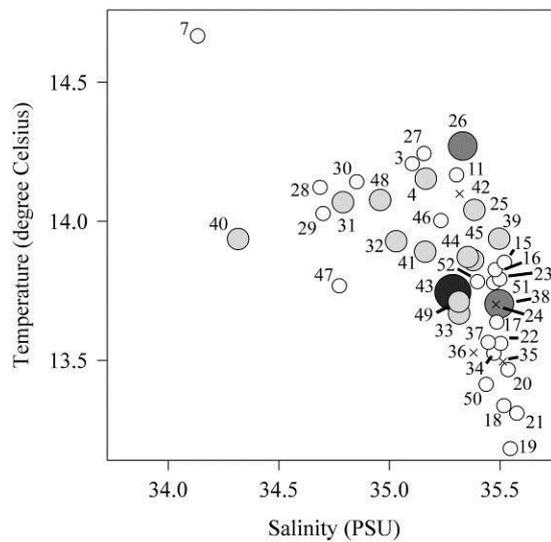


Figure 2.4. Environmental context in which *P. noctiluca* occurred in the North subregion.

Temperature and salinity (3 m subsurface) were measured at each station by means of an on-board temperature sensor and thermosalinograph. Sampling station number is indicated to facilitate comparison with Figure 2.3.

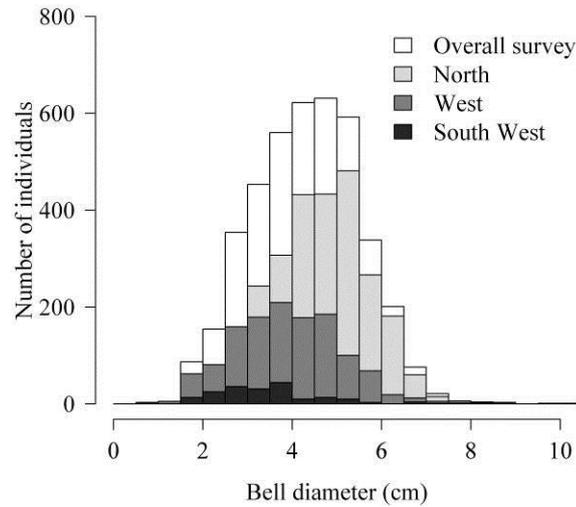


Figure 2.5. Size distribution of *P. noctiluca* caught during the IGFS in 2009.

Data are for the N (light grey, $N = 2,640$), W (grey, $N = 1,276$) and SW (dark grey, $N = 195$) subregions. The distribution for the overall survey is also represented (in white, $N = 4,116$). The five individuals caught in the S subregion are not shown.

4. Discussion

Our results show that the broad-scale distribution of *P. noctiluca* in the Northeast Atlantic is marked by a high level of heterogeneity at both small (between consecutive stations) and large (between subregions) scales (Figure 2.2 and Figure 2.3).

At the large scale, there was a clear north–south gradient, with largest catches in the N subregion, intermediate and small catches in the W and SW subregions, and an almost total absence in the S subregion (Figure 2.2). Drivers of this observed interregional variation are uncertain (especially given the delay between sampling in the N and the other subregions), but the highest densities in the N (Figure 2.2 and Figure 2.3) are most likely explained by the advection of a large pulse of oceanic water from the Rockall Trough (Figure 2.1) onto the continental shelf. The actual origin of *P. noctiluca* in the Rockall Trough area is uncertain, but with *P. noctiluca* generally considered to be a warm-water species (Russell, 1970), it is likely that either the Shelf Edge Current (a mid-water current running northward along the slope of the European continental shelf from the Iberian Peninsula up to Norwegian waters, White and Bowyer, 1997) or the North Atlantic Current (the branch of the Gulf Stream flowing toward Europe, Schmitz and McCartney, 1993) is the ultimate driver of the northern limit of the species (Figure 2.1). Fraser (1968) showed that, in the north, the overflow of oceanic waters peaks in September/October, but in the other areas sampled here, the seasonality of oceanic inflows is more uncertain. However it is of note that historical records report the presence

of *P. noctiluca* off the southwest coast of Ireland in November and even December in some years (reviewed in Russell, 1970). Offshore, over the Rockall Trough (Figure 2.1), the presence of the species has been documented in September, October, and November 2007 (Doyle et al., 2008; Baxter et al., 2010). The absence of the species in the south (except at two stations in the southwest of the survey area) likely reflects the relative isolation of the Celtic Sea from oceanic inputs at that time of year, as also indicated by the absence of salps in the catches there (Figure 2.2).

At a smaller scale, the high level of heterogeneity between stations reflects how jellyfish can form large highly localized aggregations. This horizontal patchiness was most striking in the N, with one estimated catch of >23,000 *P. noctiluca* (27.1 kg ha⁻¹) contrasting with its absence at the previous station, just 17 km away (Figure 2.3). Similar local heterogeneity in the catch of *P. noctiluca* has been documented in the Adriatic Sea using data from an ichthyoplankton survey (Piccinetti and Piccinetti-Manfrin, 1991), suggesting that this result is likely not a sampling artefact. The formation of such horizontal patchiness is usually a result of local hydrographic conditions (Graham et al., 2001), such as a current frontal system (Vanhöffen 1896, cited in Russell, 1970), a convergence zone (Piccinetti and Piccinetti-Manfrin, 1991; Sabatès et al., 2010), or the presence of Langmuir cells (Larson, 1992; Doyle et al., 2008). Unfortunately, there are no data available on the configuration of local currents at the time of the survey at a scale that could allow investigation of such patterns.

Within the N subregion, where catches of *P. noctiluca* were largest, analysis of environmental conditions at the different stations revealed that the species was found within a small temperature range (13.2–14.7°C), but within a relatively broad salinity range (34.13–35.58 psu; Figure 2.4). Therefore, although there was a large variation in individual catches (and similar variation in bell diameters between catches; Figure 2.5) in the N subregion, this variation could not be attributed to any particular environmental variable. Individual catches of *P. noctiluca* in the W and SW subregions were associated with lower temperatures but similar salinity values as in the N subregion, but because the timing of these hauls were from <4 to >9 weeks after the initial hauls, no broad-scale comparison between all stations sampled was possible. In the Mediterranean Sea, the species experiences much higher salinity (>37 psu) and temperatures (>23°C) (Piccinetti and Piccinetti-Manfrin, 1991; Yahia et al., 2003).

The insights into the distribution of *P. noctiluca* provided by our data are of main interest to the aquaculture industry. Indeed, as mentioned in the Introduction, *P. noctiluca* has

already caused serious damage to the industry (Merceron et al., 1995; Doyle et al., 2008; Hay and Murray, 2008). Considering that the aquaculture industry generates thousands of jobs and several million euros each year within the EU, and is expected to expand to meet the decline in wild fisheries catch (FAO, 2000), the potential threats posed by *P. noctiluca* blooms assume great importance.

Worryingly, our data highlighted the presence of large aggregations of *P. noctiluca* in an area where many aquaculture facilities are concentrated (Figure 2.3). This provides an interesting snapshot at a given time that could serve as a basis to develop early warning systems. Indeed, the recent application of a particle-tracking model to jellyfish spatial dynamics (Moon et al., 2010) indicates the potential for developing forecasting systems to plot the trajectory of these large aggregations and to estimate the probability that they may impact on aquaculture facilities. Data such as ours could be useful in defining realistic initial conditions for such simulations. In the meantime, mitigation measures such as the development of cost-effective barrier systems to deflect jellyfish incursions, e.g. bubble nets, need to be considered.

An additional use of jellyfish bycatch datasets collected over several years can be in supporting tools to investigate how climate and jellyfish occurrence/abundance are related (reviewed by Purcell, 2009). One of the best examples of such use comes from the Eastern Bering Sea, where more than 20 years of bycatch data from quantitative bottom-trawl surveys have described how jellyfish abundance in that area is responding to successive regional climate shifts (Brodeur et al., 2008a). Those results demonstrate that, although bottom-trawl surveys are not designed to sample planktonic species, they can still provide useful indices of jellyfish biomass. We believe that the data from the IGFS have the potential to provide such time-series for *P. noctiluca*, provided that species-specific records are maintained. Indeed, although other scyphozoan species tend to peak in summer (Doyle et al., 2007a; Houghton et al., 2007), some are found during autumn (Figure 2.2), and our results show that a catch of 0.18 kg ha^{-1} in the N subregion ($56^{\circ}20'N$ $7^{\circ}37'W$) consisted of >200 *P. noctiluca*, and that a similar catch (by weight) in the S subregion ($51^{\circ}38'N$ $7^{\circ}24'W$) was of a single *R. octopus* of 1.6 kg. The same happened, to a lesser extent, with catches of salps or *A. aurita* (Figure 2.2).

To conclude, it appears that jellyfish bycatch data not only provide information on the distribution of *P. noctiluca* at a scale and a resolution that has not been possible before in the Northeast Atlantic, but also offer one of the best available options to record year-on-year variations in the abundance of the species there. More generally, we believe that

such data can provide the necessary baseline to investigate how jellyfish populations are responding to changes in marine ecosystems (Richardson et al., 2009). For that reason, therefore, we urge that efforts to record jellyfish bycatch at a species level be maintained in future, and perhaps also extended to other national and international fisheries surveys.

Acknowledgements

Many thanks are expressed to all those involved in the IGFS of 2009; and to Kenneth D. Black (Scottish Marine Institute) and Hamish Rodgers for providing information on the locations of Irish and Scottish finfish farms. Temperature and salinity data were kindly provided by the Irish Marine Institute.

Chapter 3

Inter-annual and inter-regional distributions and abundances of *Aurelia aurita* and *Cyanea* spp. across the Irish Sea

Chapter 3 – Inter-annual and inter-regional distributions and abundances of *Aurelia aurita* and *Cyanea* spp. across the Irish Sea

The chapter presents data from year 2007 – 2010, collected by TB (2009 and 2010), MKS Lilley (2007 and 2009), SE Beggs (2007 – 2010) and D Haberlin (2010). TB performed all data analysis and writing up of the results as presented here.

Abstract

Identifying interactions between scyphomedusae and other components of the ecosystem requires information on their distribution and abundance. Four years (2007-2010) of jellyfish bycatch from a juvenile gadoid fish survey were analysed. An average of 76 stations distributed all across the Irish Sea basin were sampled each year, providing for the first time, spatially explicit information on the abundance of scyphomedusae for both the eastern and western part of the Irish Sea. Data from CTD profiles were extracted to investigate relationships between jellyfish abundance and environmental parameters (temperature, salinity, stratification index). Contrasting inter-annual variations of abundance were observed between different regions of the Irish Sea for *Aurelia aurita* and *Cyanea* species. No formal relationships could be found with environmental parameters. However, *A. aurita* were found to have a higher average biomass per individual in stratified waters than in mixed waters; potentially reflecting the difference of seasonal dynamics in the productivity of the different ‘marine landscapes’ of the Irish Sea. Such contrasting regional dynamics in jellyfish abundances should be considered when addressing potential interactions between scyphomedusae and other components of the ecosystem (e.g. fish larvae).

1. Introduction

Scyphozoan jellyfish are receiving increased recognition as key components of marine ecosystems (Pauly et al., 2009). Examples of ecological processes that they contribute to include: benthic-pelagic coupling (Pitt et al., 2008; Yamamoto et al., 2008), nutrient cycling (Pitt et al., 2009a), and control of invasive species outbreaks (Purcell and Cowan, 1995; Hosia and Titelman, 2011). However, the primary concern about jellyfish is about their potential impacts on commercially important species (especially fish) through competition and predation (Lynam et al., 2005b). For example, most scyphozoan jellyfish

feed primarily on crustaceans (mostly cladocerans and copepods) and gelatinous zooplankton (e.g. ctenophores, hydrozoans, or other scyphozoans), but are also known to feed on fish eggs, fish larvae and small juvenile fish (Purcell, 1991; Purcell and Arai, 2001; Barz and Hirche, 2007). Furthermore, as jellyfish populations may be increasing globally in response to climate change, overfishing, and modifications of coastal environments (e.g. eutrophication and the development of artificial structures), the impacts of jellyfish blooms (reviewed by Richardson et al., 2009) may be exacerbated.

A recent study has demonstrated that the Irish Sea pelagic ecosystem has undergone deep modifications since the 1980s, with the mean overall jellyfish biomass increasing in the western part of the basin since 1994 (Lynam et al., 2011, see Appendix B). The most abundant jellyfish species found in the Irish Sea is the moon jellyfish, *Aurelia aurita*. However, other species can be very abundant locally. These species are the barrel jellyfish (*Rhizostoma octopus*), the lion's mane jellyfish (*Cyanea capillata*), the blue jellyfish (*Cyanea lamarckii*), and the compass jellyfish (*Chrysaora hysoscella*) (Russell 1970). As mentioned in Chapter 1, the analysis of stranding events around Ireland and Wales (during 2003-2006) suggested that different jellyfish species occurred in distinct environments within the Irish Sea (Doyle et al., 2007a; Houghton et al., 2007). This spatial component of the different species is therefore a key element if the potential for competition with, and predation on, other species is to be established. This is particularly pertinent for fish species which may have spatially restricted spawning and nursery grounds (Fox et al., 2000; Armstrong et al., 2001; Bunn et al., 2004).

The Irish Sea is a complex environment, composed of different 'marine landscapes' (Golding et al., 2004). It is a semi-enclosed sea between Ireland and Great Britain. It opens into the Celtic Sea through Saint Georges Channel in the south, and onto the Malin Shelf through the North Channel in the north. The Irish Sea basin can be subdivided into two regions based on its bathymetry. The region east of the Isle of Man is relatively shallow with depths < 50 m, and is characterised by important river runoffs and the existence of a salinity front in Liverpool Bay. Conversely, the region west of the Isle of Man is characterised by a channel 100-150 m deep, running along a north-south axis between the St George's Channel and the North Channel (Figure 3.1). This region becomes seasonally stratified during spring and summer. The eastern and western regions present contrasting environments, within which ecological processes (e.g. primary production, fish spawning) present contrasting dynamics. In particular, seasonal production differs between mixed and stratified regions (Gowen et al., 1995), while spawning of commercially important species (fish and crustaceans) concentrates in

specific spawning grounds (Heffernan et al., 2004), and fish larvae are not randomly distributed (Dickey-Collas et al., 1996; Bunn et al., 2004). In consequence, any investigation of the potential for interaction of jellyfish with fish requires analysis of the spatial distribution of jellyfish.

Lynam et al. (2011) provided a solid analysis of the inter-annual variations and long-term evolution of the abundance of scyphomedusae in the western part of the Irish Sea. Their study was based on jellyfish bycatch data from the juvenile gadoid fish survey organised in the Irish Sea in late-May-early-June every year. Their analysis showed how the inter-annual variability of the mean jellyfish abundance correlated with sea surface temperature (SST), salinity and secondary production. The objective of the present chapter is to use similar data to describe, for the first time, the distribution and abundance of the different scyphozoan species in both the western and eastern parts of the Irish Sea. In contrast to the 15 year time-series available for the western part (Lynam et al., 2011), only 4 years of species-specific data are available across the entire basin (i.e. eastern and western basins of the Irish Sea). The present work therefore focuses on describing the spatial aspect of the records, and demonstrates how it varies from year to year. In addition, relationships between jellyfish abundance and environmental conditions defining the different ‘marine landscapes’ that make up the water column of the Irish Sea (i.e. temperature, salinity and stratification) are considered.

2. Methods

2.1. Data collection

Data on the distribution and abundance of scyphomedusae were collected during the annual juvenile gadoid fish survey organised by Agri-Food and Biosciences Institute, Northern Ireland (AFBI) in 2007, 2008, 2009 and 2010, using the *RV Corystès*. Each survey was organised as two legs. During the first leg (usually the last week of May), sampling stations located in the western Irish Sea were sampled. During the second leg, stations from the eastern half were sampled first (usually the first week of June) and then western stations were sampled a second time (second week of June) (Figure 3.1 and Table 3.1). The number of stations varied slightly from year to year depending on logistical and natural constraints (e.g. mechanical breakdown, bad weather). Details on sampling dates and numbers of stations for each region are presented for each year in Table 3.1.

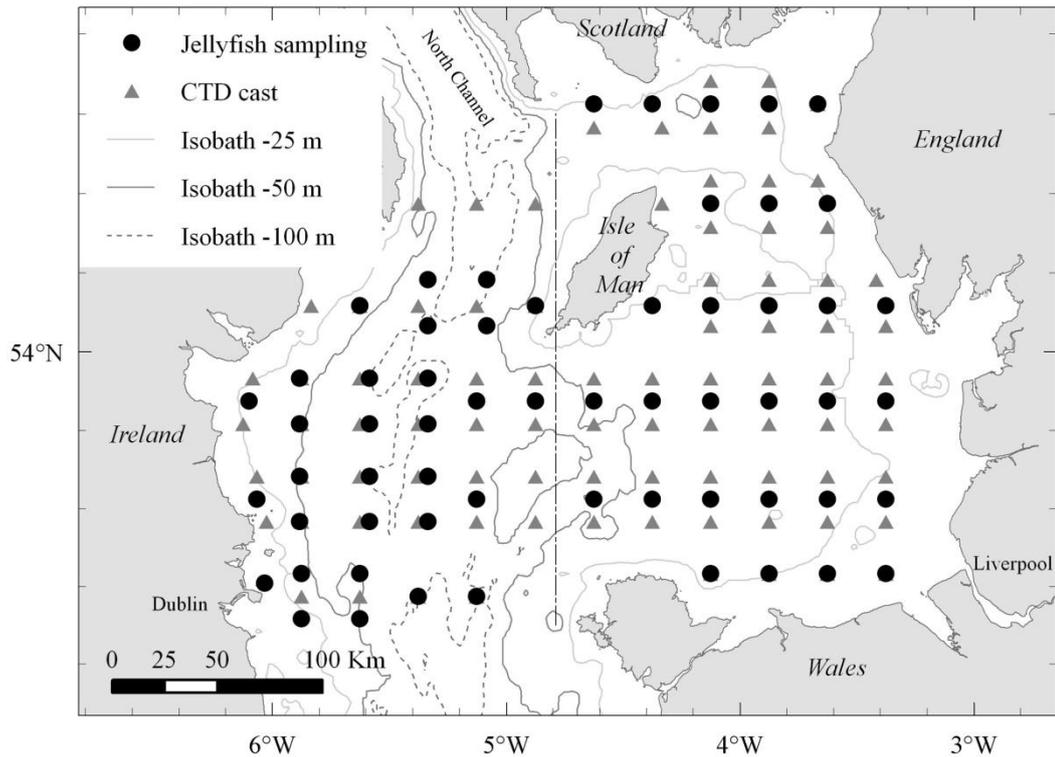


Figure 3.1. Sampling stations in the Irish Sea.

Details on the temporal organisation of the survey, for each year between 2007 and 2010 are presented in Table 3.1.

Sampling was by a 5 m² Methot Isaacs Kidd-net (5 mm mesh size, see Methot, 1986) towed in a single v-shaped profile at different stations distributed throughout the Irish Sea (Figure 3.1). Deployment was down to 3 m from the bottom and towing speed was adjusted to keep sampling-time within 10 min. At shallow stations, two consecutive v-shaped profiles were conducted within 10 min. A mechanical flowmeter (General Oceanics Model 2030R) was attached to the centre of the MIK net frame. Sampling was always at night time.

The catch was sorted as soon as the net was on board. Since 2007, scyphozoan jellyfish have been identified to species or genus level, and the total wet mass and the number of individuals per species recorded. Large catches were subsampled and the overall count and species-specific weight deduced from the fraction subsampled. For each station, the catch biomass (g) and the number of individuals were standardised by the volume filtered (m³), calculated from flowmeter readings.

Table 3.1. Sampling effort in the Irish Sea between 2007 and 2010.

Number of valid jellyfish sampling stations (N) and dates (in dd/mm) between which sampling took place in the eastern and western Irish Sea each year. Note that the western Irish Sea was sampled twice a year (Leg 1 and Leg 2).

Year	Leg 1		Leg 2			
	West		East		West	
	Dates	N	Dates	N	Dates	N
2007	29/05 – 01/06	24	03/06 – 08/06	27	10/06 – 14/06	25
2008	27/05 – 01/06	27	01/06 – 06/06	26	06/06 – 10/06	23
2009	26/05 – 30/05	25	02/06 – 06/06	26	06/06 – 11/06	30
2010	11/05 – 15/05	30	09/06 – 11/06	14	05/06 – 09/06	29

2.2. Environmental parameters

During daytime, a Gulf-VII fast plankton sampler (280 μm mesh) was deployed at a network of stations slightly different than the one used for MIK sampling, but covering the same area (Figure 3.1). In 2008, 2009, and 2010, a CTD profiler (SeaBird – SBE19plus) recording temperature and salinity, was attached to the GULF VII sampler. As for the MIK net, deployment was in v-shaped profiles (w-shaped profiles at shallow stations), down to 3 m from the bottom. The speed was adjusted so that sampling occurred within 15 min.

Data from CTD profiles were averaged by 0.5 m-depth bins. At each station, for each parameter, a ‘composite’ profile was calculated using the mean of the downward and upward value of each 0.5 m-depth bin. A running median filter (window width = 5 points) was run on the data to eliminate possible spikes in the profile. Profiles were visually inspected and validated. Then for each station, several parameters were extracted from the resulting composite profile:

- Maximum depth of the profile.
- Near surface temperature and salinity, calculated as the mean of the values between 2 and 3 m from the surface.
- Bottom temperature and salinity, calculated as the mean of the values from 2 m above the maximum depth of profile and the maximum depth of profiles.

In addition, a stratification index was calculated for each profile. The index proposed by Simpson (1981) was used. This index characterises the quantity of work (J m^{-3}) required to bring complete vertical mixing of the water column and is defined as follows:

$$\phi = \frac{g}{h} \int_{-h}^0 (\bar{\rho} - \rho) z dz$$

Where g is the acceleration of gravity (9.807 m s^{-2}), h is the maximum depth of the profile, ρ is the density at depth z , and $\bar{\rho}$ the average density of the profile.

The near surface salinity and Simpson stratification index were used to identify different types of water mass. Following Dickey-Collas et al. (1996), we used values of $\phi \leq 10$, and $\phi \geq 20$, to discriminate between mixed, intermediate and stratified waters. A value of near surface salinity of 33.5 was used to discriminate between ‘high salinity’ and ‘low salinity’ waters, and delimit marine landscapes as suggested by Golding et al. (2004) (these authors used a winter salinity of 34 as a limit).

In order to describe the environmental context of the catch, each jellyfish catch was associated with the data extracted from the closest CTD profile. For 48 sampling stations, the CTD was cast at approximately the same location where the jellyfish were caught. Sixty-nine jellyfish sampling stations were localised at mid-distance between two CTD stations; in this case we used the mean values calculated from the two profiles. Finally, for 95 jellyfish stations values from nearby stations (max distance = 21.7 km, 90% quantile = 6.5 km) were used. Twenty-five stations were excluded from the analysis involving environmental parameters due to the lack of corresponding CTD data. Elapsed time between CTD and jellyfish sampling ranged from < 1 hour to 4.5 days, with a median of 12.5 hours.

2.3. Statistical analysis

For each species, the existence of inter-annual differences of abundance across the entire basin was tested using Wilcoxon rank-sum tests. Similar procedures were used to test for differences between regions, and between years within each region. When comparing data from one year to data from another one, if an entire area had not been sampled both years, data from this area were excluded from the data of the year during which it had been sampled (e.g. the southern part of the eastern Irish Sea was not sampled in 2010,

therefore data collected in that area in other years were not taken into account when comparing these years with 2010). Statistics were performed on both volume-standardised biomass data (g m^{-3}) and density data ($\text{ind. } 100 \text{ m}^{-3}$).

The existence of differences in the distributions of *A. aurita* and *Cyanea* spp. was tested using the modified Cramér-von Mises statistic proposed by Syrjala (1996). It is a non-parametric inferential statistic to test for difference of spatial-distributions between two populations, and is particularly adapted to species that exhibit aggregative behaviour (Syrjala, 1996; Brodeur et al., 2002). The null hypothesis of the test is that the normalized distributions of the two populations (in our case species) are the same. The Syrjala-test is sensitive to differences in distribution, but is insensitive to differences in abundance between the two populations. The level of significance of the difference is determined by a randomization test. The Syrjala-test was also used to test for significant inter-annual differences in the distribution of each species. In this case, for each pair-comparison, the samples compared were restricted to stations sampled both years. A total of 999 iterations were used for the randomization procedure.

Spearman's rank correlation coefficient was used to investigate the possible existence of an association between *A. aurita* and *Cyanea* spp., since some studies have suggested significant interactions between *A. aurita* and *C. capillata* (Båmstedt et al., 1997; Hansson, 1997a). Correlation between jellyfish abundance (biomass and densities) and the available environmental parameters (see section 2.2.) were also investigated with Spearman's rank correlations.

All statistical analyses and computing were conducted in R (R Development Core Team, 2011). The 'oce' package was used to calculate densities from CTD profiles (Kelley, 2011). The Syrjala test was computed using the 'ecespa' package (De la Cruz, 2008). The detailed results of all statistical tests are reported in Appendix A.

3. Results

3.1. Catch summary

Between 2007 and 2010, a total of 306 valid tows were conducted with scyphozoan jellyfish present in 95.4% of them. The mean volume filtered ($X \pm \text{SD}$) was $4,671 \pm 1,788.95 \text{ m}^3$ (range 1,412 – 11,720 m^3). Depth in the sampling area was between 4 and 130 m (mean = 61.4 m). The summary of catches for each year is presented in Table 3.2.

Considering the data from the second leg (entire Irish Sea in early June), the overall annual mass (wet weight) of jellyfish catch was estimated to be 178, 312, 636, and 243 kg in 2007, 2008, 2009 and 2010 respectively. Overall, *Aurelia aurita* represented 77.7% of the catches (wet weight) and *Cyanea* spp. (*Cyanea lamarckii* and *Cyanea capillata*) 21.5%, however the contribution of each species varied greatly between regions and between years (Table 3.2). Large *C. capillata* and *C. lamarckii* can be easily distinguished by their colours (*C. capillata* is red-brown, *C. lamarckii* is blue). However, small medusae of both species can have a transparent yellowish coloration. Species identification has therefore to be based on the number of tentacles and the presence or absence on the muscle folds of pit-like intrusions from the gastrovascular cavity (Russell 1970). Unfortunately, time and logistical constraints during the cruise did not allow for reliable observations of these characteristics, and results are therefore reported at the genus level. The only other scyphozoan caught was the compass jellyfish (*Chrysaora hysoscella*), but it was only marginally present (totals of 16 individuals in 2007, 131 in 2008, 1 in 2009, and 1 in 2010).

To avoid bias due to delay in sampling, only data from stations sampled during the second leg were considered for further analysis. The overall mean ($X \pm SD$) volume standardised biomass of *A. aurita* in early June was $1.32 \pm 3.92 \text{ g m}^{-3}$ (median = 0.13 g m^{-3} , $N = 200$), and for *Cyanea* spp. it was $0.34 \pm 0.74 \text{ g m}^{-3}$ (median = 0.09 g m^{-3} , $N = 200$).

3.2. Inter-annual variations of abundances and distributions of scyphomedusae across the study area

Across the entire basin, significantly higher abundance (biomass and densities) of *Cyanea* spp. were found in 2007 compared with other years (Wilcoxon rank-sum test, detailed results presented in Appendix A), whereas *A. aurita* was significantly more abundant in 2009 (Figure 3.2, Tables A.1 and A.2).

The distribution of each species across the study area in early June significantly differed from one year to the next (Syrjala tests on density data, Table A.3 and Table A.4 for full details). Spearman's rank correlation coefficient was used to investigate the association between the two species. The biomass (g m^{-3}) of *A. aurita* was positively and significantly correlated with the biomass of *Cyanea* spp. only in 2007 and 2008.

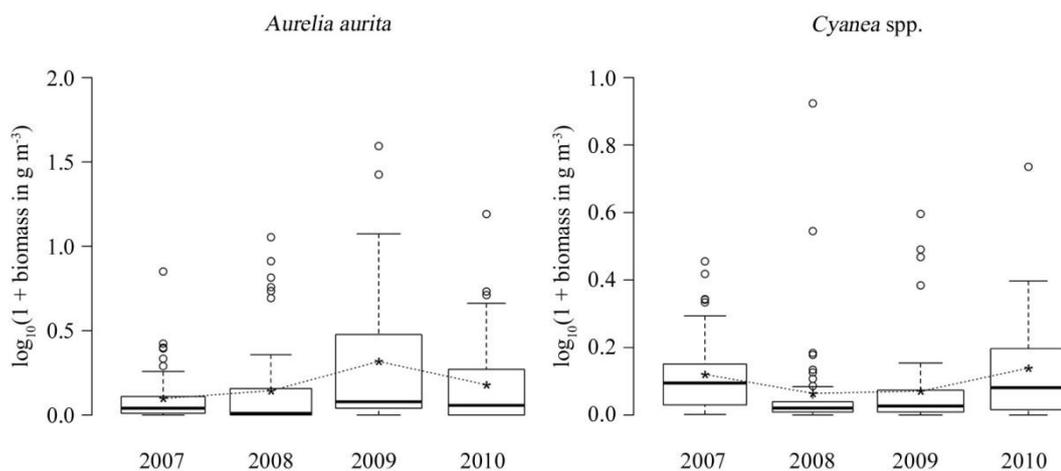


Figure 3.2. Inter-annual variations of biomass of *A. aurita* and *Cyanea* spp.

Data from the East and West (second sampling only) of the Irish Sea are combined here. Dashed lines were drawn between annual means (marked by black asterisks) to guide the eye. Statistical comparisons between years are presented in Tables A.1 and A.2 of appendix A.

No significant correlation was found for any year when considering densities (ind. 100 m⁻³) (Table A.5). When comparing the distribution of the biomass of the two species, *A. aurita* was found to be significantly differently distributed across the Irish Sea from *Cyanea* spp. in 2008 and 2010; when densities were considered, the distribution of the two species was significantly different in every year except in 2009 (Table A.6).

3.3. Inter-regional variations of jellyfish abundance

Within the study area, the eastern and western regions exhibited contrasting inter-annual patterns in abundance and densities of *Aurelia aurita* and *Cyanea* spp. (Figures 3.3 and 3.4). The differences in abundance between the eastern and western regions were more pronounced for *A. aurita*, however, their statistical significance varied from year to year (Tables A.7 and A.8). In the western part (data from early June only), the biomass per volume (g m⁻³) of *A. aurita* did not vary significantly between years, while for *Cyanea* spp. only the catches from 2007 were found to be significantly higher than those in other years. The densities (ind. 100 m⁻³) of both species were significantly different in 2007 from all other years (lower for *A. aurita*, higher for *Cyanea* spp.; see Table 3.2 and details of statistics in Tables A.9, A.10, A.11, and A.12).

In the eastern part, most inter-annual variations were statistically significant for both species when considering volume-standardised biomass (g m⁻³) (Tables A.9 and A.11). Most inter-annual variations of density of *A. aurita* were also found to be significant;

however, inter-annual variations of density (ind. 100 m⁻³) of *Cyanea* spp. were non-statistically significant (except when comparing 2007 with 2009, Table A.10 and A.11). For *A. aurita*, the northern part of the east basin exhibited a particular high degree of inter-annual variations with large quantities caught there in 2009, while in 2010 and 2008 only small catches occurred in that region (Figures 3.3 and 3.4). In fact, the median density (ind. 100 m⁻³) of *A. aurita* in the eastern Irish Sea in 2009 was >22 times higher than the median density of 2008 (and 6.7 and 9.3 times higher than in 2007 and 2010 respectively, see Table 3.2).

In the western part, no significant change was observed that year compared with other years. Unfortunately insufficient sample size, did not allow for comparison of distribution patterns within each region using the Syrjala statistics as was done for distributions across the entire basin.

Table 3.2. Catches of *A. aurita* and *Cyanea* spp. in the Irish Sea between 2007 and 2010.

Each year, the western region was sampled twice (see Table 2.1 for details). “Frequency pres.” is the frequency of occurrence of each species in the sampling events of each region; “% total catch” is the contribution of each species to the overall wet weight of scyphomedusae for each region.

	West 1					West 2					East					West 2 and East				
	2007	2008	2009	2010	overall	2007	2008	2009	2010	overall	2007	2008	2009	2010	overall	2007	2008	2009	2010	overall
<i>All scyphomedusae</i>																				
n stations	24	27	25	30	106	25	23	30	29	107	27	26	26	14	93	52	49	56	43	200
Frequency pres.	0.96	0.93	0.92	0.87	0.92	1.00	0.96	1.00	0.83	0.97	1.00	0.92	1.00	1.00	0.98	1.00	0.94	1.00	0.95	0.98
Total catch (kg)	103	21	87	94	305	81	197	305	187	770	97	115	331	56	599	178	312	636	243	1369
<i>Aurelia aurita</i>																				
Frequency pres.	0.83	0.52	0.60	0.70	0.66	0.80	0.83	0.87	0.76	0.81	0.85	0.54	0.96	0.64	0.76	0.83	0.67	0.91	0.72	0.79
% total catch	0.73	0.68	0.91	0.97	0.85	0.48	0.95	0.83	0.86	0.83	0.60	0.32	0.97	0.09	0.71	0.54	0.72	0.91	0.69	0.78
Mean	0.71	0.11	0.84	1.21	0.73	0.31	1.58	2.36	1.42	1.45	0.43	0.23	3.49	0.10	1.18	0.37	0.86	2.89	0.99	1.32
Median	0.15	0.007	0.16	0.005	0.029	0.16	0.24	0.19	0.38	0.21	0.06	0.0023	0.29	0.010	0.049	0.10	0.023	0.20	0.139	0.13
SD	2.18	0.18	1.93	2.29	1.87	0.45	2.82	7.26	2.84	4.29	1.19	0.80	5.87	0.28	3.47	0.91	2.11	6.60	2.41	3.92
Maximum	10.57	0.49	8.61	7.24	10.57	1.65	10.32	38.25	14.52	38.25	6.09	3.94	25.63	1.08	25.63	6.09	10.32	38.25	14.52	38.25
Mean	0.30	0.08	0.37	1.86	0.71	0.10	0.70	1.51	0.68	0.78	0.50	0.35	3.72	0.10	1.27	0.31	0.52	2.52	0.49	1.01
Median	0.10	0.01	0.08	0.04	0.04	0.06	0.12	0.14	0.17	0.12	0.06	0.02	0.40	0.06	0.06	0.06	0.02	0.24	0.09	0.09
SD	0.81	0.13	0.97	3.47	2.07	0.12	1.38	5.07	1.38	2.86	1.41	1.05	5.13	0.17	3.18	1.03	1.21	5.18	1.16	3.02
Maximum	3.92	0.42	4.75	12.01	12.01	0.46	5.47	27.48	6.71	27.48	7.11	4.07	17.76	0.63	17.76	7.11	5.47	27.48	6.71	27.48
<i>Cyanea spp.</i>																				
Frequency pres.	0.96	0.89	0.84	0.67	0.83	1.00	0.91	0.93	0.90	0.93	1.00	0.85	0.88	1.00	0.92	1.00	0.88	0.91	0.93	0.93
% total catch	0.19	0.30	0.09	0.03	0.12	0.49	0.05	0.17	0.13	0.16	0.41	0.63	0.02	0.91	0.28	0.44	0.26	0.09	0.31	0.22
Mean	0.18	0.05	0.08	0.02	0.08	0.34	0.08	0.37	0.22	0.26	0.40	0.48	0.09	1.06	0.43	0.37	0.29	0.24	0.49	0.34
Median	0.09	0.02	0.05	0.01	0.03	0.23	0.05	0.09	0.08	0.08	0.24	0.03	0.06	0.96	0.14	0.24	0.048	0.06	0.205	0.09
SD	0.23	0.08	0.10	0.03	0.14	0.42	0.11	0.73	0.33	0.48	0.43	1.49	0.10	1.07	0.96	0.42	1.10	0.55	0.77	0.74
Maximum	0.99	0.39	0.36	0.12	0.99	1.85	0.53	2.94	1.42	2.94	1.62	7.39	0.43	4.44	7.39	1.85	7.39	2.94	4.44	7.39
Mean	0.43	0.23	0.22	0.13	0.24	1.11	0.18	0.87	0.16	0.58	1.79	3.56	0.59	0.83	1.81	1.46	1.97	0.74	0.38	1.15
Median	0.25	0.107	0.13	0.0752	0.1093	0.25	0.14	0.16	0.12	0.16	1.12	0.4746	0.40	0.502	0.564	0.60	0.163	0.25	0.171	0.24
SD	0.60	0.36	0.23	0.15	0.37	2.42	0.14	1.79	0.13	1.55	2.23	10.70	0.63	0.85	5.84	2.33	7.91	1.38	0.58	4.18
Maximum	2.51	1.36	0.81	0.55	2.51	11.88	0.51	8.20	0.56	11.88	9.44	52.87	2.70	2.63	52.87	11.88	52.87	8.20	2.63	52.87

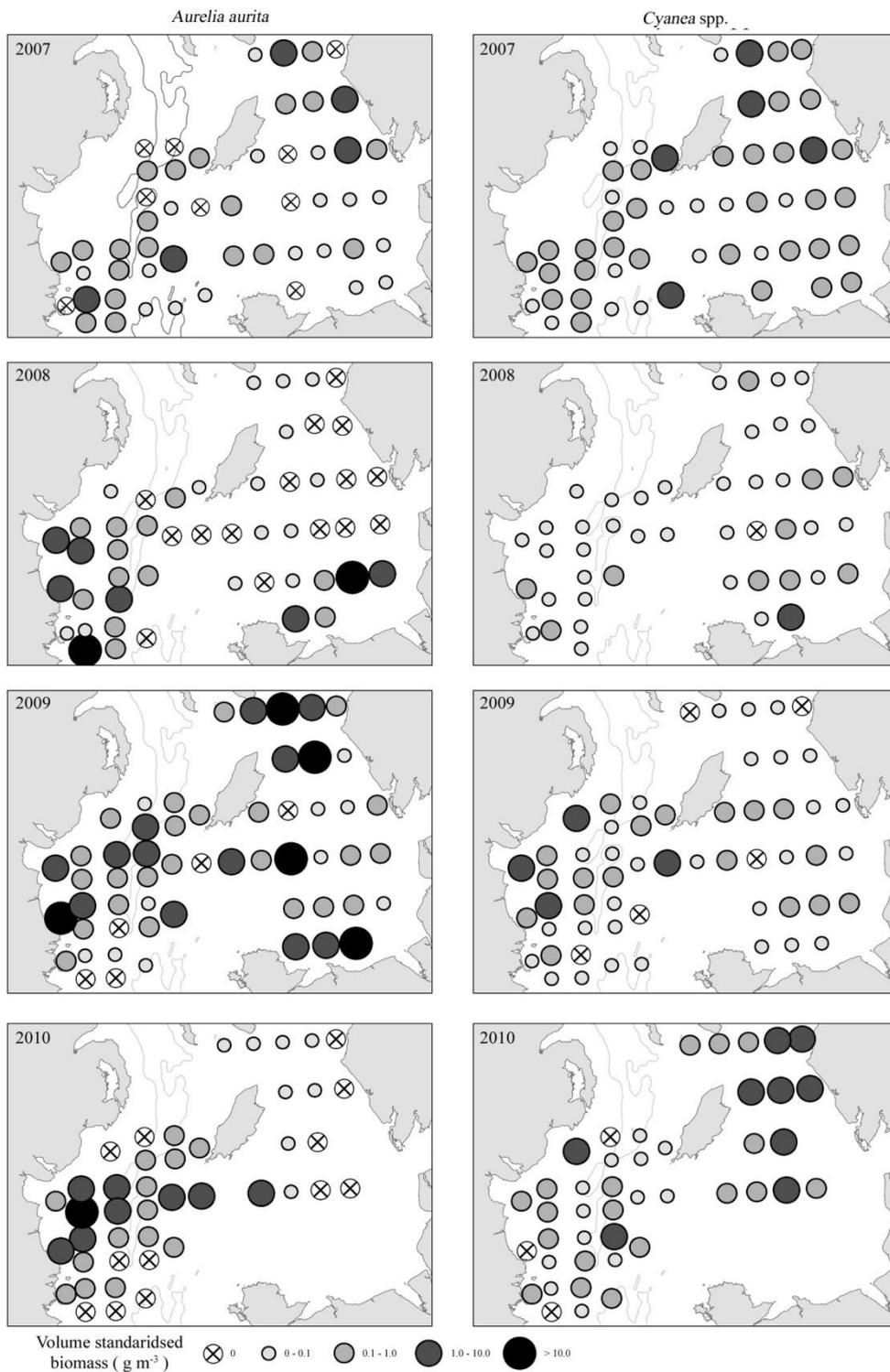


Figure 3.3. Volume standardised biomass (g m^{-3}) of *A. aurita* and *Cyanea* spp. in the Irish Sea in early June 2007-2010.

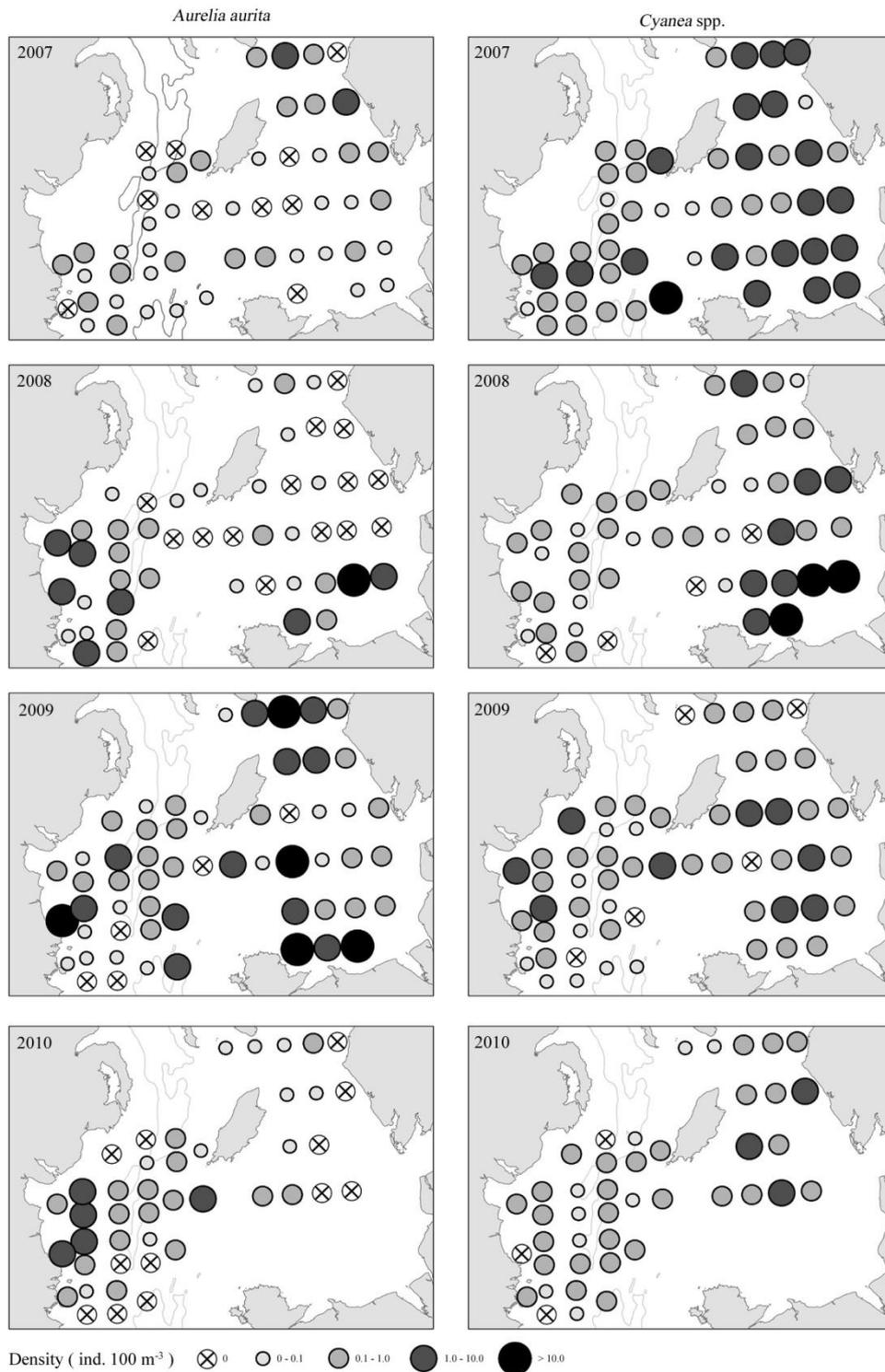


Figure 3.4. Densities (ind. 100 m⁻³) of *A. aurita* and *Cyanea* spp. in the Irish Sea in early June 2007-2010

3.4. Environmental context

The distribution of near-surface temperatures, salinity, and limits of mixed and stratified waters during sampling in early June 2008, 2009 and 2010 are presented in Figure 3.5. The eastern and western parts of the Irish Sea exhibited contrasting inter-annual variability. For example, temperature was higher in the west in 2010 compared with 2009, but no marked inter-annual difference was observed in the east. Conversely, important differences in salinity between 2009 and 2010 were observed in the east, but they were only moderate in the west (Figure 3.5).

Significant correlations were found between the abundance (both density and biomass) of *Cyanea* spp. and the various environmental parameters tested (positive correlations with temperatures, negative with salinities and depth), except in the case of the stratification index. The abundance of *A. aurita* was found to be significantly correlated (negatively) only with near-surface temperatures. The density of *A. aurita* was also significantly correlated with depth (Table 3.3).

3.5. Jellyfish condition

In the absence of exhaustive individual bell diameter and wet weight data, an estimated average mass (wet weight) per individual (g ind.^{-1}) was calculated for each station and for each species, by dividing the catch biomass by the total number of individuals in the catch.

For both *A. aurita* and *Cyanea* spp. the ratio was greater to a highly significant extent in the west region compared with the east (*A. aurita*: $W = 5,277$, $p < 0.001$, $N_{\text{west}} = 81$, $N_{\text{east}} = 69$; *Cyanea* spp.: $W = 5,973$, $p < 0.001$, $N_{\text{west}} = 100$, $N_{\text{east}} = 87$) (Figure 3.6). When considering water types, the ratio was found to be greater to a highly significant level in high salinity stratified waters than in high salinity mixed waters (*A. aurita*: $W = 572$, $p < 0.001$, $N_{\text{stratif}} = 45$, $N_{\text{mixed}} = 45$; *Cyanea* spp.: $W = 1,106.5$, $p = 0.001$, $N_{\text{stratif}} = 58$, $N_{\text{mixed}} = 58$). In low salinity waters the ratio was also higher in stratified than in mixed (Figure 3.7), but the difference was not statistically significant.

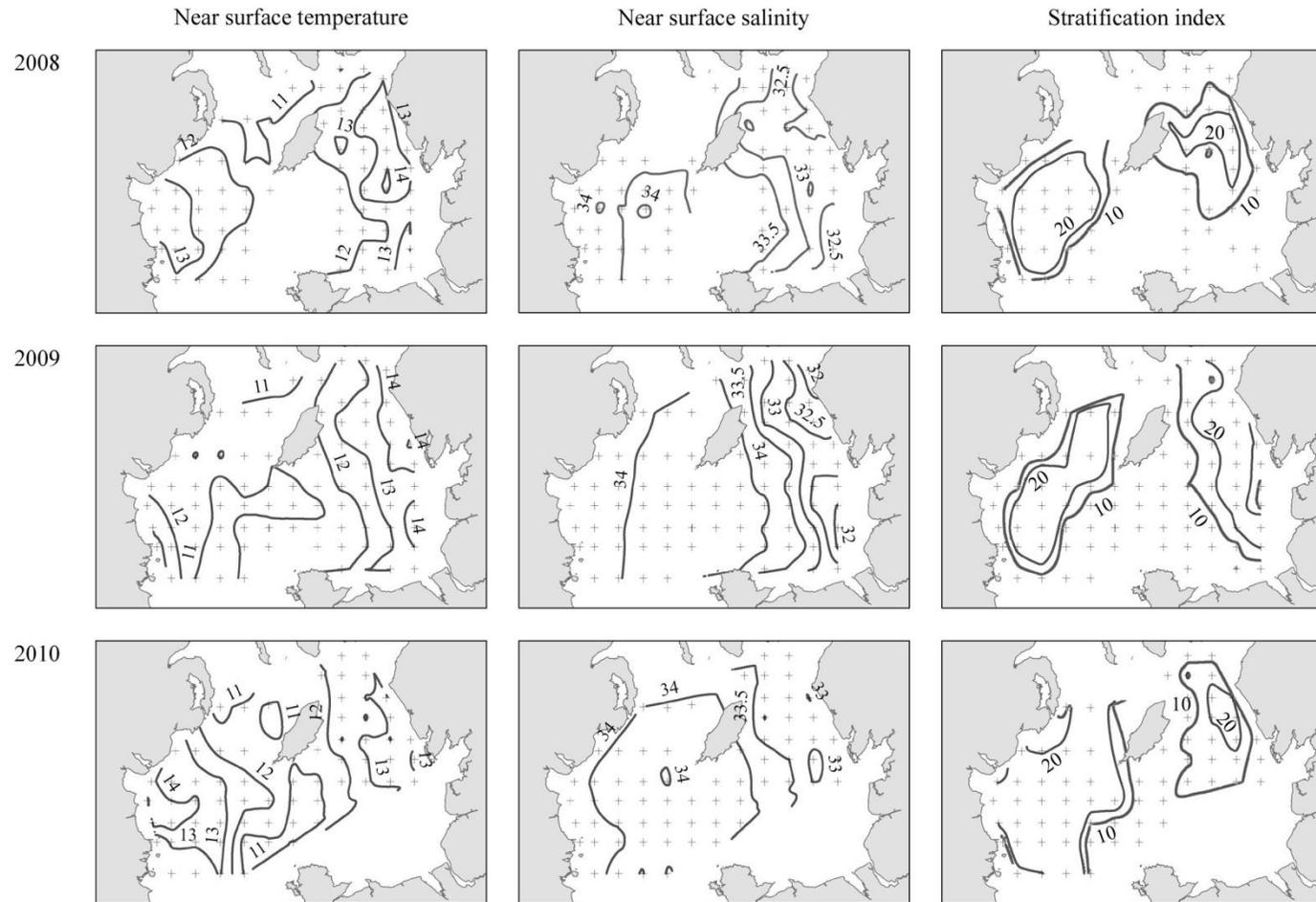


Figure 3.5. Near surface temperature and salinity, and stratification index in the Irish Sea in early June 2008-2010.

For the stratification index, only the 10 and 20 isolines were drawn as they are the values delimiting stratified and mixed waters. Lines were generated after natural neighbour joining interpolation (grey crosses mark the positions of sampling stations).

Table 3.3. Correlations between scyphomedusae abundance and condition index with environmental parameters.

rho is Spearman's rank correlation coefficient and *p* the associated *p*-value. Near surface and bottom salinity and temperatures are labelled as 'surface' and 'bottom' in the table. See material and methods for further details.

		<i>Aurelia aurita</i>						<i>Cyanea</i> spp.					
		Biomass (g m ⁻³)		Density (ind. 100 m ⁻³)		Condition index (g ind ⁻¹)		Biomass (g m ⁻³)		Density (ind. 100 m ⁻³)		Condition index (g ind ⁻¹)	
		rho	<i>p</i>	rho	<i>p</i>	rho	<i>p</i>	rho	<i>p</i>	rho	<i>p</i>	rho	<i>p</i>
Temperature	Mean	0.060	0.387	0.092	0.185	-0.067	0.414	0.290	<0.001	0.362	<0.001	-0.003	0.963
	Surface	0.173	0.012	0.150	0.030	0.246	0.002	0.392	<0.001	0.326	<0.001	0.241	0.001
	Bottom	-0.026	0.706	0.019	0.785	-0.160	0.051	0.193	0.005	0.299	<0.001	-0.108	0.144
Salinity	Mean	-0.094	0.182	-0.128	0.068	0.267	0.001	-0.274	<0.001	-0.408	<0.001	0.059	0.431
	Surface	-0.082	0.245	-0.107	0.128	0.223	0.007	-0.269	<0.001	-0.369	<0.001	0.007	0.929
	Bottom	-0.093	0.187	-0.130	0.064	0.282	0.001	-0.260	0.000	-0.400	<0.001	0.072	0.336
Stratification index		0.125	0.075	0.066	0.346	0.384	<0.001	0.130	0.063	-0.011	0.874	0.281	<0.001
Depth (m)		-0.039	0.500	-0.121	0.036	0.316	<0.001	-0.249	<0.001	-0.366	<0.001	0.087	0.148

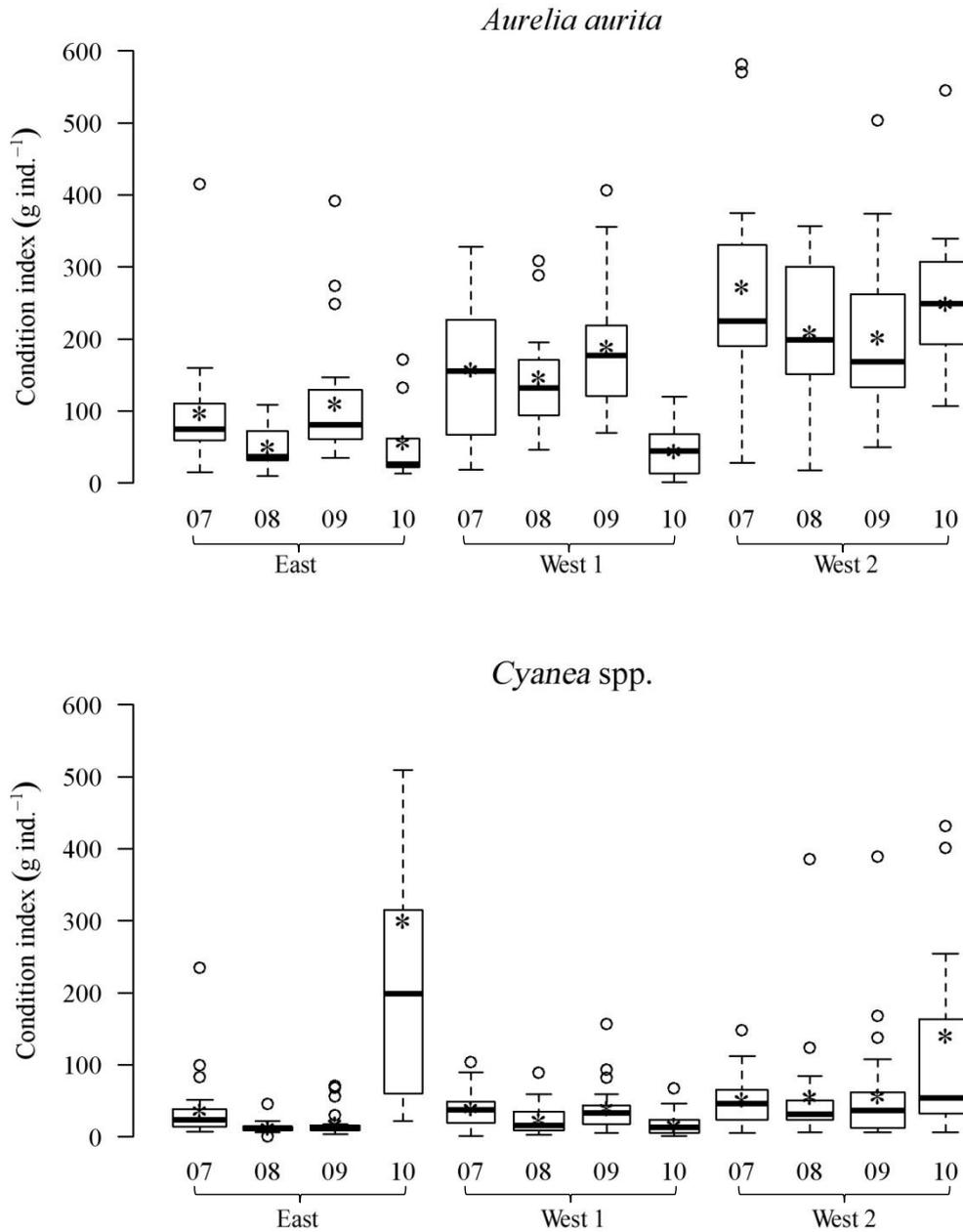


Figure 3.6. Inter-annual and inter-regional variations of the condition index (g ind.⁻¹) of *A. aurita* and *Cyanea* spp.

Years and region are indicated in x-axis. West 1 and West 2 refer to sampling of the western region of the Irish Sea during the first and the second leg of each year, respectively. Please note that to avoid too much distortion of the bottom graph, higher limit of y-axis of *Cyanea* spp. was limited: as a result the following 2 points from 2010 are not visible: a point at 1,849.2 g ind.⁻¹ in the eastern region, and a point at 978.5 g ind.⁻¹ in the western region (2nd leg).

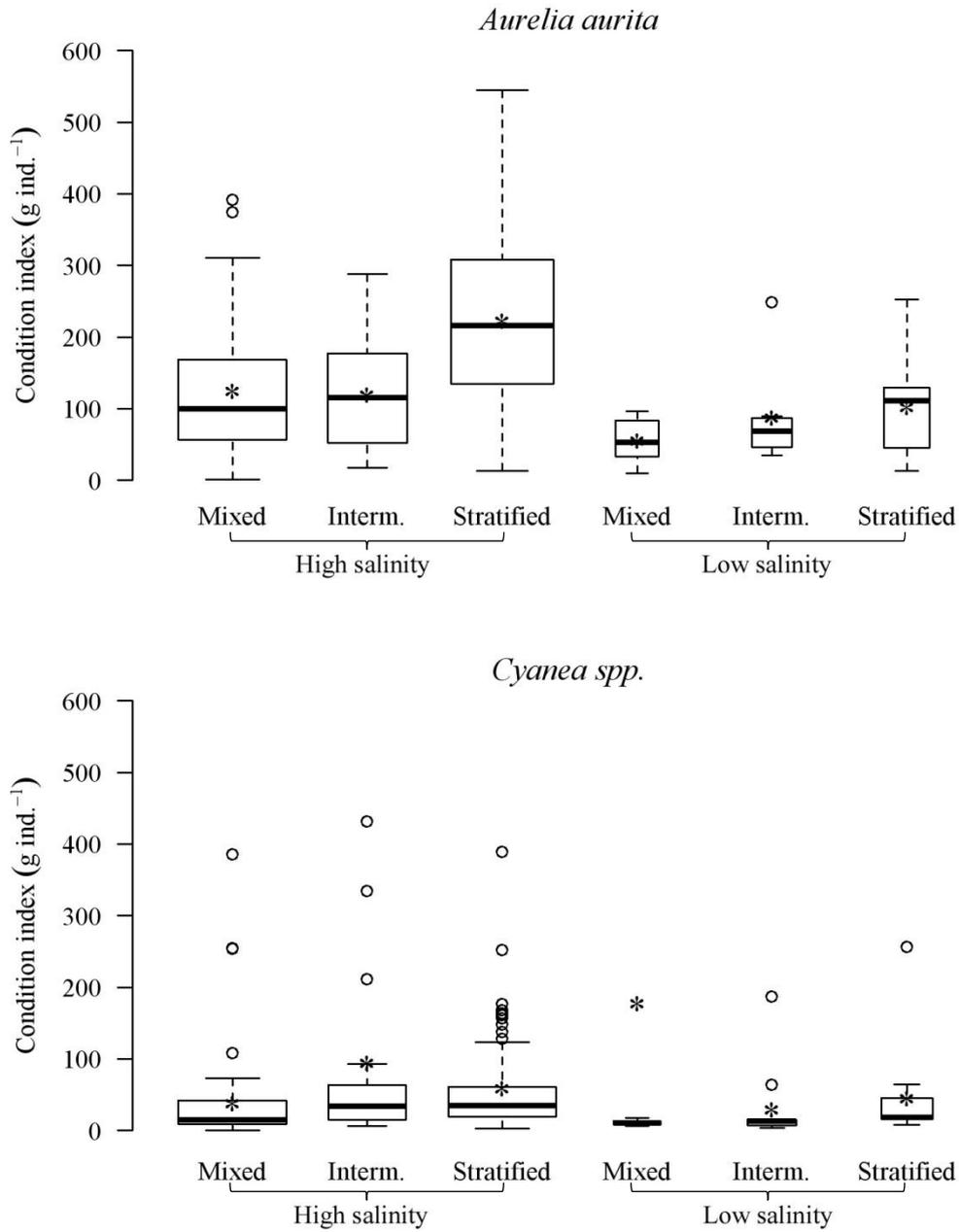


Figure 3.7. Variations in the condition index of *A. aurita* and *Cyanea* spp. in different water types.

The definition of the different water types was based on the stratification and the near-surface salinity in early June each year; see material and methods for details. Please note that to avoid too much distortion of the bottom graph, higher limit of y-axis of *Cyanea* spp. was limited: as a result the following 2 points are not visible: a point at 978.5 g ind.⁻¹ in intermediate highly saline waters and a point at 1,849.2 g ind.⁻¹ for mixed and low salinity waters.

4. Discussion

The distributions and abundances of *Aurelia aurita* and *Cyanea* spp. were found to vary differently between years and between regions, indicating the existence of regional specific dynamics, with catches from the eastern part of the Irish Sea basin exhibiting more year to year variability than the catches from the western part of the basin. Within the eastern part of the basin, contrasting dynamics were recorded between the north and south.

With only four years of data, it would be unreasonable to try to establish definitive conclusions concerning the factors driving the inter-annual variations reported here. In the western Irish Sea, the catches of all scyphomedusae (without species-specific details) have been recorded since 1994 and analysis of the resultant 15 year time series (1994-2009) showed that the annual mean catch (volume-standardised biomass) correlated positively with sea surface temperatures from the previous 18 months and with the copepod biomass of the previous year, but negatively with spring precipitation (Lynam et al., 2011; see Appendix B). These findings highlighted the importance of (i) food availability to the previous jellyfish generation, and (ii) environmental conditions that can influence polyp growth and the production of ephyrae.

Considering the differences in the morphology of the eastern and western regions of the Irish Sea basin, it would not be surprising that environmental factors varied differently from year to year in each of these regions. In particular, the eastern region is much shallower and under a noticeably stronger influence of rivers runoff than the western region (Dickson and Boelens, 1988); two factors that can only add to the variability of the system. The data presented in the current work provide snap-shots of environmental conditions in each basin in early June 2008, 2009, and 2010, and confirm that environmental factors do not vary in the same way from year to year in the different regions of the basins (Figure 3.5). Comparable regional-specific inter-annual variations were documented in the North Sea, where jellyfish populations of hydrographically distinct regions of the basin responded differently to the North Atlantic Oscillation (Lynam et al., 2005a).

Some differences were observed in the inter-annual variations of jellyfish abundances depending on whether abundances were considered in terms of biomass or densities (Figures 3.3 and 3.4, and Tables A.9 to A.12). Such discrepancies probably indicate that the factors that influence the rate of production of medusae (via polyp strobilation and

ephyral development), and those that influence the rate of individual medusan growth, are likely to be different.

The ratio (wet weight / number of individuals) was used in the present study as an ‘index of condition’ reflecting the average wet weight per individual for each species, in each catch. Interestingly, for both species, the ratio was significantly higher in the western region than in the eastern region; suggesting that, at the time of the survey, individuals in the west were on average larger than in the east (Figure 3.6). Differences in the timing of the onset of the production season might help to explain these differences of size. Coastal areas in the western part of the basin (east coast of Ireland) are known to have a production season starting early in the year (March-April) followed by production in more offshore regions (May-June) (Gowen et al., 1995). Conversely, the spring bloom seems to occur in May in Liverpool Bay (eastern Irish Sea) (Foster et al., 1982), and data from the Continuous Plankton Recorder programme indicated a peak in the colour index (an index of phytoplankton abundance) in June, followed by a peak in copepod abundance in July in this region (Edwards and Johns, 2003). Therefore, if the production of medusae is in tune with the production season (following the classical match-mismatch hypothesis of Cushing, 1974), younger (and therefore smaller and lighter) medusae might be expected in the eastern region in comparison with the western region at the time of the survey.

Within the western region (or more exactly within ‘highly saline waters’), the average wet weight per individual of both species was significantly higher in stratified waters than in mixed waters (Figure 3.7). Several studies have reported that the stratified region of the western Irish Sea supports a higher daily primary production and zooplankton biomass (or standing stock) than mixed regions (Fogg et al., 1985; Williams et al., 1994; Gowen et al., 1995). Such a difference might provide better feeding conditions for scyphomedusae in the stratified region, and may explain the higher wet weight per individual observed, as well as the significant correlation observed between the condition indices of both species and stratification indices (Table 3.3). Such links between food availability and stratification has been suggested by other authors for sprat larvae in the Irish Sea (Coombs et al., 1992).

In terms of environmental conditions, the abundances of *Cyanea* spp. were significantly correlated with most environmental parameters (mean, near-surface, and near-bottom temperature and salinity), whereas the abundances of *A. aurita* were not, except for near-surface temperature (Table 3.3). Considering the size (as indicated by the median of the

condition index) of the medusae caught during the early June cruise, it is likely that *A. aurita* (median condition index = 130.6 g ind⁻¹) have been present in the water column for few months, but this is much less likely for most Cyaneidae medusae (median = 25.8 g ind⁻¹). The production of medusae of each species seems therefore to take place at different times, with medusae of *Cyanea* spp. produced closer to the sampling date (i.e. later in the year) than medusae of *A. aurita*. Therefore one could expect that the densities of *A. aurita* would be under the influence of environmental conditions that prevailed earlier in the season, and its biomass under the influence of local food conditions (Lynam et al., 2011) but also temperature which can affect the growth rate of medusae (Hansson, 1997b); whereas for *Cyanea* spp. environmental conditions at the time of the survey may still reflect the conditions that influenced the production of medusae by the polyps. Alternatively, correlations with environmental parameters may simply reflect the correlations or the absence of correlation of jellyfish abundance with depth.

Several diet and feeding studies have demonstrated that fish eggs and larvae can contribute to the diet of *C. capillata* and *A. aurita* (e.g. Titelman and Hansson, 2006; Barz and Hirche, 2007). For example, Möller (1984) reported an average of 4.4 herring larvae (*Clupea harengus*) present in the gastric pouch of juvenile *A. aurita* (6 to 50 mm in bell diameter) in a Swedish fjord in May 1979, and observed up to 49 larvae in the stomach of a single 68 mm medusa. Contrasting dynamics in the outbreak of medusae in different regions of the Irish Sea might therefore have serious implications for other components of the ecosystems, and in particular for fish populations. Indeed, the results of the present study show how the abundance of jellyfish is highly variable in the eastern part of the basin, a region in which are localised important spawning and nursery grounds for many fish species (Fox et al., 1997; 2009; Bunn et al., 2004). In fact, Heffernan et al. (2004) estimated that most Irish Sea spawning of commercially important species occurs in the eastern Irish Sea (56% of Plaice spawning occurs in the east of the Irish Sea, 59% of Cod, 79% of Haddock, and 88% of Whiting). However, fish spawning in the Irish Sea peaks in early to mid-March, and peak numbers of fish larvae occur in late-April (Bunn et al., 2004). Without reliable knowledge of the abundance of jellyfish during these months it is difficult to say whether they have a significant impact on fish eggs and larvae. As mentioned above, it is likely that *A. aurita* medusae have been present in the water column for some months before the survey, but this is less likely for most Cyaneidae. Furthermore, with a diet composed mostly of meso-zooplankton, both *A. aurita* and *Cyanea* spp. could potentially be in competition for food with zooplanktivorous fish (Purcell and Arai, 2001; Barz and Hirche, 2007). Conversely, some juvenile fish are

found living in association with scyphomedusae, and *Cyanea* spp. in particular (Nagabhushanam, 1965; Russell, 1970). By swimming along with the jellyfish, these juvenile fish probably escape from visual predators and, as they grow, start feeding on the jellyfish itself (Lynam and Brierley, 2006). This shows how the identity of the species involved, as well as their respective development stage, are critical elements in defining which type of interactions can take place between scyphomedusae and fish. A study of the diet of *A. aurita* and *Cyanea* spp. in the Irish Sea is needed to establish once and for all whether or not these species prey on fish eggs and larvae, and to determine the extent to which their diets overlap with those of planktivorous fish species (Barz and Hirche, 2005; Brodeur et al., 2008b; Suchman et al., 2008; Pitt et al., 2009a).

In summary, *Aurelia aurita* and *Cyanea* spp. can be found from one side of the Irish Sea to the other, both in inshore and offshore waters. However, their distributions and abundances exhibit contrasting inter-regional and inter-annual dynamics. Between 2007 and 2010 the variability in the abundance of both species was greater in the eastern than in the western part of the basin, and this is likely linked to a greater variability of environmental conditions in the east. Such contrasting patterns of variability confirm the importance of including the spatial and temporal dynamic dimension in any effort aimed at addressing the ecological impact of jellyfish in the Irish Sea, and in particular their interaction with different developmental stages of fish. The data presented in this chapter, represent the first description of the distribution of the abundance of scyphomedusae throughout the entire Irish Sea. As such they could be used to estimate the early summer biomass of jellyfish in the system and inform numerical models (e.g. biomass in EcoPath). However, the inter-regional variations observed in the condition index highlight an important limitation of jellyfish bycatch datasets collected during annual fisheries survey organised at fixed dates: the potential risk that a delay in the timing of the production may result in a lower catch biomass that ends up being interpreted as a ‘low’ year of jellyfish abundance. The integration of density data in the index used to study long term patterns of inter-annual variations might help in limiting this bias in regions marked by a high degree of variability. In addition, monitoring of the seasonal dynamics of the abundance of *A. aurita* and *Cyanea* spp. could help to address this issue, and would also be essential before the bycatch data presented here could be extrapolated to estimate jellyfish abundance at peak season (see next Chapter).

Chapter 4

Monitoring of the seasonal dynamics of scyphomedusae in the Irish Sea

Chapter 4 – Monitoring of the seasonal dynamics of scyphomedusae in the Irish Sea

This chapter was accepted for publication in a similar form in *Marine Biology* under the reference:

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TB and DH conducted the ferry surveys. DH conducted the camera trials (with help of TKD) and the picture analysis. JEP and TKD conducted the net tow trials. TB analysed the data and wrote manuscript with contributions of DH, TKD, JEP and all others.

Abstract

At-sea distributions of large scyphozoan jellyfish across the Irish Sea were studied using visual surface counts from ships of opportunity. Thirty-seven surveys were conducted along two > 100 km long transects between Ireland and the UK from April to September in 2009 and 2010. Five species were recorded but only *Aurelia aurita* and *Cyanea capillata* were frequently observed. The first formal description of the seasonal changes in the abundances and distributions of these two species in the study area is provided. The highest densities of these species were more likely to be found ~ 30 km offshore, but large aggregations were present both in coastal and offshore waters. Evidence for aggregations of medusae along physical discontinuities was provided by coupling jellyfish observations with simultaneous records of environmental parameters. The value of surveys from ships of opportunity as cost-effective semi-quantitative tools, to develop local knowledge on jellyfish abundance, distribution, and phenology is discussed.

1. Introduction

There is concern that climate change (Purcell, 2005; Brodeur et al., 2008a), overfishing (Lynam et al., 2006), eutrophication of coastal waters (Arai, 2001), and the development of artificial structures along coastlines (e.g. marinas, aquaculture facilities, see Lo et al., 2008) can result in a proliferation of gelatinous organisms with dramatic impacts on human activities (Mills, 2001; Purcell et al., 2007; Richardson et al., 2009). However, the reality of suspected global patterns of increased abundance of jellyfish has not been formally established (Mills, 2001; Haddock, 2008), and the absence of long-term baseline data makes it difficult to address this topic (Purcell, 2009).

Some studies have established links between environmental parameters and the inter-annual variability of jellyfish abundance (Goy et al., 1989; Brodeur et al., 2008a; Kogovsek et al., 2010; Lynam et al., 2011). However, because of the complexity of the physical and biological processes at play in marine systems, these relationships based on local or regional datasets do not necessarily apply to other locations. For example, Lynam et al. (2005a) have described how the abundance of scyphozoan jellyfish exhibits contrasting responses to the North Atlantic Oscillation in different regions of the North Sea basin, due to differences in local hydrographical conditions. Therefore, any attempt to address the likelihood of jellyfish populations increasing in a specific region requires the development of a local knowledge of their frequency of occurrence, their abundance, and their broad-scale distribution in that region.

Previously, Doyle et al. (2007a) suggested that visual surveys using ships of opportunity (ShOps) could provide a cost-effective option to build up datasets of jellyfish abundance. Visual surveys from ShOps consist of conducting surface counts from an observation platform on a ship as it sails (or steams) along its regular route. A ShOp can be a research vessel cruising between sampling stations or a ferry-boat regularly crossing between two islands or two sides of a bay. Seabird and marine mammal observers use this approach on a regular basis (Warren et al., 2009), and it can be adapted to any easily identifiable object present on the surface of the sea e.g. algal rafts (Hobday, 2000; Hinojosa et al., 2010), pieces of macro-litter (Hinojosa and Thiel, 2009), or large medusa stages of scyphozoan jellyfish (Doyle et al., 2007a; 2008). With the development of numerical models and on-board sensing equipment (e.g. FerryBox device, Balfour et al., 2007), it is now possible to couple such observations with environmental parameters.

In order to investigate the seasonality and at-sea distributions of the main scyphozoan jellyfish species in the Irish Sea, frequent field surveys using ShOps were conducted between Ireland and Wales from mid-April to late-August – early-September in 2009 and 2010. In addition, trials using camera still-images were conducted in order to test the reliability of the surface counts. Net tows were made to determine if surface counts reflected jellyfish biomass throughout the water column, as recommended by Purcell (2009). Results are discussed with regards to information on other environmental variables as provided by different sources of data (model outputs, in situ measurements, published data), and highlight some of the original advantages associated with the use of ShOps to monitor jellyfish relative abundance.

2. Methods

2.1. Study area

The Irish Sea is a semi-enclosed sea separating the islands of Great Britain and Ireland (Figure 4.1). In the north, the North Channel links the Irish Sea to the Atlantic Ocean, while in the south the St George's Channel links the Irish Sea to the Celtic Sea. The western Irish Sea is characterised by a net northward flow (annual average of $2.5 \text{ km}^3 \text{ days}^{-1}$, Dabrowski et al. 2010), that varies in intensity seasonally.

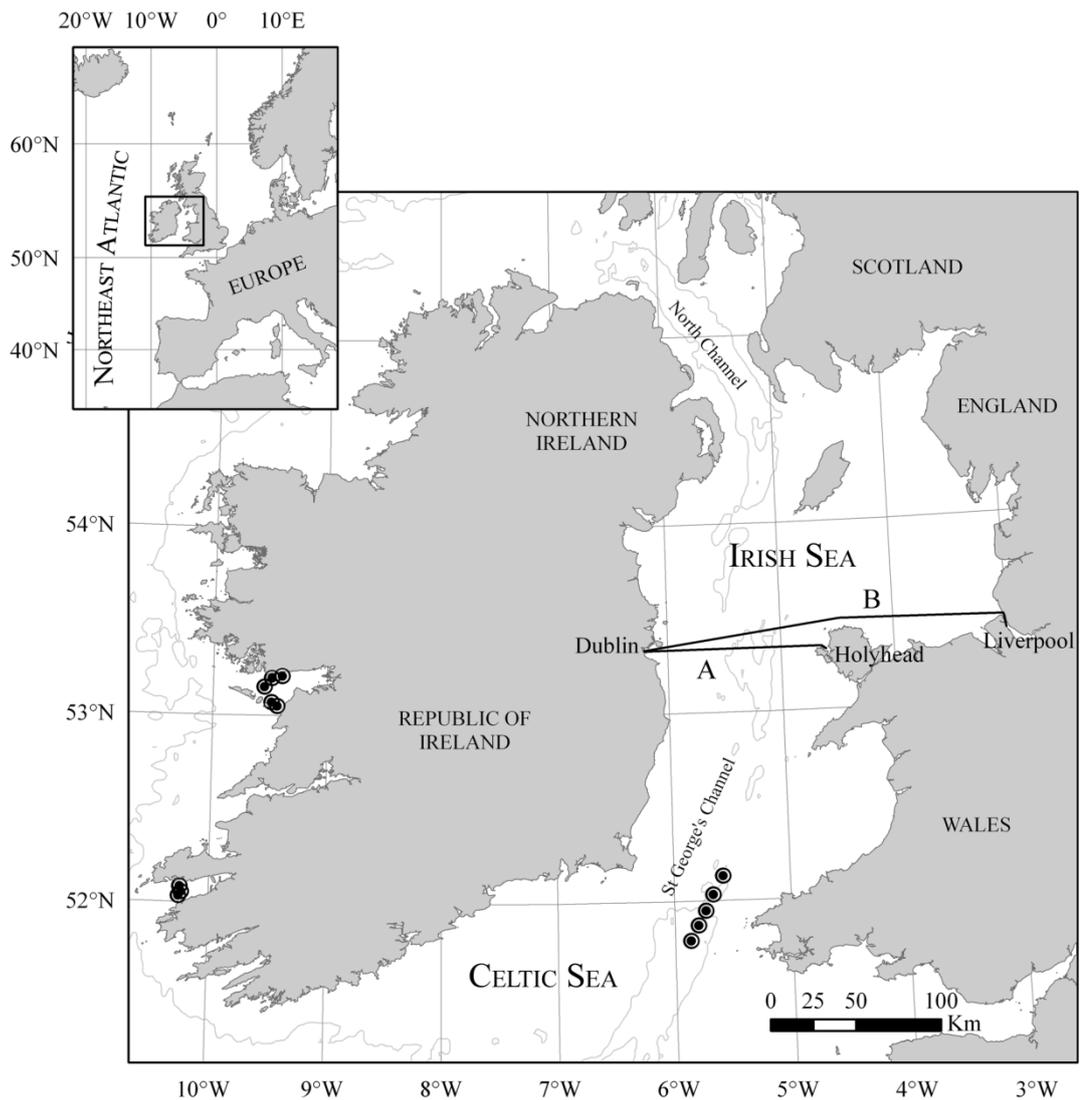


Figure 4.1. Study area for visual enumeration of scyphomedusae in the Irish Sea in 2009 and 2010.

Ferry-routes A and B are represented by black lines. Black dots denote positions where oblique net tows were performed during a research cruise between 16 and 21 June 2009. The 100 m isobath is represented by a thin grey line. Projection on the Irish National Grid was used to map the close-up of the study area.

From spring to early-autumn a counter-clockwise cold pool gyre forms in the western part of the Irish Sea (Horsburgh et al., 2000; Hill et al., 2008). This gyre and the development of a strong thermal stratification at the entrance of the North Channel cause a significant decrease of the northward flow from June to September. The flow only resumes with the breakdown of the stratification. From time to time, the net flow can be reversed to a southwards direction under the effects of winds, in particular during the first few months of the year (Dabrowski et al., 2010).

2.2. Data collection

The methodology used for the surveys was adapted from Doyle et al. (2007a). An observer placed on the outside deck of a ferry visually identified jellyfish to species level and estimated their numbers per 5-min intervals using six categories of abundance: 0, 1 – 10, 11 – 50, 51 – 100, 101 – 500 and > 500. The scyphozoan species present in the Irish Sea (*Aurelia aurita*, *Rhizostoma octopus*, *Chrysaora hysoscella*, *Cyanea capillata* and *Cyanea lamarckii*) have medusae that grow large enough (> 10 cm in bell diameter) and differ sufficiently in shape and colour that medusae swimming at the surface can be identified relatively easily. The number of individuals for which there was any doubt on the species identification was recorded in a separate category. Sampling was for 15 min (i.e. three 5-min counts per sampling period) with 5-min breaks between successive

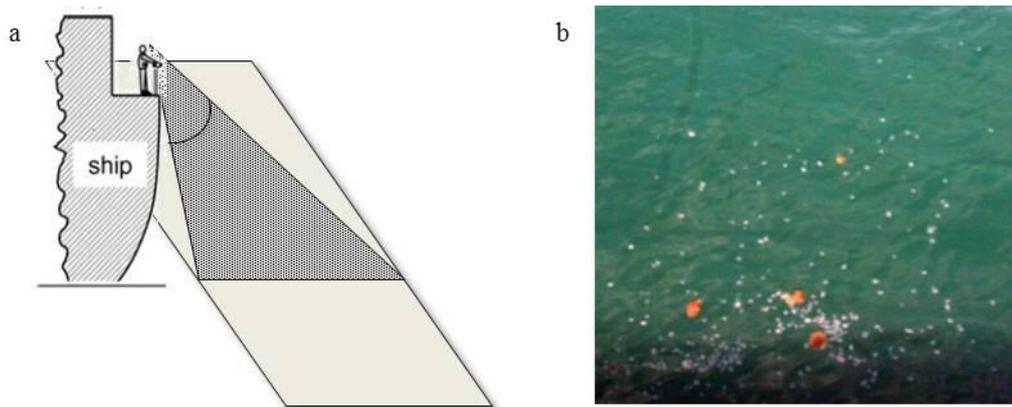


Figure 4.2. Using ships of opportunity to monitor the surface abundance of scyphomedusae. (a) Schematic of the survey setting showing how the width of field of view can be derived from the height of the deck where the observer stands, the height of the observer and the angle of the field of view (adapted from Doyle et al. (2007)). (b) Picture of individual *A. aurita* (white dots) and *C. capillata* (red larger dots) at the surface captured during one of the survey (picture by D. Haberlin).

Table 4.1. Dates of ferry surveys across the Irish Sea in 2009 and 2010.

Please note that two surveys were conducted on each sampling day along ferry-route A.

Route	Year	Date of survey
Ferry Route A	2009	20 Apr; 03 May; 22 May; 22 Jun; 10 Jul; 25 Jul; 13 Aug; 11 Sept
	2010	22 Apr; 12 May; 21 May; 12 Jun; 24 Jun; 12 Jul; 29 Jul; 15 Aug; 31 Aug
Ferry Route B	2009	07 Aug
	2010	16 Jun; 29 Jul

samples. A longer break (20 – 25 min) was taken at about mid-cruise to avoid potential bias due to observer tiredness. The position of the break was slightly shifted from two consecutive surveys (way over and way back), to avoid leaving any area totally unsampled. GPS positions were taken every 5 min using a handheld GPS. Sea state (Beaufort scale) and glare (as defined by Houghton et al., 2006b) were recorded at least every 15 min. An inclinometer and basic trigonometry were used to evaluate the width of the field of view surveyed. Consistency between observers ($N = 4$) was informally tested every time a new observer was involved. A formal trial where two observers conducted independent counts was completed on the 20 August 2010, in parallel with the camera trial (see section 2.6). All surveys were planned based on a maximum of a 3-day weather forecast of relatively low wind (sea-state 0 – 3 maximum) and no or moderate cloud coverage.

Between April and September 2009 and 2010, 34 individual surveys (16 and 18 per season, respectively) were conducted on-board MS Ulysses, one of the ferries linking Dublin (Ireland) and Holyhead (Wales, UK) (ferry-route A, Figure 4.1). The two ports are ~ 105 km apart and both an outward (Dublin-Holyhead crossing) and a return leg (Holyhead-Dublin crossing) were conducted on each day of survey (~ 3.5 h each way). Details are presented in Table 4.1. The observation deck was 27.5 m above the waterline (company information) and the field of view was estimated to be 50.2 m wide.

Three additional surveys were conducted on the 7 August 2009, 16 June 2010, and 29 July 2010 on board the Liverpool Viking, a ferry linking Dublin (Ireland) to Liverpool (England, UK) (ferry-route B, Figure 4.1). In this case, because the return journey is at night-time, jellyfish were only recorded on the way over, leading to 3 transects of ~ 200 km. Because of the transect length (journey ~ 6.7 h), the protocol was adapted so that a 20-min break was taken after four 15-min sampling-periods and a longer break of 1 h was taken at the middle of the crossing. The observation deck was 18.75 m above the

waterline (company information) and the field of view was calculated to be 43.3 m wide. These additional surveys were conducted to explore the potential of linking jellyfish observations with in situ environmental data provided by the ‘FerryBox’ carried by the Liverpool Viking (see section 2.5).

2.3. Seasonal trend

The lower and higher limit of the categories of abundance, the distance travelled (derived from GPS positions), and the width of the field of view were used to estimate a minimum and maximum density for each 5-min interval (reported in individuals per 1,000 m²). Note that the last category is an open one (> 500) and therefore the maximum densities are by definition underestimated.

2.4. Distribution patterns

To investigate distribution patterns across the transect, the section surveyed (ferry-route A) was first divided into 10 sections of 10.5 km each (using Dublin 53.34°N 6.20°W, as the 0 km point). Each 5-min count was then allocated to its corresponding section based on the position of the mid-point between the start and end-point of the 5-min period, compared with the start and end-point of each 10.5 km section. To guarantee that each section had at least one observation, data from each survey day (two surveys) were pooled. This pooling procedure was used because individual 5-min counts were based on the time since departure of the ferry and therefore the exact position where the nth count occurred varied between different surveys. The change in the spatial distribution of jellyfish along the transect was characterised by considering the number of 5-min counts of each category of abundance for each of the 10.5 km-wide transect sections. Finally, the position of the average density of medusae through the season was addressed by considering the position of the ‘centre of jellyfish density’ along the transect. This parameter was defined by the following expression:

$$D_i = \frac{\sum_{j=1}^k d_j m_j}{\sum_{j=1}^k d_j}$$

where D_i is the position of the centre of density for the i^{th} day; m_j is the distance from the closest coast of the middle point of the j^{th} section; d_j is the average density (number of jellyfish per 1,000 m²) within the j^{th} section; and k is the number of sections. Effectively,

D_i is the average of the distance from the coast of the central point of each 10.5 km section, weighted by the average density of jellyfish in each section. Densities per section were calculated using the mid-points of the class of abundance recorded for each 5-min counts, rather than presenting several values of D_i based on the minimum and maximum density estimates. Points of coordinates 53.343°N, 6.204°W and 53.331°N, 4.619°W were used as references to calculate distance from the coast (one point on each side of the transect).

2.5. Environmental data

Daily surface and bottom temperatures and salinity along ferry-route A (Figure 4.1) were provided by the National Oceanography Centre (NOC), Liverpool, UK (<http://noc.ac.uk/>). The data were from outputs of the Irish Sea high resolution POLCOMS model (1/40 degree in longitude and 1/60 degree in latitude) extracted for 63 points distributed along ferry-route A (more details can be found on the NOC website). The daily means of these 63 points from 1 January 2008 to 1 October 2010 were considered to describe general conditions along the transect.

Along ferry-route B (Figure 4.1), in situ environmental data were collected by a FerryBox carried by the ship as part of the FerryBox project (<http://www.ferrybox.org>), meaning that data were collected simultaneously with the jellyfish surveys (for details on the FerryBox device see Balfour et al., 2007). Surface temperature, salinity, and chlorophyll, which were sampled every 10 s along the route, were considered for our study. GPS coordinates associated with sampling values were corrected for the 5-min lag between sampling (water intake) and sensor measurement due to the large sea chest of the ferry. A moving median with a width of 2 min was applied to smooth the series. Chlorophyll data must be considered with caution as they have not undergone quality control. The FerryBox data are also managed at NOC.

2.6. Camera trial

To address the accuracy of visual counts, a camera trial was conducted at the same time as visual surveys on a portion of 19.64 km of ferry-route A on the 15 August 2010. A digital still SLR camera (Canon 350D) was mounted on a tripod on the observation deck of the survey ship and pointed towards the water at an oblique angle (51°), aligning the lower edge of the field of view with the outside edge of the ship's wash. This was done to

provide the camera with a relatively constant composition and focus within the field of view. The camera was connected to a laptop and a remote capture tool was used to automatically take a picture (3,456 x 2,034 pixels) every 3 s and to store it on the hard drive of the computer. The camera, computer and GPS were synchronised before the survey, subsequently allowing every image taken within each 5-min sample-period to be easily identified by time.

The horizontal and vertical angles of view of the camera (α) were estimated to be 63.3° and 44.7° respectively, using the following equation:

$$\alpha = 2 \tan^{-1} \frac{d}{2f}$$

with d the sensor dimension (22.2 mm length x 14.8 mm height) and f the effective focal length (35 mm) (Marcos et al., 2008). The dimensions of the photographed area were calculated using trigonometry, specifically using the following equation: $d = h \times \tan \alpha$, where d is the horizontal distance from the camera, h is the height of the camera and α is the angle in radians. The resultant image surface area was $\sim 1,286 \text{ m}^2$ and the number of individual jellyfish in each slide was counted. Counts were then pooled in each 5-min time-period and compared with visual counts corresponding to the same time interval.

2.7. Net tow trials

In order to compare surface densities as estimated by visual surveys with sub-surface densities, opportunistic pelagic trawls were conducted during a zooplankton/algal raft cruise in June 2009 with concomitant visual surveys from the same vessel (RV Celtic Voyager). In total, 13 pelagic trawls were conducted using a 4 m^2 Methot Isaacs Kidd (MIK) frame net with a 5 mm mesh (Methot, 1986). Five trawls were conducted in the Irish Sea, three in Dingle Bay and five in Galway Bay (Figure 4.1). The net was towed in a single oblique profile through the water column to various depths depending on the locality. In the Irish Sea, tow depths varied between 24 and 65 m (bottom depth 94 – 117 m); in Dingle Bay depth was between 9 and 12 m (bottom depth 36 – 45 m) and in Galway Bay all nets were deployed to a depth of between 19-24 m (bottom depth 32 – 47 m). An impellor flowmeter recorded the volume filtered during each tow. The distance travelled and volume filtered averaged $1.23 \pm 0.55 \text{ km}$ and $3,851 \pm 852 \text{ m}^3$ (range 2,924 – 5,562 m^3), respectively. All jellyfish in the catch were counted and identified to species.

Table 4.2. Numbers of individual *R. octopus*, *C. lamarckii*, and *C. hysoscella* observed during ferry surveys in 2009 and 2010.

Species	Year	Date (n _{Dublin-Holyhead} -n _{Holyhead-Dublin})
<i>Rhizostoma octopus</i>	2009	20 Apr (22-12); 03 May (1-5); 22 May (1-1)
	2010	22 Apr (2-2); 21 May (1-0); 24 Jun (0-1); 29 Jul (2-1)
<i>Cyanea lamarckii</i>	2009	22 Jun (70-9); 10 Jul (3-0); 25 Jul (22-6); 13 Aug (0-15)
	2010	-
<i>Chrysaora hysoscella</i>	2009	10 Jul (56-36); 25 Jul (12-5); 11 Sep (0-1)
	2010	-

3. Results

3.1. Surveys along ferry-route A

A total of 34 individual surveys were conducted between Dublin and Holyhead in 2009 ($N = 16$) and 2010 ($N = 18$), details are presented in Table 1. The mean ($X \pm SD$) speed of the ship was $35.7 \pm 6.5 \text{ km h}^{-1}$ or 19.3 ± 3.5 knots, $N = 798$. The mean ($X \pm SD$) surface area surveyed in each 5-min count was $149,418 \pm 27,192 \text{ m}^2$, $N = 798$. The mean ($X \pm SD$) number of 5-min observations per survey was 23.5 ± 3.6 , $N = 34$. Bad conditions or unexpected events caused gaps in the records for five surveys in 2010: 12 May (only 12 and 18 5-min records), 21 May (only 15 5-min records on Dublin-Holyhead crossing), 12 June (only 18 5-min records on Dublin-Holyhead crossing), and 29 July (only 15 5-min records on Holyhead-Dublin crossing).

During the 2 years of monitoring, five scyphozoan species were observed: *Aurelia aurita*, *Chrysaora hysoscella*, *Cyanea capillata*, *Cyanea lamarckii*, and *Rhizostoma octopus*. During both years, *A. aurita* and *C. capillata* were frequently observed throughout the season, whereas the other species were encountered on a more irregular basis. The proportion of individuals that were too small or too deep to be confidently identified was usually low (< 10 individuals per survey in 27 out of 34 surveys), except for 2 days in 2009 (22 June and 10 July) when more than 100 individuals (with up to 45 individuals in one 5-min time-period) could not be successfully identified in Dublin Bay. However, the identification of *A. aurita* and large *C. capillata* was very reliable, so further analyses were only conducted for these two species. Information on the sightings of other species is presented in Table 4.2.

3.2. Seasonal abundance of *Aurelia aurita*

In 2009, *A. aurita* was observed for the first time on 22 June with more than 100 individuals counted per 5 min on seven occasions on each crossing. An overall mean density of 0.26 – 1.49 ind. 1,000 m⁻² was calculated for this day, using respectively the lowest and highest limit of the count categories for each 5-min records of the day (Figure 4.3). The maximum abundance of *A. aurita* was observed on 25 July with a mean density of 0.67 – 1.53 ind. 1,000 m⁻² for the Dublin-Holyhead crossing. However, because the highest category is open (> 500), the maximum count underestimates the true maximum abundance present at the peak period (see section on camera trials). By 13 August 2009, numbers of *A. aurita* had dramatically decreased with only two 5-min counts in the 50–100 category and no observations in the two highest categories, leading to an overall mean density of 0.015 – 0.04 ind. 1,000 m⁻² for the day. In 2010, *A. aurita* was first detected on 21 May with two single individuals observed on the Holyhead-Dublin crossing. The maximum abundance was observed on 29 July with a mean density of 0.76 – 1.23 ind. 1,000 m⁻² for the Dublin-Holyhead crossing. The season extended later in 2010 than in 2009 with relatively high abundances still being observed on 15 August (mean density of 0.32 – 0.68 ind. 1,000 m⁻² for the day). The overall mean density was down to 0.007 – 0.039 ind. 1,000 m⁻² by 31 August (Figure 4.3), with only four 5-min periods with more than 10 individuals counted.

3.3. Seasonal abundance of *Cyanea capillata*

In 2009, *C. capillata* was first detected on 22 June (six counts in the 1–10 category on the outward leg and eight on the return leg) and the mean density along the transect was 0.0018 – 0.018 ind. 1,000 m⁻² (Figure 4.3). In 2010, two individuals were sighted as early as 12 May. In both years, the maximal abundance was observed during the mid-August survey (13 August 2009 and 15 August 2010) and the maximum daily mean density was significantly higher in 2010 (0.074 – 0.265 ind. 1,000 m⁻²) than in 2009 (0.013 – 0.055 ind. 1,000 m⁻²) (Wilcoxon's rank-sum test, $W = 587.5$, $N_{2009} = 51$, $N_{2010} = 47$, $P < 0.001$). In 2009, densities of *C. capillata* had decreased by 11 September with only few individuals observed. In 2010, the monitoring ended on 31 August and at that time, *C. capillata* densities had started declining but were still at a relatively high level (daily mean 0.049 – 0.170 ind. 1,000 m⁻²). *Cyanea capillata* usually did not form dense aggregations like *A. aurita*: 75% of observations were 1-10 individuals per 5-min count, whereas for *A. aurita* only 38.5% of observations fell in that category and all other

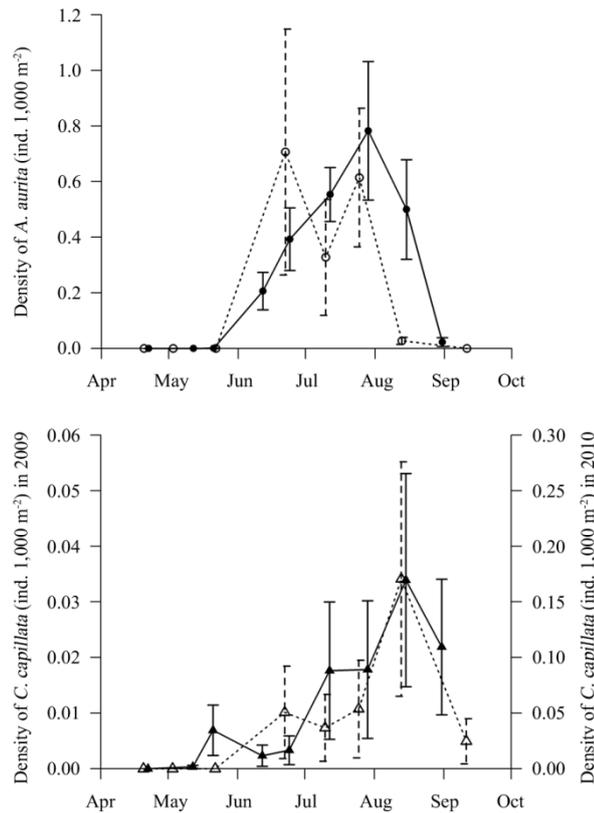


Figure 4.3. Seasonal occurrence of *A. aurita* and *C. capillata* between Dublin and Holyhead in 2009 and 2010.

Vertical bars show the range between the low and high mean daily estimates of density for each day of sampling. Lines were drawn through the middle point of vertical bars for visual aid (middle points marked by circles for *A. aurita* and by triangles for *C. capillata*). Data from 2009 are marked by open symbols and dashed lines, while data from 2010 are marked by solid lines and symbols. Note additional y-axis for *C. capillata* highlighting higher densities in 2010 than in 2009; for *A. aurita* densities were of the same order both years.

observations in the higher categories. However, on three occasions, > 100 individuals of *C. capillata* were counted during a 5-min count (12 July 2010, 29 July 2010, and 15 August 2010 – for *A. aurita*, such counts occurred 66 times), showing that density of *C. capillata* can also be locally high (maximum density estimates of 3.21 ind. 1,000 m⁻² for the > 100 individual 5-min count on 29 July 2010).

3.4. Spatial patterns and seasonal changes in the distributions of *Aurelia aurita* and *Cyanea capillata*

Aurelia aurita and *C. capillata* were not homogeneously distributed along the transects. The details of the distribution of 5-min categories in the different sections of the ferry-route A are presented in Figure 4.4a. High numbers of *A. aurita* (> 500 ind. per 5-min

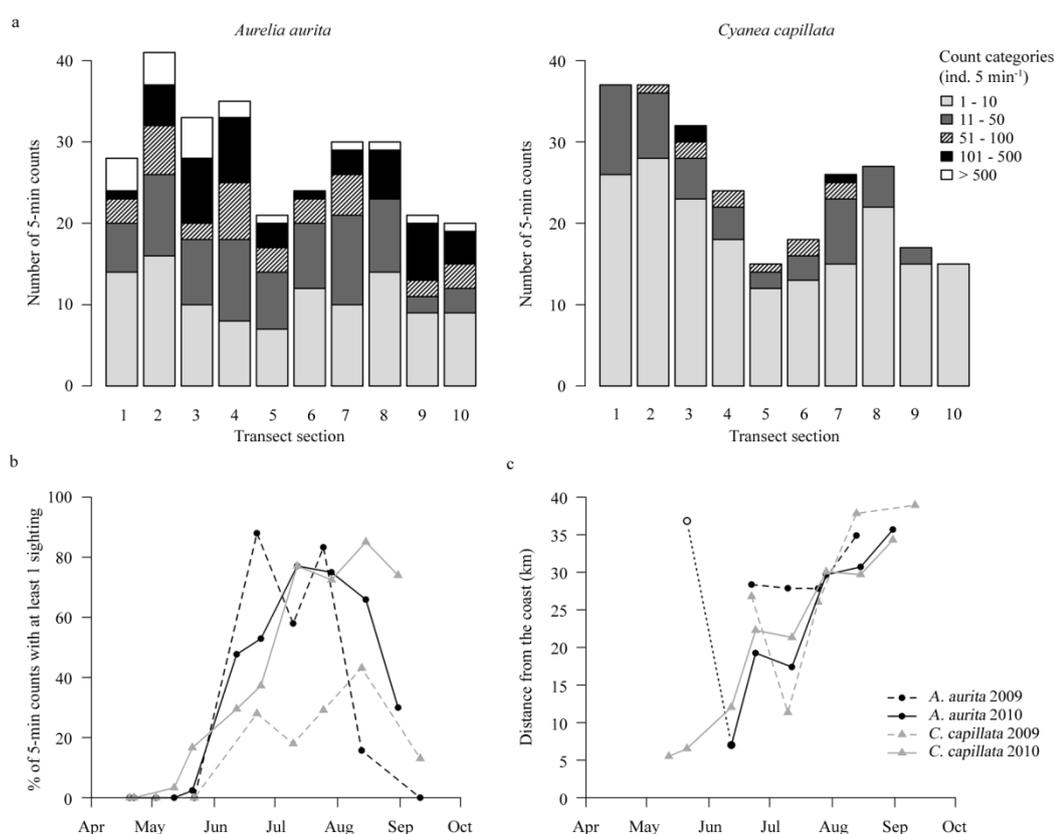


Figure 4.4. Spatial patterns and season changes in the distribution of *A. aurita* and *C. capillata* between Dublin and Holyhead in 2009 and 2010.

(a) The total number of 5-min counts of each category of abundance for each species, for each 10.5 km section of the Dublin-Holyhead transect (ferry-route A), in 2009 and 2010; (b) the % of 5-min counts with at least one medusa sighting; and (c) the distance from the coast of the centre of density of *A. aurita* (black dots) and *C. capillata* (grey triangles) for each day of survey, in 2009 (dashed lines) and 2010 (solid lines). Please note that in (a) the 0-count category is not represented; and that in (c) the first value for *A. aurita* in 2010 (open circle) was due to the detection of only 2 individuals on that day.

count) were encountered at least once in most sections of the transect (all except for the central section extending from 53 to 63 km offshore). The section with the highest number of > 500 ind. counts ($N = 5$) was the section from 21 to 32 km off Dublin (section 3 on Figure 4.4a). Counts of 51 – 100 *C. capillata* per 5 min occurred in every section from 10 to 70 km offshore (from the Irish coast). The counts of > 100 *C. capillata* occurred in section 21 – 32 km off the Irish coast, and the section 32 – 42 km off the Welsh coast (sections 3 and 7 on Figure 4.4a).

In order to illustrate how each species was distributed across the study area and how this pattern of distribution changed with time (e.g. over the season), the proportion of 5-min sampling-periods during which at least one jellyfish was observed, was considered for

each survey-day (Figure 4.4b). In 2009, *C. capillata* was first observed in only 28.0% of the 5-min counts ($N = 49$, 22 June), but this proportion went up to 43.1% in mid-August ($N = 51$). In contrast, in 2010, *C. capillata* was present in up to 85.1% of 5-min sampling-periods ($N = 47$, 15 August), almost consistently found in every patch of water observed. *Aurelia aurita* was already widely distributed (88.0% of $N = 50$ 5-min counts) when first observed in 2009 (22 June); whereas in 2010, the species was initially observed during only 1 of the 42 sampling-periods (21 May), and then progressively spread across the transect to be found in up to 77.1% of the sampling-period in mid-July ($N = 48$). In both years, the distribution of *A. aurita* increased earlier than *C. capillata*. In 2010, the centre of density of both species exhibited a progressive displacement from coastal areas to more offshore areas throughout the season (Figure 4.4c). In 2009, this pattern was not as marked, though for both species the centre of density during the last survey of 2009 was further offshore than during any other survey of the year.

3.5. Environmental conditions along ferry-route A

The mean daily water temperature (both surface and bottom) along ferry-route A followed an annual cycle marked by a progressive increase from early-March to mid-August before decreasing from late-August to late-February of the following year (Figure 4.5a). There was a slight decrease in both the minimum and maximum temperatures observed each year during the period considered (2008 – 2010). Indeed, the minimum mean daily surface temperature was 8.1°C in 2008, 7.5°C in 2009, and 7.1°C in 2010, while the maximum mean daily surface temperature was 16.1°C in 2008, 16.0°C in 2009, and 15.5°C in 2010. A slight difference between overall mean daily surface and bottom temperatures formed from 10 April to the first week of October in 2009. The same pattern occurred in 2010, at least until the end of August. The overall difference along the transect was low with a mean maximum difference between surface and bottom temperatures of only 0.9°C in 2009 (14 August) and 1.2°C in 2010 (8 July). The highest difference was found in the middle of the transect (deepest section) where surface temperature was up to 3.10°C warmer than bottom temperatures in 2009 (1 August) and 3.5°C in 2010 (9 July). The salinity along the transect (Figure 4.5b) was characterised by a rapid increase in the late-summer and early-autumn months (+0.4 from 11 August to 1 November 2008 and +0.3 between 17 October and 20 November 2009). Salinity did not return to the initial level after the seasonal increase in either year. However, salinity started to decrease after mid-April in 2010.

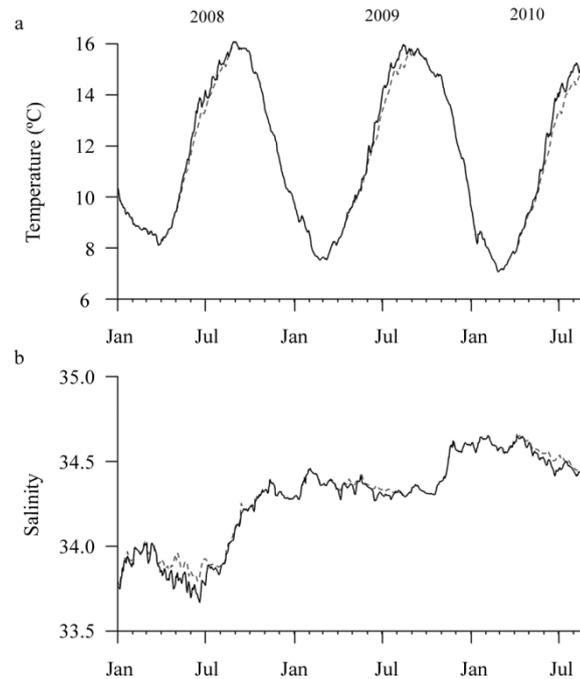


Figure 4.5. Mean daily temperature and salinity between Dublin and Holyhead.

Surface and bottom (a) temperature and (b) salinity from 1 January 2008 to 1 September 2010. Surface temperature and salinity are illustrated by continuous black lines, bottom temperature and salinity by dashed grey lines. Data are daily means from high resolution model outputs along ferry-route A ($N = 63$ points, material and methods for details).

3.6. Distribution patterns along ferry-route B in relation to environmental parameters

A total of three surveys between Dublin and Liverpool (ferry-route B) were conducted (7 August 2009, 16 June 2010 and 29 July 2010) (Figure 4.1 and Table 4.1). The mean speed ($X \pm SD$) of the ship was 32.5 ± 5.2 km h⁻¹ or 17.5 ± 2.8 knots, $N = 150$. The mean ($X \pm SD$) surface area surveyed in each 5-min count was $117,395 \pm 19,768$ m², $N = 150$. As with ferry-route A, the main jellyfish species present were *A. aurita* and *C. capillata*. Other species encountered were: *R. octopus* (one individual recorded on 16 June 2010, at position 53.5181°N, 3.4319°W) and *C. lamarckii* (three times 1 – 10 individuals on 7 August 2009; five times 1 – 10 and one time 11 – 50 individuals on 16 June 2010; four times 1 – 10 individuals on 29 July 2009). The number of individuals that could not be identified was low in August 2009 (six times 1 – 10 individuals and two times 11 – 50) and July 2010 (one 1 – 10 count and one 11 – 50 count). In June 2010, the numbers of individuals that could not be identified was much higher; with unidentified individuals in 60% of the 5-min counts ($N = 48$), and five counts with more than 50 individuals (among which, one of more than 100 individuals). This high number of unidentified individuals

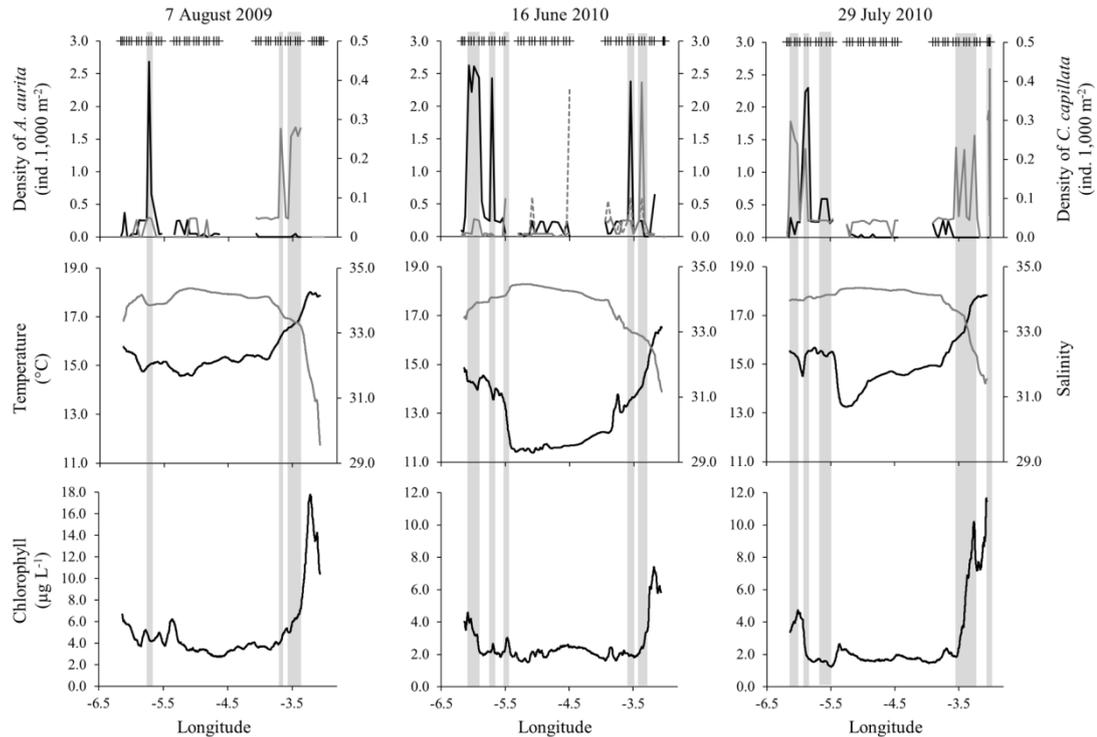


Figure 4.6. Distributions of *A. aurita*, *C. capillata*, and variation of environmental parameters between Dublin and Liverpool.

The density of *A. aurita*, temperature and chlorophyll are illustrated in black; the density of *C. capillata* and salinity in grey. In July 2010, large numbers of *Cyanea* sp. that could not be identified to species level occurred; they are illustrated by a dashed dark grey line. Crosses in the top panel indicate the mid-position of 5-min time periods of sampling. Regions with high medusae densities are highlighted by vertical grey areas. Please note changes in y-axis scale for densities of *C. capillata* (June 2010) and chlorophyll (August 2009). Jellyfish densities were calculated using the mid-point of the category of abundance for each 5-min count.

can mainly be explained by the presence of many small *Cyanea* spp. individuals for which it was not possible to visually determine whether they were *C. lamarckii* and/or *C. capillata*.

For each survey, variations of surface densities of *A. aurita* and *C. capillata* along the transect were considered in parallel with the in situ surface temperature, salinity, and chlorophyll measured by the FerryBox device (Figure 4.6). In August 2009, *A. aurita* was mostly present on the western part of the transect, with highest densities ~ 20 km offshore (101 – 500 ind. per 5 min, or 0.90 – 4.47 ind. 1,000 m⁻²). The temperature and salinity records indicated that the position corresponded to a decrease in temperature followed by a decrease in salinity as the ship entered a relatively less saline water-mass. Interestingly, the peaks of *A. aurita* corresponded to small peaks in chlorophyll concentration. In July 2010 (Figure 4.6), a similar pattern of a very high density of *A. aurita* localised in a

region of a physical discontinuity ~ 13 km offshore (with a marked temperature change) was observed. In addition, on the same day, surface densities of *A. aurita* decreased with the entrance of the ship into the colder central waters. In June 2010 (Figure 4.6), the species was present both in coastal and central waters, although far more abundant in coastal areas (and in particular just 2.6 km offshore, at the end of Dublin Bay). The association with physical discontinuities was not as marked as during the other surveys. Numbers of *C. capillata* observed in August 2009 were low compared to numbers observed in 2010 (Figure 4.6). While individuals were regularly encountered all along the crossing, the highest densities (up to 0.100 – 0.456 ind. 1,000 m⁻² in a 5-min count) were observed on the eastern side of the transect. The increase in *C. capillata* densities seemed to follow the progressive change in environmental conditions as the ferry entered the waters of Liverpool Bay (indicated by increase of chlorophyll and temperature and decrease of salinity, Figure 4.6). *Cyanea capillata* were far more abundant in 2010 as already shown by the seasonal survey along route A (Figure 4.3). During the two Dublin-Liverpool surveys conducted that year, the highest densities of *C. capillata* were also found on the eastern side of the transect, in the region corresponding to an increase of temperature and chlorophyll (Figure 4.6). In July 2010, *C. capillata* was observed in the estuary of the River Mersey, right up to Liverpool city itself. On the western part of the transect, a relatively large aggregation of *C. capillata* was localised ~ 37 km offshore in June 2010 (> 50 individuals per 5-min count, or a density range of 0.39 – 0.76 ind. 1,000 m⁻²). This was precisely the limit between coastal and more central waters as shown by the change in temperature and salinity (Figure 4.6). The numbers were only limited while cruising in central waters. The large aggregation of smaller individuals of *Cyanea* spp. for which it was not possible to confidently identify the species (*C. capillata* and/or *C. lamarcki*), was located in the middle of the central waters and was not associated with any noticeable change in temperature, salinity or chlorophyll.

3.7. Camera trial

The camera trial was conducted along a distance of 19.64 km with 805 images recorded. At the same time two people conducted 8 independent 5-min visual surveys (Figure 4.7). In total, 207 individuals of *C. capillata* and 5,869 *A. aurita* were counted from the photographs. Visual counts by two different observers were 230 and 286 for *C. capillata*, and 1,373 and 1,197 for *A. aurita*. The maximum count of *A. aurita* in one picture was 1,308 individuals which corresponded to an estimated density of 1.02 ind. m⁻². Within the

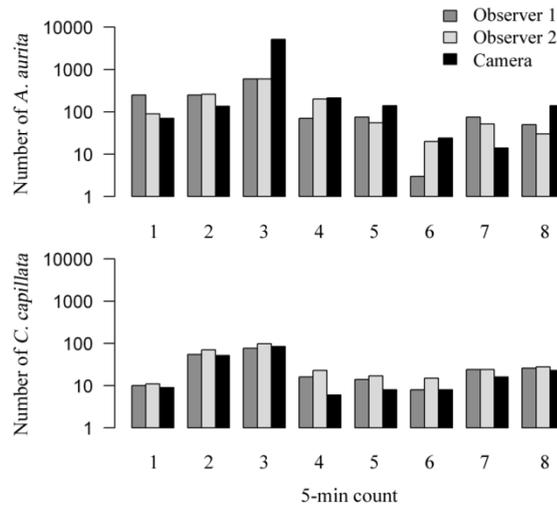


Figure 4.7. Comparison of surface counts of jellyfish by two observers with numbers derived from image analysis.

Please note that the y-axis scale is logarithmic.

picture, clusters of up to 24.2 ind. m⁻² could be observed. For *C. capillata*, up to 20 individuals were counted in one still image (0.016 ind. m⁻²). Visual counts by different observers were in close agreement with counts from camera records for *C. capillata* (Wilcoxon rank-sum test: $W_{\text{observer1-observer2}} = 25.5$, $P = 0.53$; $W_{\text{observer1-camera}} = 40.5$, $P = 0.40$; $W_{\text{observer2-camera}} = 45.5$, $P = 0.17$). In the case of *A. aurita*, the counts based on the camera pictures were very similar to the “live-counts” for low densities, with less agreement when *A. aurita* densities were high (Figure 4.7). However, these differences were not statistically significant (Wilcoxon rank-sum test: $W_{\text{observer1-observer2}} = 35.5$, $P = 0.75$; $W_{\text{observer1-camera}} = 31.5$, $P = 1$; $W_{\text{observer2-camera}} = 29.0$, $P = 0.79$).

3.8. Net tow trials

A total of 13 oblique tows were conducted with concomitant surface counts, in three different regions (Figure 4.1). Jellyfish catches were dominated by medusae of *A. aurita* (bell diameter 5–36 cm). Some *C. larmarckii* and *C. hysoscella* were recorded. When few or no jellyfish were observed from the surface, few or no jellyfish were caught in the net (Figure 4.8). Only one large surface aggregation was observed and no large jellyfish catch was recorded. The data were too few and variable to confidently establish a relationship between surface counts and sampled biomass; however, at low jellyfish abundances, the correspondence was approximately 1 ind. 1,000 m⁻² to 1 ind. 1,000 m⁻³ (Figure 4.8).

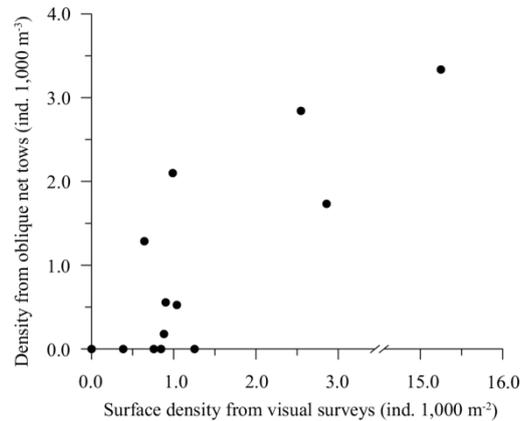


Figure 4.8. Comparison of densities of *A. aurita* from oblique net tows with surface densities from visual counts.

Net tows and visual counts were conducted simultaneously. Location of sampling stations is figured in Figure 4.1. Please note break on x-axis.

4. Discussion

Purcell (2009) encouraged greater implementation of large-scale sampling methods for assessing the broad-scale distribution of jellyfish for the effective management of our oceans. Here, 37 transects (> 100 km each) were conducted across the Irish Sea over two sampling seasons (June–September 2009 and 2010). Such extensive temporal and spatial coverage (overall total of 79 h of observations, 4,170 km travelled and $136.8 \times 10^6 \text{ m}^2$ surveyed) provides a unique opportunity to investigate the seasonality of the surface abundances and distributions of the two main scyphozoan jellyfish species of the Irish Sea.

Aurelia spp. are cosmopolitan jellyfish that can form very dense aggregations under a broad range of environmental conditions (see review by Lucas, 2001). In Europe, the different populations of *A. aurita* exhibit a large degree of variability in their dynamics and in particular regarding the timing of occurrence of the medusa stage (Lucas, 2001). When considering the detrimental impacts that large aggregations of *Aurelia* spp. can have on human activities (e.g. aquaculture, Baxter et al., 2011), and concerns over potential competition of the species with fish for zooplankton resources (Purcell and Arai, 2001; Richardson et al., 2009; Lynam et al., 2011); addressing the question of when and where large aggregations of *A. aurita* occur is critical. By monitoring at-sea surface abundances, the present study provides some answers to these questions for the Irish Sea for the first time. The findings of medusae being present from late-May to late-August–early-September (Figure 4.3) are in agreement with the general seasonality of the species

in other locations around the UK (Russell, 1970). However, the first observations of adult medusae have sometimes been reported to occur as early as April, this discrepancy with the present study may be due to the methodology underestimating the youngest (smallest) medusae. *Cyanea capillata* on the other hand, is considered a boreal species and is present on both sides of the Atlantic. The seasonality of its occurrence in the Irish Sea as described in the results (Figure 4.3) is consistent with previous observations of large medusae not being recorded in UK waters before June, and with a peak period from July to September (Russell, 1970). However, bycatch data from juvenile-gadoid fish-surveys in the north-western Irish Sea show the presence of the species as early as mid-May in 2010 (see Chapter 3). Comparisons of our data with the analysis of beach strandings in the same region by Doyle et al. (2007a), suggest that strandings of *A. aurita* occur throughout the season when the species is present, whereas strandings of *C. capillata* seems to concentrate only at the end of the season (Doyle et al. (2007a) described that 90% of *C. capillata* strandings occurred from 26 June to 17 September in the period 2003–2005). However, this comparison should be considered with caution as the records are from different years and as we show here that abundance and seasonality can vary from year to year.

Indeed, the seasonal pattern of occurrence of *C. capillata* was comparable in 2009 and 2010, but the species was far more abundant in 2010 (Figure 4.3). The factors responsible for the inter-annual variability in the abundance of *C. capillata* are unclear but several factors could be involved:

(1) Temperature. In 1965, Verwey (cited in Russell, 1970) suggested that the occurrence of high abundances of *C. capillata* on the Dutch coast in 1963 was due to the preceding cold winter. As the Irish Sea and the North Sea are the southern limit of the distribution area of *C. capillata* in Western Europe, one might expect that unusually cold conditions would lead to higher abundances there. The winter of 2009–2010 was actually marked by a noticeably negative North Atlantic Oscillation Index (NAOI, NOAA, 2011), which translated into an unusually cold (Dungan et al., 2010) and dry winter over north-western Europe. However, although a decrease in daily surface and bottom water temperature along the transect was observed between 2008 and 2010, it was only moderate (Figure 4.5a)

(2) Salinity. A higher salinity was experienced in 2010 compared with 2009 and 2008 (Figure 4.5b). The salinity in the Irish Sea is mostly controlled by (a) the inputs of more saline waters from the Celtic Sea (St George's Channel) or from the North

Channel (Figure 4.1), and (b) the river runoffs (Holt and Proctor, 2003). The increase in salinity observed late in the summers of 2008 and 2009 probably corresponded to the inflow from the North Channel being resumed after the breakdown of the seasonal stratification. The salinity may have been maintained to higher levels in 2010 as a result of the relative dryer winter (less precipitation resulting in weaker river runoffs) typical of a negative NAOI. However, *C. capillata* can be found in waters of much lower salinity (e.g. 7.0–15.5 psu in the central Baltic Sea, Barz and Hirche, 2005), and it is unlikely that the moderate increase of salinity that affected the area could be the only cause of the dramatic change in the abundance of *C. capillata* from 2009 to 2010.

(3) Hydrographical conditions. In the absence of information on polyps and ephyrae, it is impossible to say whether the observed *C. capillata* are local populations or if they were advected there (Barz and Hirche, 2005). In spring and summer, the formation of the seasonal gyre in the Western Irish Sea strongly affects the oceanography of the area: the overall northward flow is stopped and the cyclonic current associated with the gyre significantly increase the retention time in the region (Dabrowski et al. 2010). The study area is at the extreme southern limit of the gyre and it is likely that a slight change in the position of the gyre may modify its retention effect. Similarly, the resumption of the northward flow after the breakdown of the seasonal stratification could play an important part in the timing of the end of the season as recorded by the methods presented here (i.e. a decrease in jellyfish abundance could be due to advection to the north rather than the senescence of jellyfish). In contrast, the recorded decline of *A. aurita* is unlikely to be linked to this phenomenon as it occurred before the breakdown of the stratification in 2009 and 2010. However, strong wind events could also overwhelm the effect of the gyre and advect medusae away from the study area (Lynam et al., 2011).

Collection of additional data is required to elucidate the factor(s) that drive the differences in abundance of *C. capillata* from year to year, but also those that drive the end of the season for both species. It will also help determine whether 2010 had an exceptionally high abundance of *C. capillata* or if 2009 was unusually low, as in the absence of reliable baseline data it is impossible to conclude on this aspect (Brewer, 1989). Our observations, however, illustrate how sustained long-term data collection by regular surveys from ships of opportunity, coupled with other data (e.g. hydrographic models, FerryBox), could help in investigating the links between climate, oceanographic conditions, and jellyfish abundance. Additionally, the use of ferry-survey data can be used to validate and complement existing fisheries bycatch datasets (Brodeur et al.,

2008a; Bastian et al., 2011) by providing the possibility of detecting phenological changes in the dynamics of jellyfish populations; something that fisheries surveys that are run once a year (sometimes before or after peak jellyfish season) cannot do (Lynam et al., 2011).

Furthermore, detailed information on the seasonality of presence of medusae is critical to address the role of these organisms in the dynamics of the ecosystem. Lynam et al. (2011) provided a description of the average seasonality of primary production together with copepod and cnidarian abundances (using phytoplankton colour index, copepod biomass and cnidarian index, respectively) in the Irish Sea using data from the Continuous Plankton Recorder survey (CPR, for details see Richardson et al., 2006). Comparisons of these CPR records with the data presented here, show that the peak season of *A. aurita* (June to early-August) matched the peak period of copepod biomass in the Irish Sea, and that *C. capillata* peaked after *A. aurita* (Figures 4.3, and 4.9 adapted from Lynam et al. 2011 with permission from authors). This chronology is coherent with *A. aurita* feeding mostly on meso-zooplankton (mostly cladocerans and copepods, Barz and Hirche, 2005) and *C. capillata* feeding on meso-zooplankton and gelatinous organisms, especially *A. aurita* (Båmstedt et al., 1997; Hansson, 1997a; Barz and Hirche, 2007). Although it has been previously suggested that *C. capillata* could control populations of *A. aurita* (Båmstedt et al., 1994), in this case it is unlikely as the season of *A. aurita* was shorter in 2009 when there were far fewer *C. capillata* than in 2010 (Figures 4.3 and 4.9). Furthermore, records of cnidarian occurrence in CPR samples, as presented by Lynam et al. (2011), showed that sub-surface gelatinous zooplankton is abundant in the Irish Sea from May to October (monthly average over 18 years from 1991 to 2008, see Figure 4.9). The present study on the other hand, described a significant decrease in the abundance of the large scyphomedusae as early as mid-August for *A. aurita*, and early-September for *C. capillata* (Figures 4.3 and 4.9). These findings highlight the importance of restricting the use of CPR data as a proxy of scyphomedusae distribution or inter-annual abundance, to regions and months for which correlations have been clearly demonstrated (Lynam et al., 2010; 2011).

Beyond this overall average picture across the study area, our results highlighted that medusae were not homogeneously distributed across the Irish Sea. There were differences in speed and extent of the spatial spread, both between species and between years (Figure 4.4b). The centre of density of each species exhibited a progressive displacement from coastal to more offshore areas, and large aggregations of both *A. aurita* and *C. capillata*

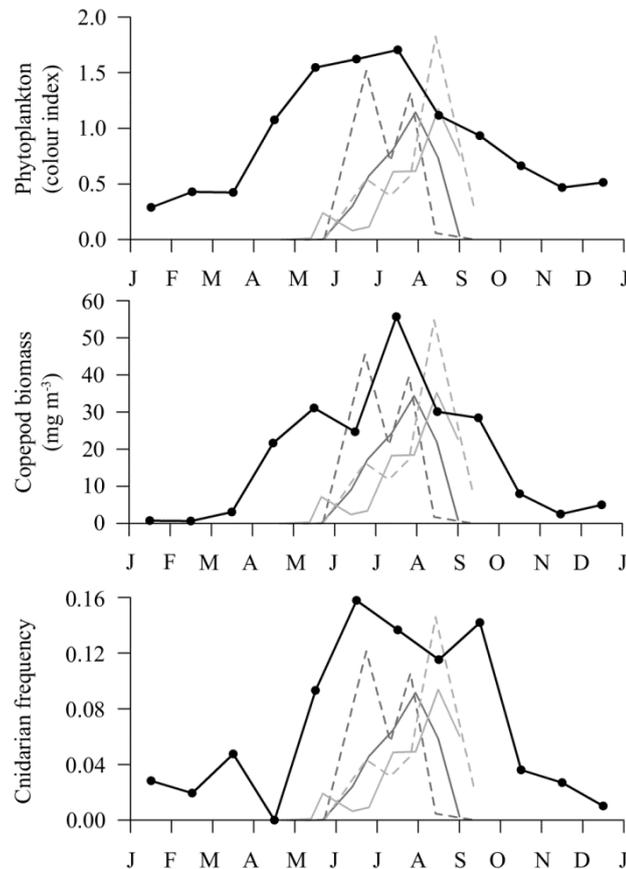


Figure 4.9. Seasonality of different components of the ecosystem of the Irish Sea.

Monthly phytoplankton colour-index, copepod biomass (mean from 1989 to 2008) and cnidarian frequency (mean from 1991 to 2008) are illustrated by solid black lines and are adapted (with permission from author) from data of the Continuous Plankton Recorder for the Irish Sea presented in Lynam et al. (2011). The variation of densities of *Aurelia aurita* and *Cyanea capillata* in 2009 (dashed lines) and 2010 (solid lines) are displayed in dark and light grey respectively. Jellyfish information is presented here only to facilitate comparison of seasonality with CPR records. Note that to that purpose, jellyfish data were transformed so that they all fit on the same axis (by dividing each individual mid-density value by the sum of values of the corresponding year and species), and therefore no comparison of abundance between year and species should be made. Actual values of density for *A. aurita* and *C. capillata* are presented in Figure 4.3.

were more likely to be found in the section between 20 and 30 km offshore, along ferry-route A (Figure 4.4c). Furthermore, the observation of the highest densities occurring at physical discontinuities (Figure 4.6) may reflect the effect of such discontinuities acting as barriers, stopping large numbers of medusae that probably originated in coastal areas (where polyps are more likely to be found) from being advected to more offshore waters. In addition, *Aurelia* sp. are known to actively swim against the shear flow present at physical discontinuities; a behaviour that can lead to the formation of aggregations of

Aurelia sp. in these highly productive regions (Floodgate et al., 1981; Rakow and Graham, 2006).

Another interesting finding of the current study was the existence of groups of several *C. capillata* very close to each other, with more than 100 individuals counted in 5 min on several occasions, and up to 20 individuals counted in a single still image during the camera trial. For *A. aurita*, the use of a camera revealed local densities as high as 24.2 ind. m⁻². This is much higher than the maximum density that could be calculated using categorical counts during an average 5-min period (i.e. 500 individuals over 149,419 km² = 0.003 ind. m⁻²). The generalisation of the use of digital cameras can therefore significantly improve the accuracy of the counts (Figure 4.7) and the frequency and spatial resolution at which data are collected. By doing so it will also facilitate the comparison between surveys conducted on different ships, in different areas. Indeed, the current method based on categorical counts during a set period of time makes the density estimate dependent on the speed of the ship from which the survey is conducted. The use of digital camera also opens the way for new fine-scale investigations on the surface aggregation patterns across large areas (albeit only in day time with current technology). Such information could then be used to inform dynamic spatial ecosystem models or to map prey-fields for the predators of gelatinous plankton, such as the endangered leatherback turtle *Derموchelys coriacea* or the ocean sunfish *Mola mola* (Houghton et al., 2006a; 2006c). It will also have implications for marine planning as it can help to identify areas where the probability of negative interactions of jellyfish with human activities is high.

Different methods are currently available for acquiring broad-scale data on jellyfish distribution and biomass (e.g. acoustic surveys, jellyfish by-catch on fish-surveys, aerial surveys, see Purcell, 2009). Each of these methods presents different advantages and limitations with regards to (1) the spatial and temporal scale they cover, (2) the species they sample, (3) their cost and the ease of implementation, and (4) the type of data they provide. The main limitations of ferry-surveys are: lack of control over the route surveyed; dependency on good weather conditions; the restriction to large, easily identified species present at the surface during daytime (albeit bioluminescent species can be surveyed by night-time); and the lack of information on the densities and biomass of jellyfish in the water column. Our net tows were insufficient to reliably convert surface counts of jellyfish into densities in the water column. This last point is critical to address in future work so that results from visual surveys can be converted into quantitative abundance and biomass (Purcell, 2009; Lilley et al., 2011). Furthermore, the vertical

distributions of jellyfish could differ due to diel vertical migrations, ontogenetic and/or seasonal changes (Hays, 1995; Barz and Hirche, 2005). Recent progress in understanding the diving behaviour of jellyfish by the use of miniaturised time-depth loggers may provide useful ways to address these issues (Hays et al., 2008; 2011; Lilley, 2010; and Chapter 5 of present work).

Ultimately, the choice of method should ideally only be driven by the aim of the study. However, the available resources are often a key constraint. In this context, visual surveys from ShOps provide a reliable cost-effective tool to monitor the relative spatial and temporal distributions of jellyfish across continuous transects (the price of return ticket on ferry-route A in 2010 was ~ €30, while dedicated ship-time on an Irish research vessel costs ~ €8,000 per day). Moreover, the method could easily be implemented at much smaller spatial scales than that of the present study (e.g. a small ferry frequently commuting between two sides of a bay or a harbour). We believe that, over several years, data from these surveys can constitute invaluable local baselines and time-series to investigate the drivers of the inter-annual variations of jellyfish populations, even in regions with limited research capacities and resources.

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Chapter 5

Acoustic tracking of *Cyanea capillata*

Chapter 5 – Acoustic tracking of *Cyanea capillata*

This study was conceived and realised with TK Doyle. TB performed all the data analysis and writing up.

Abstract

Scyphomedusae are generally perceived to passively drift with the currents. However, several studies have suggested that in some cases, scyphomedusae exhibit active behaviours that can affect their distributions. A full understanding of the distribution patterns of scyphomedusae at both large and local scales therefore requires an appreciation of the degree to which they are able to move independently of currents. In Ireland, the lion’s mane jellyfish, *Cyanea capillata*, is a serious risk to recreational open water swimmers. The horizontal and vertical movements of this highly venomous species were investigated in the vicinity of a popular swimming spot in Dun Laoghaire (Co. Dublin, Ireland) using acoustic tracking techniques. Acoustic transmitters were deployed for several hours (range 2.7 – 7.7 h) on 5 individual *C. capillata*. Individual jellyfish travelled between 1.64 and 5.9 km, and exhibited a variety of vertical behaviours during the tracking. The mean vertical speed calculated from > 2-min long continuous upward and downward movements was 1.22 m min^{-1} (SD = 0.86, $N = 33$). The horizontal movements of the tracked individuals broadly followed the local currents (as indicated by drogue deployments), which were driven by the tidal cycle, resulting in a “back and forth” movement of the jellyfish in the study area. However, at times, the speed of travel of the tracked individuals differed from the speed of travel of surface drogues. The present study demonstrates that, although challenging, the deployment of acoustic transmitters on *C. capillata* is feasible and opens the way to more detailed studies on the movements of this ‘problematic’ species.

1. Introduction

The understanding of the distribution patterns of scyphomedusae (Chapters 2 to 4) and the development of efficient strategies to mitigate their potential detrimental impacts on human activities requires an understanding of their movements. Indeed, although hydrographical parameters often play an important role in re-distributing and aggregating scyphomedusae (see review by Graham et al., 2001; and discussion of previous chapters),

several studies have suggested that scyphomedusae can exhibit swimming behaviours that can also actively affect their distributions (Albert, 2011).

For example, in Saanicht Inlet (British Columbia, Canada), *Aurelia aurita* exhibited daily migrations that are oriented toward the sun (Hamner et al., 1994). In marine lakes of Palau, *Mastigias* sp. also exhibited oriented swimming behaviours (Hamner and Hauri, 1981), but with a different orientation of swimming in each lake. Shanks and Graham (1987) artificially deflected individual *Stomolopus meleagris* from their natural swimming trajectory and observed that all of them quickly re-orientated either towards the bearing they were originally heading on, or its reciprocal course (i.e. $\pm 180^\circ$). With regard to vertical movements, the existence of synchronous and asynchronous diel vertical migrations have been documented in several species (Madin et al., 1996; Arai, 1997; Schuyler and Sullivan, 1997; Kaartvedt et al., 2007). In addition, Albert (2009) suggested that *Aurelia labiata* can modify its swimming behaviour to avoid becoming damaged or stranded on rocks in Roscoe Bay (Canada). It has also been suggested (Albert, 2007) that some species could use tidally synchronous vertical migrations to maintain their position within a certain area (i.e. by adjusting their depth during the ebb and flow to avoid being dispersed offshore), but to date, this hypothesis has not been validated (Albert, 2010).

For several decades the use of electronic loggers has allowed investigations of detailed horizontal and vertical movements of many marine vertebrates (see reviews by Kooyman, 2004; and by Block, 2005). Recently, miniaturization of these devices has allowed their deployment on pelagic invertebrates (e.g. Gilly et al., 2006; Hays et al., 2008). Few studies of this type have so far been conducted on jellyfish. Seymour et al. (2004) used acoustic tracking techniques to investigate the horizontal movements of a species of box jellyfish (Cubozoa) (see also Gordon and Seymour, 2009); while Hays et al. (2008; 2011) have pioneered the deployment of small archival tags on scyphomedusae, allowing them to collect detailed vertical movements of *Chrysaora hysoscella* and *Rhizostoma octopus* (one data point collected per minute). Finally, in Japan, Honda et al. (2009) used a mixed approach by deploying satellite pop-up archival tags and acoustic tags on *Nemopilema nomurai*, which allowed them to investigate both the horizontal and vertical movements of this ‘giant’ jellyfish that can reach a diameter of 2 m and a mass of 200 kg.

Along the coasts of the Irish Sea, the lion’s mane jellyfish, *Cyanea capillata*, is a source of concern for many recreational open water swimmers, with several reported cases of people requiring medical attention after being stung (Tom Doyle, *pers. comm.*). To

investigate horizontal and vertical movements of this highly venomous species in the vicinity of a heavily used swimming area (the Forty Foot, Dun Laoghaire, Co. Dublin), acoustic tracking of individual specimens of *C. capillata* was undertaken in July 2010.

2. Methods

2.1. Device attachment

Electronic tags measuring pressure and acoustically transmitting data every 2 s were used for this study (VEMCO V9 continuous transmitters: each 9 mm in diameter, 45 mm in length, weighing 3.5 g in water). The acoustic tag was attached with fishing line to a cable tie which was then attached to the oral arms of *C. capillata* by a snorkeler. *Cyanea capillata* are extremely fragile and because of the skirt-like folds of oral arm tissues, they have no obvious attachment point such as the single solid peduncle found near the bell in *R. octopus*, *N. nomurai*, or *C. hysoscella*. Therefore, the snorkeler had to carefully feel his way around the oral arms to identify and separate out an individual arm before wrapping a cable tie around it (Figure 5.1). It was critical to avoid any pull on the jellyfish oral arms, bell, or even on the transmitters once attached, as such force could easily tear or rip the jellyfish. This attachment procedure was further complicated by the highly venomous

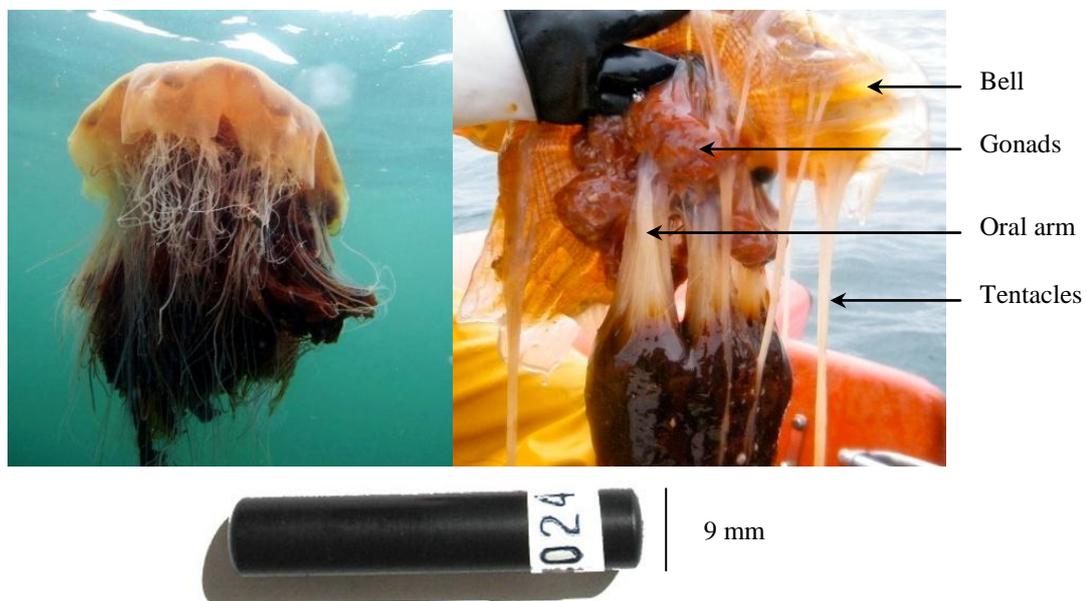


Figure 5.1. Images of *C. capillata* in and out of the water, and the acoustic tag.

Note separation of the oral arms (right-hand picture); the acoustic transmitter was attached to one of these, using a nylon cable tie. Pictures of *C. capillata* by Damien Haberlin and Vanessa Mazza. Picture of the acoustic tag is from californiafishtracking.ucdavis.edu.

nature of the species. All snorkelers wore wetsuits, gloves, hoods and a mask; any exposed skin was covered by plain petroleum jelly (Vaseline®).

Before deployment, a float was attached to the tag to make the jellyfish easily identifiable when right at the surface. Once deployed, the buoyancy of the float was adjusted in-situ so that the float was only slightly buoyant in the top 2 m of water. After deployment, one or two snorkelers observed the animal for several minutes to visually check that the tag and float were not hampering its movement. The signal transmitted by the tag was detected using a hydrophone hand-held in the water from a 5.1 m RIB. The hydrophone was linked to a receiver (VEMCO VR100), allowing real time visualisation and automatic recording of the data (depth) and of the strength of the signal (in dB) emitted by the acoustic tag.

2.2. Horizontal movements

During each tracking trial, a directional hydrophone was used to re-locate the animal. When in the water, the hydrophone received the signal sent by the tag and the strength of this signal was read on the acoustic receiver. At each relocation trial, the boat was moved toward the direction from which the strongest signal was received (at a given distance from the tag, the signal strength is maximum when the directional hydrophone points in the direction of the tag). When the depth information transmitted by the tag indicated that the jellyfish was at the surface, the animal was searched for until visually observed. Its position was then recorded using a handheld GPS (Garmin). When the signal indicated that the jellyfish was at depth, triangulation was used to estimate the position of the jellyfish. In practice, this was accomplished by moving the boat until a strong signal was received (> 80 dB). Then, GPS coordinates were recorded, and a compass bearing toward the direction pointed by the directional hydrophone was taken. The boat was then moved off by a few hundred metres in a different direction and a new GPS point and compass bearing recorded. For each relocation trial, 2 to 4 points with bearing readings were taken. The intersection point of the lines drawn from these different points in the direction of corresponding bearings was taken as the jellyfish's estimated position. When the lines did not exactly intersect due to imprecisions inherent in measurements from a RIB (i.e. continuously moving and rocking platform, time lapse between successive positions), the coordinates of the middle-point between the two points where the strongest signal was recorded were used as an estimate of the position of the jellyfish. For each relocation trial,

the intermediate time between the first and final points of the relocation trial was used as a time-stamp for the estimated jellyfish position.

To compare the horizontal movements of the tracked individuals with local currents, a drifting cruciform drogue (drifter) was deployed close to the jellyfish immediately after deployment of the tag. A handheld GPS was attached to the drogue and was set to automatically record its position every minute. At times, when the jellyfish and the drogue had drifted apart and there was a real danger of losing sight of the latter, the drogue was recovered and redeployed next to the jellyfish. This also ensured that the movements of the drogue reflected the hydrographical conditions next to the jellyfish rather than several hundred metres away.

Distances between successive GPS positions were calculated using the haversine formula (implemented in the R ‘geosphere’ package from Hijmans et al., 2011). This was also used to calculate distances between the jellyfish and the drogue. Horizontal travel speed was calculated by dividing these distances by the elapsed time between the time-stamps of successive positions.

2.3. Vertical movements

The tag transmitted depth reading every 2 s. Noise in the signal was filtered by deleting all records with a signal strength < 60 dB (60 dB was arbitrarily chosen after consideration of the high number of impossible depth records occurring below this value in the depth vs. signal-strength scatterplot). As depth readings could only be recorded when the hydrophone was in the water (which was not possible when the boat was on the move), the record was non-continuous. Depth records were therefore visually analysed rather than using automatic algorithms. Obvious long descent or ascent movements were extracted, and a vertical speed was calculated for each of them by fitting a line through the points using a least square procedure (the slope of fitted line was taken as the vertical speed). Depth readings from the echo-sounder of the RIB were taken on several occasions during tracking trials to estimate the depth of the seabed.

Five tracking trials were conducted between the 5th and 23rd July 2010 in the vicinity of Dun Laoghaire (Co. Dublin, Republic of Ireland). Details of sampling dates, time and locations of tag deployment and recovery are presented in Table 5.1.

Table 5.1. Acoustic tracking of *C. capillata* in July 2010.

ID	Size (cm)	Date	Deployment			Recovery			Duration (h)	<i>N</i> relocations	Distance travelled (km)	Mean vertical speed (m min ⁻¹)
			Time	Lat	Lon	Time	Lat	Lon				
J05	26	05-Jul	11:10	53.2898	-6.1073	17:54	53.3043	-6.1490	6.73	10	4.10	0.78 (<i>N</i> = 10)
J12	48	12-Jul	12:29	53.2886	-6.1062	15:56	53.2603	-6.1007	3.45	4	5.66	1.61 (<i>N</i> = 5)
J20	25	20-Jul	16:40	53.3052	-6.1282	19:21*	53.3084	-6.1509	2.68	4	1.64	0.53 (<i>N</i> = 7)
J21	35	21-Jul	11:06	53.2877	-6.1091	18:48*	53.3102	-6.1401	7.70	5	5.94	1.63 (<i>N</i> = 3)
J23	35	23-Jul	10:47	53.2883	-6.1081	15:20	53.2728	-6.0916	4.55	7	2.81	1.97 (<i>N</i> = 8)

* tag was not recovered, this is the last relocation position

3. Results

Five individual *Cyanea capillata* were followed, each for several hours (ranged from 2.68 to 7.7 h), with a minimum of 4 relocations for each individual (max = 10). The total horizontal distance travelled varied between 1.64 and 5.94 km, with a mean speed (\pm SD) of $0.24 \pm 0.12 \text{ m s}^{-1}$. Details for each tracked individual are presented in Table 5.1, and Figure 5.2 presents the successive estimated positions of each jellyfish.

3.1. Horizontal movements

Overall, the tracked individuals and drogues moved in the same direction (i.e. with the current), with a marked change in the direction of travel being observed for both the jellyfish and the drogues at the times corresponding to the turn of tide. However, in all trials the jellyfish and the drogue progressively drifted apart (Figure 5.2). The speed of this drift between the jellyfish and the drogue was highly variable (Table 5.2). Nevertheless, the jellyfish and the drogue exhibited comparable travel speeds at the beginning and the end of each trial, sometimes for several hours, suggesting that part of the divergence of their trajectories may be due to divergent small-scale hydrographical features. In fact, on the 23/07, the trajectories of the drogue suggest the presence of small eddies in the study area (Figure 5.2). However, each tracking also showed that, at times, the drogue travelled twice as fast as jellyfish (Figure 5.3). It was not possible to consistently link this with any obvious parameters (e.g. state of tide).

Table 5.2. Measures of drift between the trajectories of jellyfish and drogues.

Date bloa	Drogue deployment	Max drift distance (m)	Time since drogue deployment (h)	Time since beginning of tracking (h)
05-Jul	1	442	2.50	2.58
	2	382	1.20	3.87
	3	366	2.68	6.73
21-Jul	1	1,006	4.57	4.57
	2	2,689	1.60	6.70
	3	769	0.70	7.70
23-Jul	1	751	0.88	0.80
	2	1,299	1.15	2.23
	2	505	1.80	2.88
	3	82	0.25	3.32

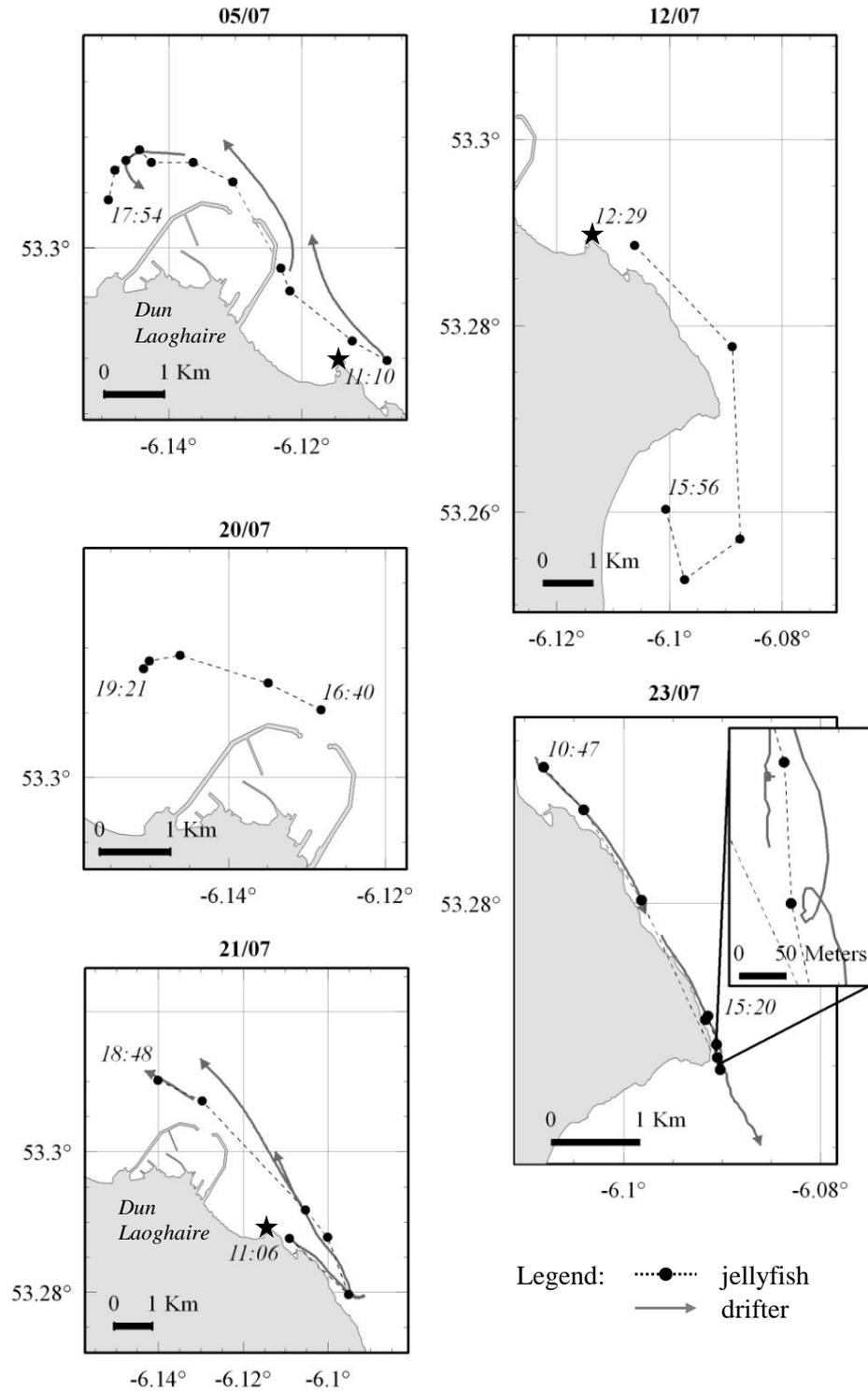


Figure 5.2. Acoustic tracking of five *C. capillata* in July 2010.

Time of tag deployment and recovery is indicated. On 05/07, 21/07, and 23/07, drogues, each equipped with a GPS, were deployed near the jellyfish position and repositioned during the trial. Grey arrows show the GPS tracks of these drogues. Note the close up on the drogue trajectory on the 23/07 showing the presence of small scale eddies in the tracking areas. A black star marks the location of the Forty Foot, a famous place in Ireland for open-water swimming.

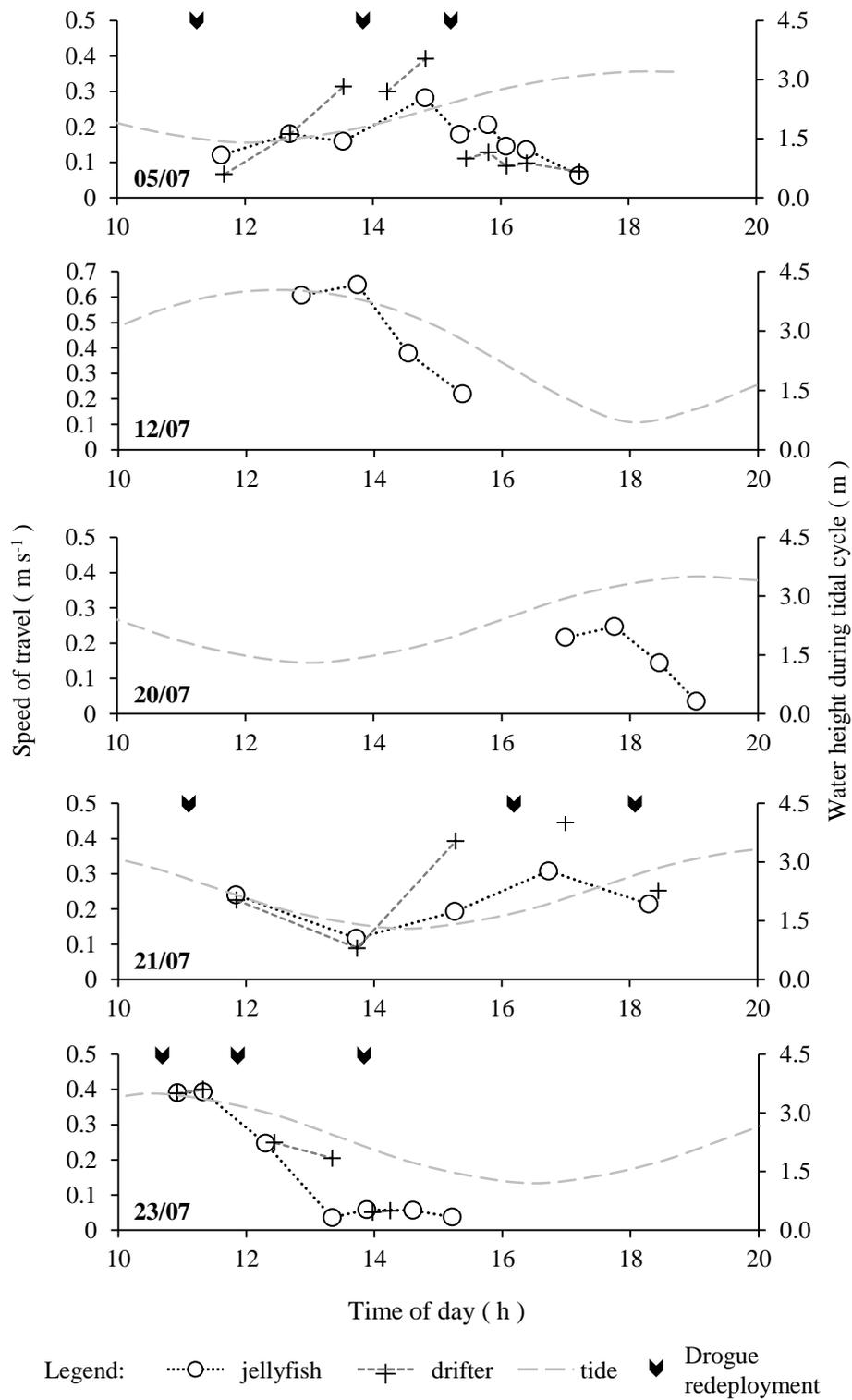


Figure 5.3. Speed of travel of jellyfish and drogues during tracking trials.

Open circles are for speed of jellyfish, black crosses for speed of the drogue. Black chevrons indicate times when the drogue was initially deployed and then manually moved closer to the jellyfish during the trials. Variation of water height during the tidal cycle of each day is shown (light grey dotted line) as an indication of tidal state (tidal cycle simulated using tide table for Dublin and the rule of twelfths).

3.2. Vertical movements

Every tracked jellyfish exhibited a range of vertical movements (Figure 5.4). On several occasions, v-shaped movements (i.e. from the surface to the bottom and back to the surface) were observed. Some of the tracked individuals (12 July, 23 July) spent long periods of time at the surface. Conversely, sometimes, the animals spent several minutes close to the bottom before swimming upwards again.

Thirty-three > 2 min-long (range 2 – 18 min) upward or downward continuous moves ($n = 16$ and 17 respectively) were extracted from the time-depth records. The variations of depth between these movements ranged between 2.2 to 8.3 m. Least squares procedure was used to fit a line through each of these individual movements and to deduce the associated vertical speed (i.e. the slope of the line, all R^2 values associated with fitted lines > 0.80). The overall mean vertical speed was 1.22 m min^{-1} (range = $0.29 - 3.98 \text{ m min}^{-1}$, median = 0.93 m min^{-1} , SD = 0.86). Upward movements were significantly faster (median speed = 1.47 m min^{-1} , SD = 0.75, $N = 16$) than downward movements (median speed = 0.55 m min^{-1} , SD = 0.92, $N = 17$) (Wilcoxon rank-sum test, $W = 69$, $p = 0.015$). Large individuals exhibited greater vertical speeds than smaller ones (Table 5.1).

4. Discussion

Understanding the movements of individual scyphomedusae is a necessary step towards an understanding of their spatial dynamics. In that regard, the present work was the first attempt to record the movements of the lion's mane jellyfish in the vicinity of an area where swimmers often encounter this highly venomous species.

The deployments of loggers on *Cyanea capillata* represent additional difficulties compared with other jellyfish species. Unlike box-jellyfish (Seymour et al., 2004; Gordon and Seymour, 2009), *C. capillata* cannot be caught by a landing-net and brought to the surface without damaging the individual. The deployment of the tag on *C. capillata* therefore had to be done underwater. This has also been the case for studies on other scyphozoan species, but in *C. capillata*, the absence of an easily accessible body-part (peduncle in *Rhizostoma octopus*, base of the oral arms for *Chrysaora hysoscella*) around which to attach the device, and the potential serious consequences of being stung by *C. capillata*, makes this operation even more complicated (Figure 5.1). These difficulties, added to the necessity of good weather to operate from a RIB, account for the small sample size of the present study. However despite these limitations, the data collected provided valuable information.

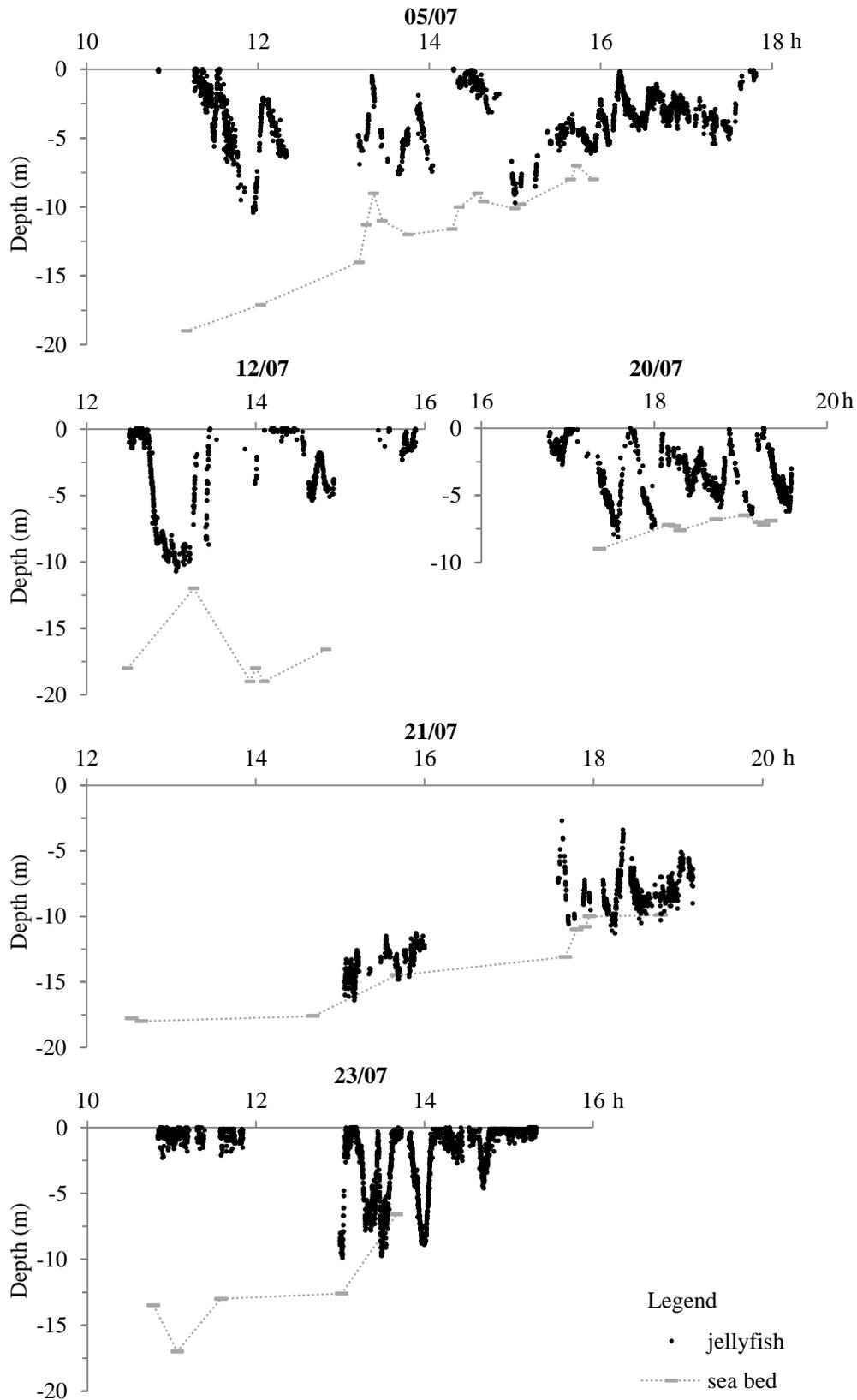


Figure 5.4. Dive records of the five *C. capillata* tracked in July 2010. Depths of seabed as indicated by RIB echo-sounder are shown by grey ticks and dotted lines.

The first finding of the present work was that individual *C. capillata* moved in the direction of the prevailing currents (Figure 5.2), and these were mostly driven by the tidal cycle. As a result, we observed that the tracked *C. capillata* were moving along the shore in a direction predictable from the time of the day and the state of the tide. In addition, during each tracking trial we recorded a change in the predominant direction of the jellyfish horizontal movement, and the timing of this change was closely matched with the turn of the tide (Figure 5.2). This suggests that, in Dublin Bay, the tidal cycle drives *C. capillata* in a “back and forth” movement with the likely consequence of greatly increasing the residency time of the species within the area (although records over a complete tidal cycle would be necessary to precisely document and assess the retention effect of this tidal flow). Interestingly, after acoustically tracking several *Chironex fleckeri* (Cubozoa, box jellyfish), Gordon and Seymour (2009) concluded that the travel rate of this species was influenced by the tidal flow in estuarine habitats, but not in coastal non-estuarine habitats. As box jellyfish are active visual predators, Gordon and Seymour (2009) suggested that their horizontal travel-rate may reflect their feeding activity rather than the effect of the currents (and therefore that differences between estuarine and coastal habitats may be due to prey availability changing with tidal state in estuarine habitats, but remaining relatively the same throughout the tidal cycle in coastal areas). Box jellyfish like *C. fleckeri* have a robust and quite solid bell and are capable of rapid swimming (Shorten et al., 2005), and are therefore more likely to be able to achieve greater independence of hydrographical conditions than scyphomedusae like *C. capillata*, which have a far more flexible and fragile bell. However, the fact that in the present work, the jellyfish and the drogue were found to drift apart, and that the travel speed of the drogue was at times twice that of the scyphomedusae, may suggest that *C. capillata* has some ability to limit horizontal displacements away from the main tidal flow. For example, the most extreme case of divergence between jellyfish and drogue in this study was 1,300 m in 1.15 h, quite a significant displacement. Interestingly, individual *C. hysoscella* tracked in Ventry harbour (Co. Kerry, Ireland) (Lilley, 2010) were found to travel significantly more slowly than drifters deployed at the same time. However, Lilley’s study was based on visual tracking of surface floats tethered to the jellyfish, and the author could not exclude the possibility that the observed differences in horizontal speed may be due, at least to some degree, to the drag caused by the tether (Lilley, 2010). Acoustic tracking technology such as that used in the present study, greatly reduces the problem of the drag, nevertheless, a larger sample size would be necessary to reliably test for differences between the horizontal speed of *C. capillata* and the speed of the local

currents. Tracking of the giant jellyfish *Nemopilema nomurai* tracked in the Sea of Japan, suggested that horizontal movements of the species were driven by the currents (Honda et al., 2009).

The second finding of the present study was that the tracked individuals exhibited a variety of vertical behaviours (Figure 5.4). In situ-observations of different species of Scyphozoa have revealed that scyphomedusae spend 93-100 % of their time actively swimming (Costello et al., 1998); a behaviour probably linked to the importance for feeding and respiration of the flow created by each pulsation of the bell (Costello and Colin, 1995). More specifically, Costello et al. (1998) described how *C. capillata* could swim upwards for long periods and how, once at the surface the animals often stopped swimming and passively sank, but sometimes orientated themselves downwards and actively swam to the bottom. The types of behaviours observed in the current study ranged from v-shaped dives to extended times spent either at the surface or at the bottom (Figure 5.4). The mean vertical speed of *C. capillata* was of the same order of magnitude as that reported for other scyphozoan species of comparable size studied in the wild (Table 5.3). The differences between upward and vertical speeds reported here perhaps reflect the active upward swimming vs. passive downward sinking patterns described by Costello et al. (1998). Interestingly, a variety of different types of vertical movements have also been reported for other scyphozoan species whose swimming behaviours have been investigated in the wild. For example, several day-long records of the vertical movements of *R. octopus*, obtained via archival time-depth loggers, revealed the existence of different types of behaviours and important degrees of inter-individual variations in the time-budgets of these respective behaviours (Lilley, 2010; Hays et al., 2011). Such inter-individual variations were also observed in the vertical movements of several *N. nomurai* equipped with archival satellite tags in Japan: some individuals exhibited clear diurnal dive patterns, one other individual spent several days at depth, while another spent several days close to the surface (Honda et al., 2009). Finally, asynchronous vertical migration patterns have been clearly demonstrated in a population of *P. periphylla* of the Lurefjord (Norway) (Klevjer et al., 2009). Future work on *C. capillata* should therefore involve increasing the length and the quality of vertical movement records so that time-budgets for each type of behaviour, for each individual, can be calculated, and the existence of patterns related to tidal or diurnal cycles can be investigated. The issue of collecting non-continuous records could be overcome by using a hydrophone that can remain permanently in the water (Honda et al., 2009), or by

combining the use of acoustic pingers with the use of archival tags (although the weight of a multi-tag assemblage might become an issue).

To summarise, despite many limitations, the present study demonstrated that, although challenging, the deployment of acoustic transmitters on *C. capillata* is possible, and opens the way to more detailed study on the movements of this venomous species.

Table 5.3. Vertical swimming speed of different scyphozoan species.

Species (Number of individuals)	Bell diameter (cm)	Vertical speed (m min ⁻¹)			Method	Reference
		Mean*	SD	Range (min – max)		
<i>Cyanea capillata</i> (N = 5)	25 – 48	1.22	0.86	0.29 – 3.98	Acoustic tag	This study
<i>Chrysaora hysoscella</i> (N = 15)	19 – 33	1.14	0.64	0.39 – 2.32	Archival time depth recorder (TDR)	Hays et al. (2008)
<i>Rhizostoma octopus</i> (N = 6)	~ 60	Range of medians: 0.72 – 1.33	-	Max ascent 3.17 m min ⁻¹ Max descent 3.16 m min ⁻¹	Archival time depth recorder (TDR)	Lilley (2010)
<i>Peryphilla peryphilla</i> (N = 701)	3 – 6	0.618	1.07	90% of individual speed between +1.56 m min ⁻¹ (up) and -2.22 m min ⁻¹ (down)	Echogram analysis	Klevjer et al. (2009)
<i>Nemopilema nomurai</i> (N = 14)	60 – 160	6.73	2.39	1.8 – 10.2 m min ⁻¹	Direct observation	Honda (2009)

* save in the case of *Rhizostoma octopus*, for which only the median vertical speed for each tracked individual was available.

Chapter 6

General Discussion

Chapter 6 – General Discussion

As worldwide concern about jellyfish outbreaks and their consequences on human activities have risen, our limited knowledge of the ecology of scyphomedusae and other gelatinous organisms has become increasingly obvious. In recent years, much progress has been made in identifying the ecological processes that scyphomedusae contribute to (see Chapter 1), and one of the main challenges is now to refine and quantify the nature of these contributions. The necessary first step in doing so is to evaluate the abundance of scyphomedusae and investigate their distribution patterns across extended spatial scales (Purcell, 2009). However, the cost involved in organising dedicated surveys is a major obstacle in achieving this goal. A solution to overcome this problem is to use the opportunities provided by existing programmes, such as annual fisheries surveys and other such ships of opportunity (e.g. Hay et al., 1990; Brodeur et al., 1999).

The present work shows how, by recording jellyfish bycatch at species level during the Irish groundfish survey (IGFS), detailed information on the distribution of *P. noctiluca* was made available for an area > 160,000 km² around Ireland (Chapter 2); a scale never reached before for this species in the Northeast Atlantic (and only rarely in the Mediterranean Sea). Furthermore, the data collected during the IGFS revealed how this species, although unequally distributed, was present all over the continental shelf North and West of Ireland during the last quarter of 2009 (and again in 2010: T. Bastian; *pers. obs.*). These findings complement the results from opportunistic plankton tows, visual surface counts (Doyle et al., 2008), and reanalysis of samples from the CPR programme (Baxter et al., 2010; Licandro et al., 2010), that previously demonstrated the widespread presence of the species off the Irish continental shelf in autumn 2007 and 2008. This demonstrates the extent to which *P. noctiluca* is a common member of the autumnal planktonic community of the waters off the North and West coast of Ireland. Considering the risk posed by the species for farmed fish in coastal waters (Doyle et al., 2008; Hay and Murray, 2008), its widespread presence over the shelf represents a legitimate source of concern for the Irish aquaculture industry. It also calls for further investigations of the species' role in the ecosystem, especially in terms of interactions with fish (Malej, 1989; Giorgi et al., 1991; Sabatès et al., 2010). Furthermore, in November 2010, jellyfish bycatch data were recorded during the second leg of the annual French groundfish survey

(EVHOE cruise) and revealed the presence of *P. noctiluca* at all sampling stations (T. Bastian; *pers. obs.*). The species is therefore most likely present throughout the waters over the western-European continental shelf. This example highlights how a potential coordinated effort to record jellyfish bycatch during fish surveys could greatly improve our knowledge of their worldwide distribution. In the case of *P. noctiluca*, such effort could provide useful time-series data to investigate the existence of possible links between the annual abundance of the species in the Northeast Atlantic and hydroclimatological factors (as has been demonstrated in the Mediterranean Sea).

The data from a different annual fish survey (Irish Sea juvenile gadoid fish survey, hereafter referred to as the ISS) was used to investigate the abundance of scyphomedusae across the Irish Sea (Chapter 3). The bycatch dataset from the 2007-2010 ISS provided the first available description of the distribution of *Aurelia aurita* and *Cyanea* spp. across the entire Irish Sea basin, both in coastal and offshore waters. It revealed how, in some areas of the basin, both species are already present high abundance as early as late-May – early-June. The analysis of this dataset also demonstrated how variable the distributions of *A. aurita* and *Cyanea* spp. can be from one year to the other, and how inter-annual variations of abundances differ in different regions of the basin. In particular, it was observed that between 2007 and 2010, the eastern half of the basin experienced a higher inter-annual variability than the western part of the basin. With major spawning grounds of commercially important fish species localised in the eastern part of the basin, the impact of such inter-annual variability on the abundance of potential predators of fish eggs and larvae should be further investigated.

Interestingly, in the western part of the basin, jellyfish bycatch data have been recorded since 1994 (but without species-specific details until 2007), and the analysis of the available time-series revealed that the inter-annual variations in the mean catch of scyphomedusae correlate positively with sea surface temperatures and copepod abundance of the previous year, and negatively with precipitations of previous months (Lynam et al., 2011; in Appendix B). As the time series of the eastern part of the basin expands, it will be interesting to test whether the regional differences in the inter-annual dynamics of *A. aurita* and *Cyanea* spp. are due to regional-specific dynamics of these environmental factors.

In addition to providing a time-series to investigate the drivers of the inter-annual variations of the abundance of scyphomedusae in the Irish Sea, the data collected during the ISS present an extra advantage: they can be considered as actual quantitative

estimates of scyphomedusae biomass at sampling sites. This was not the case for data from the IGFS. Indeed, because of the type of fishing gear used during the IGFS cruise (demersal trawl), the catch-rates (or catch-biomass) of *P. noctiluca* reported in Chapter 2 were only indices of the abundance of medusae and not an actual measure of their biomass in the area. These limitations do not apply to the ISS during which sampling is by MIK net, one of the most suitable devices for quantitative sampling of medium-sized scyphomedusae such as *Aurelia aurita* and juvenile *Cyanea* spp.. Moreover, data on the abundance and distributions of 0-group gadoid fish, fish larvae and other zooplankton are also collected during the ISS. Consequently, data from this survey represent a unique opportunity to investigate the links between the abundances of scyphomedusae and the other components of the Irish Sea ecosystem. This seems to be a critical point to address considering the potential negative (through competition and predation) or positive (acting as a shelter from visual predator, or food supply) impacts that scyphomedusae can have on fish (Purcell and Arai, 2001; Lynam and Brierley, 2006) and will therefore be the focal point of future studies.

Furthermore, Behrends and Schneider (1995) suggested that outbreaks of *Aurelia aurita* in the Kiel Bight in 1993 resulted in significantly reduced stocks of copepods, plus substantial modifications of the composition of the copepod communities. More precisely, they suggested that high densities of *A. aurita* resulted in reductions in the stocks of *Pseudocalanus* and *Paracalanus* spp. and *Oithona similis*, but little change in stocks of *Centropages hamatus* and *Acartia* spp. Now, these copepod species are precisely those for which early-life-history-stages of Irish Sea Cod, Whiting, and Haddock exhibit differential preferences that allow them to limit the competition pressures that could exist amongst them for access to zooplanktonic prey (Rowlands et al., 2008). Therefore, if Behrends and Schneider (1995) are correct, and the planktonic community changes they observed in the Kiel Bight were indeed directly due to the effect of jellyfish (rather than simply a bottom-up effects of the same environmental parameters that lead to the proliferation of jellyfish), then the possibility should be considered that, in addition to generating predation pressure on fish larvae (e.g. Möller, 1984), jellyfish outbreaks can also affect the fish community in more complex ways such as by altering the conditions of intra-guild competition amongst the early-life-stages of different species of fish. Interestingly, the highest densities of *A. aurita* recorded in the Irish Sea (up to 27.5 ind. 100 m⁻³) are very similar to densities that Behrends and Schneider (1995) considered as bloom densities in the Kiel Bight (up to 24 ind. 100 m⁻³).

Another point highlighted by the analysis of the 2007-2010 Irish Sea jellyfish bycatch data was the differences in pattern descriptions depending on whether the abundances of scyphomedusae were reported as biomass or as densities. In particular, in 2010, the significantly higher biomass of *Cyanea* spp. in the eastern part of the basin than in 2007-2009, was not due to significant higher numbers of individuals than the previous years, but to individuals being larger on average. These findings imply that bycatch data collected only as biomass could be misleading and that it is critical that the number of individuals present in the catch is also recorded. Moreover, the average wet weight per individual was different in different hydrographical regions of the Irish Sea, with significantly larger *A. aurita* occurring in stratified than in mixed waters (Figure 3.6). It is suggested here that these variations could be linked to the differences in timing and yields of primary and secondary production in different regions of the Irish Sea.

The question of seasonal alterations in population dynamics of jellyfish, and of their inter-annual variations is important to address as it is undoubtedly a potential source of bias in time series built on bycatch dataset collected at fixed dates every year (Lynam et al., 2011). Accordingly, a monitoring programme using ships of opportunity was implemented (Chapter 4), in order to reveal the seasonal variability in the abundance of scyphomedusae in the Irish Sea, and complement the ‘snapshots’ of jellyfish distributions provided by the analysis of the Irish Sea bycatch dataset (Chapter 3). The data collected during summers 2009 and 2010, along the ~100 km long transect between Dublin and Holyhead, are the first available records of the seasonal abundance and distribution of medusae at such a scale and resolution anywhere in the Irish Sea (Chapter 4). This seasonal monitoring demonstrated how both the abundances and surface distributions of jellyfish change through the season. In particular, it revealed how, early in the season, the distributional areas of *A. aurita* and *C. capillata* are relatively limited, but then progressively spread throughout the transect during the summer. In addition, by coupling these surface counts with freely available records of environmental parameters, it was possible to link some high density patches of jellyfish with the presence of hydrographical features (e.g. the front between two distinct water-masses). In terms of changes in the timing of jellyfish occurrence, the surveys suggested that *A. aurita* was slightly delayed in time in 2010 compared with 2009 (Figure 4.3).

However, if the data from the seasonal monitoring (Chapter 4) are compared with data collected during the ISS (Chapter 3), it becomes clear that the seasonal dynamics observed on the Dublin-Holyhead transect, do not reflect the seasonal dynamics of the scyphomedusae throughout the Irish Sea. Indeed, during the ferry-survey monitoring, no

A. aurita were observed before mid-June in 2009 (and only 2 in 2010), whereas bycatch data from the ISS clearly demonstrated the presence of high densities of *A. aurita* in several areas of the Irish Sea in late-May – early-June. Two possibilities could explain this result. The first one would be that the seasonality of occurrence of *A. aurita* in the regions sampled by the ferry-surveys differs from that of other regions of the Irish Sea. This could either result from a delayed production of scyphomedusae in that area (Lucas, 2001), or instead from the fact that jellyfish presence in this area would be dependent on their advection from another location (Barz and Hirche, 2005). The second possibility is that the vertical distributions of scyphomedusae change through the season and affect their detectability during the ferry surveys. Such seasonal changes in the vertical distributions of *A. aurita* and *C. lamarckii* have been observed in the Bornholm Basin of the Baltic Sea and in the Southern North Sea, respectively (Barz and Hirche, 2005; 2007). When examined in detail, data from the ISS show that, in 2009 and 2010, no *A. aurita* and only a few *Cyanea* spp. were caught at the sampling stations located close to the Dublin-Holyhead ferry route (Figure 3.4). This supports the first hypothesis (i.e. that the occurrence of these two species between Dublin and Holyhead is indeed delayed in the season compared with other regions of the basin). It would therefore be valuable to investigate the seasonal occurrence of jellyfish in other regions of the Irish Sea by using different Ferry Routes (e.g. between England or Northern Ireland and the Isle of Man).

The question of the vertical distribution of scyphomedusae remains nonetheless critical to address as it is, indeed, the main source of potential bias in using visual surface counts as a proxy of jellyfish overall abundance (Sparks et al., 2001). Unfortunately, the net tow trials presented in Chapter 3 were inconclusive, due to the lack of large aggregations in the areas where they were conducted. The ideal situation would have been to be able to conduct visual surveys simultaneously with MIK net deployments during the ISS, but as the sampling protocol of the ISS requires that fishing is only conducted at night-time, this was impossible. Therefore, access to dedicated ship time to address this question in the future seems necessary. In the meantime, successful deployments of miniaturized electronic devices on medium size scyphomedusae offer new possibilities to investigate the horizontal and vertical behaviours of jellyfish (Chapter 5). This should provide opportunities to test for patterns that can bias visual surface counts (e.g. diel vertical migration, tidally synchronous movements, ontogenic changes of behaviour).

To summarise, with access to jellyfish bycatch data, the study of jellyfish distributions in Irish waters switched from occasional samplings restricted mostly to coastal waters, to systematic regular widespread offshore sampling. Now that access to such information is

possible, it is hoped that the data collection will continue and lead to the creation of time-series of the abundance of scyphomedusae in Irish waters. These are critically required to identify the drivers of the regional and inter-annual patterns described here and to address the concerns of society about jellyfish (Haddock, 2008; Richardson et al., 2009; Purcell, 2012). However, it must be stressed that the understanding of the mechanisms by which environmental factors drives the abundance of scyphomedusae will necessarily require an understanding of how these factors influence the different stages of the scyphozoan life-cycle (Brewer and Feingold, 1991; Mills, 2001; Boero et al., 2008; Prieto et al., 2010). Finally, the approach presented in the present work (i.e. the collection and analysis of scyphomedusae bycatch data) is arguably the most straightforward and cost-effective way of collecting data on jellyfish abundance. These are urgently required to develop a reliable ecosystem approach to fisheries management (Pauly et al., 2009) and therefore, the record of jellyfish bycatch should be generalized to other fish surveys worldwide.

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APPENDIX A

STATISTIC TABLES RELATIVE TO CHAPTER 3

Inter-annual variations in the abundance of scyphomedusae throughout the Irish Sea.

Table A.1. Inter-annual variations of abundance of *Cyanea* spp. across the entire Irish Sea. Wilcoxon rank-sum test on abundance expressed in volume-standardised biomass (*b*, grey cells) and in densities (*d*, bottom-left diagonal).

<i>d</i> \ <i>b</i>	2007	2008	2009	2010
2007	-	W = 1670 N₀₇ = 52 ; N₀₈ = 43 p < 0.001	W = 1969 N₀₇ = 52 ; N₀₉ = 50 p < 0.001	W = 806 N ₀₇ = 43 ; N ₁₀ = 37 p = 0.923
2008	W = 1496 N₀₈ = 43 ; N₀₇ = 52 p = 0.005	-	W = 1312 N ₀₈ = 50 ; N ₀₉ = 56 p = 0.580	W = 480.5 N₀₈ = 42 ; N₁₀ = 43 p < 0.001
2009	W = 1754 N₀₉ = 50 ; N₀₇ = 52 p = 0.002	W = 1302 N ₀₉ = 56 ; N ₀₈ = 50 p = 0.535	-	W = 720.5 N₀₉ = 49 ; N₁₀ = 43 p = 0.009
2010	W = 1123 ; N₁₀ = 37 ; N₀₇ = 43 p = 0.002	W = 866 N ₁₀ = 43 ; N ₀₈ = 42 p = 0.748	W = 1154 N ₁₀ = 43 ; N ₀₉ = 49 p = 0.436	-

Table A.2. Inter-annual variations of abundance of *A. aurita* across the entire Irish Sea. Wilcoxon rank-sum test on abundance expressed in volume-standardised biomass (*b*, grey cells) and in densities (*d*, bottom-left diagonal).

<i>d</i> \ <i>b</i>	2007	2008	2009	2010
2007	-	W = 1389 N₀₇ = 52 ; N₀₈ = 43 p = 0.041	W = 84 N₀₇ = 52 ; N₀₉ = 50 p = 0.003	W = 822.5 N ₀₇ = 4 ; N ₁₀ = 37 p = 0.797
2008	W = 1330 N ₀₈ = 43 ; N ₀₇ = 52 p = 0.110	-	W = 830 N₀₈ = 50 ; N₀₉ = 55 p < 0.001	W = 758 N ₀₈ = 42 ; N ₁₀ = 43 p = 0.197
2009	W = 757 N₀₉ = 50 ; N₀₇ = 52 p < 0.001	W = 800 N₀₉ = 55 ; N₀₈ = 50 p < 0.001	-	W = 1272 N ₀₉ = 49 ; N ₁₀ = 43 p = 0.056
2010	W = 780.5 ; N ₁₀ = 37 ; N ₀₇ = 43 p = 0.888	W = 733 N ₁₀ = 43 ; N ₀₈ = 42 p = 0.130	W = 1304 N₁₀ = 43 ; N₀₉ = 49 p = 0.030	-

Inter-annual variations in the distribution patterns of scyphomedusae throughout the Irish Sea.

Table A.3. Inter-annual variations in the distribution of *Cyanea* spp. in the Irish Sea.

The upper-right diagonal (grey cells) present the result of the Syrjala test (Ψ value and associated p -value) conducted on volume-standardised biomass (b , g m⁻³), the lower-left diagonal (white cells) present results from test conducted on densities (d , ind. 100 m⁻³). The null hypothesis of the Syrjala test is that the distribution between years is the same.

$d \setminus b$	2007	2008	2009	2010
2007	-	$\Psi = 3.41$ $p = 0.002$	$\Psi = 1.17$ $p = 0.0599$	$\Psi = 0.76$ $p = 0.008$
2008	$\Psi = 2.54$ $p = 0.001$	-	$\Psi = 7.83$ $p = 0.001$	$\Psi = 2.05$ $p = 0.005$
2009	$\Psi = 1.17$ $p = 0.061$	$\Psi = 5.74$ $p = 0.001$	-	$\Psi = 4.00$ $p = 0.002$
2010	$\Psi = 0.76$ $p = 0.022$	$\Psi = 0.32$ $p = 0.1449$	$\Psi = 2.02$ $p = 0.007$	-

Table A.4. Inter-annual variations in the distribution of *A. aurita* in the Irish Sea.

The upper-right diagonal (grey cells) present the result of the Syrjala test (Ψ value and associated p -value) conducted on volume-standardised biomass (b , g m⁻³), the lower-left diagonal (white cells) present results from test conducted on densities (d , ind. 100 m⁻³). The null hypothesis of the Syrjala test is that the distribution between years is the same.

$d \setminus b$	2007	2008	2009	2010
2007	-	$\Psi = 5.17$ $p = 0.058$	$\Psi = 1.16$ $p = 0.553$	$\Psi = 2.23$ $p = 0.176$
2008	$\Psi = 6.74$ $p = 0.017$	-	$\Psi = 2.91$ $p = 0.009$	$\Psi = 1.19$ $p = 0.062$
2009	$\Psi = 2.27$ $p = 0.261$	$\Psi = 2.30$ $p = 0.027$	-	$\Psi = 1.95$ $p = 0.169$
2010	$\Psi = 5.69$ $p = 0.039$	$\Psi = 1.04$ $p = 0.1139$	$\Psi = 2.70$ $p = 0.037$	-

Testing for potential association between *A. aurita* and *Cyanea* spp.

Table A.5. Correlations between the annual abundance of *Cyanea* spp. and *A. aurita*.
Spearman's rank correlation test run on abundance expressed in biomass (first line) and densities (second line).

	2007		2008		2009		2010	
	<i>rho</i>	<i>p</i>	<i>rho</i>	<i>p</i>	<i>rho</i>	<i>p</i>	<i>rho</i>	<i>p</i>
Biomass (g m ⁻³)	0.230	0.049	0.416	< 0.001	0.180	0.110	-0.018	0.877
Densities (ind. 100 m ⁻³)	-0.007	0.954	0.206	0.075	0.158	0.163	-0.007	0.954

Table A.6. Comparison of annual distribution patterns of *Cyanea* spp. and *A. aurita*.
The result of the Syrjala test (Ψ value and associated *p-value*) conducted on volume standardised biomass (g m⁻³) are presented in the first line; results from the test conducted on densities (ind. 100 m⁻³) is in the second line. The null hypothesis of the Syrjala test is that the distributions of the two species are the same.

	2007	2008	2009	2010
Biomass (g m ⁻³)	$\Psi = 0.51$ <i>p</i> = 0.586	$\Psi = 9.00$ <i>p</i> = 0.001	$\Psi = 1.51$ <i>p</i> = 0.3157	$\Psi = 5.69$ <i>p</i> = 0.001
Densities (ind. 100m ⁻³)	$\Psi = 3.53$ <i>p</i> = 0.033	$\Psi = 6.46$ <i>p</i> = 0.004	$\Psi = 7.2$ 10-10 <i>p</i> = 0.8392	$\Psi = 5.93$ <i>p</i> = 0.002

Inter-regional differences in the abundance of *Cyanea* spp. and *A. aurita*.

Table A.7. Inter-regional differences in the annual abundance of *Cyanea* spp.

Comparison of differences in the volume-standardised biomass (first line) and densities (second line) of *Cyanea* spp. in the eastern and western Irish Sea using Wilcoxon rank-sum tests (H_0 : the abundances are the same in both region).

	2007	2008	2009	2010
Biomass (g m ⁻³)	W = 371 N _E = 27 ; N _W = 25 <i>p</i> = 0.549	W = 290 N _E = 26 ; N _W = 23 <i>p</i> = 0.865	W = 342 N _E = 26 ; N _W = 30 <i>p</i> = 0.435	W = 359 N _E = 14 ; N _W = 29 <i>p</i> < 0.001
Densities (ind. 100m ⁻³)	W = 464 N _E = 27 ; N _W = 25 <i>p</i> = 0.020	W = 395 N _E = 26 ; N _W = 23 <i>p</i> = 0.056	W = 476 N _E = 26 ; N _W = 30 <i>p</i> = 0.160	W = 348 N _E = 14 ; N _W = 29 <i>p</i> < 0.001

Table A.8. Inter-regional differences in the annual abundance of *A. aurita*.

Comparison of differences in the volume-standardised biomass (first line) and densities (second line) of *Aurelia aurita* in the eastern and western Irish Sea Wilcoxon rank-sum tests (H_0 : the abundances are the same in both region).

	2007	2008	2009	2010
Biomass (g m ⁻³)	W = 292.5 N _E = 27 ; N _W = 25 <i>p</i> = 0.413	W = 137 N _E = 26 ; N _W = 23 <i>p</i> < 0.001	W = 436 N _E = 26 ; N _W = 29 <i>p</i> = 0.324	W = 94.5 N _E = 14 ; N _W = 29 <i>p</i> = 0.005
Densities (ind. 100m ⁻³)	W = 389.5 N _E = 27 ; N _W = 25 <i>p</i> = 0.344	W = 171 N _E = 26 ; N _W = 23 <i>p</i> = 0.009	W = 496 N _E = 25 ; N _W = 30 <i>p</i> = 0.042	W = 125.5 N _E = 14 ; N _W = 29 <i>p</i> = 0.044

Inter-annual dynamics in the abundance of *A. aurita* and in each region of the Irish Sea.

Table A.9. Inter-annual variations of *A. aurita* biomass (g m^{-3}) in each region of the Irish Sea. Wilcoxon rank-sum tests on volume-standardised biomass of *A. aurita* from the eastern (top-right diagonal, grey cells) and western (bottom-left diagonal, white cells) half of the Irish Sea (H_0 : no difference between years).

W\E	2007	2008	2009	2010
2007	-	W = 506 N₀₇ = 27 ; N₀₈ = 26 p = 0.005	W = 170.5 N₀₇ = 27 ; N₀₉ = 26 p = 0.001	W = 178 N₀₇ = 18 ; N₁₀ = 14 p = 0.048
2008	W = 194 N ₀₈ = 17 ; N ₀₇ = 24 p = 0.800	-	W = 78 N₀₈ = 26 ; N₀₉ = 26 p < 0.001	W = 91.5 N ₀₈ = 19 ; N ₁₀ = 14 p = 0.113
2009	W = 239 N ₀₉ = 23 ; N ₀₇ = 24 p = 0.436	W = 314 N ₀₉ = 29 ; N ₀₈ = 23 p = 0.726	-	W = 237.5 N₀₉ = 19 ; N₁₀ = 14 p < 0.001
2010	W = 228 ; N ₁₀ = 23 ; N ₀₇ = 24 p = 0.309	W = 325 N ₁₀ = 29 ; N ₀₈ = 23 p = 0.882	W = 399 N ₁₀ = 29 ; N ₀₉ = 29 p = 0.743	-

Table A.10. Inter-annual variations of *A. aurita* densities (ind.100 m^{-3}) in each region of the Irish Sea.

Wilcoxon rank-sum tests on densities of *A. aurita* from the eastern (top-right diagonal, grey cells) and western (bottom-left diagonal, white cells) half of the Irish Sea (H_0 : no difference between years).

W\E	2007	2008	2009	2010
2007	-	W = 494 N₀₇ = 27 ; N₀₈ = 26 p = 0.010	W = 164.5 N₀₇ = 27 ; N₀₉ = 25 p = 0.002	W = 160 N ₀₇ = 18 ; N ₁₀ = 14 p = 0.198
2008	W = 86 N₀₈ = 17 ; N₀₇ = 24 p = 0.002	-	W = 86 N₀₈ = 26 ; N₀₉ = 25 p < 0.001	W = 84.5 N ₀₈ = 19 ; N ₁₀ = 14 p = 0.063
2009	W = 86 N₀₉ = 24 ; N₀₇ = 24 p < 0.001	W = 311 N ₀₉ = 30 ; N ₀₈ = 23 p = 0.547	-	W = 205.5 N₀₉ = 18 ; N₁₀ = 14 p < 0.003
2010	W = 129 ; N₁₀ = 23 ; N₀₇ = 24 p = 0.002	W = 316 N ₁₀ = 29 ; N ₀₈ = 23 p = 0.753	W = 454 N ₁₀ = 29 ; N ₀₉ = 30 p = 0.778	-

Inter-annual dynamics in the abundance of *Cyanea* spp. in each region of the Irish Sea.

Table A.11. Inter-annual variations of *Cyanea* spp. biomass (g m⁻³) in each region of the Irish Sea.

Wilcoxon rank-sum tests on volume-standardised biomass of *Cyanea* spp. from the eastern (top-right diagonal, grey cells) and western (bottom-left diagonal, white cells) half of the Irish Sea (H_0 : no difference between years).

W\E	2007	2008	2009	2010
2007	-	W = 520 N₀₇ = 27 ; N₀₈ = 26 p = 0.003	W = 550 N₀₇ = 27 ; N₀₉ = 26 p < 0.001	W = 56 N₀₇ = 18 ; N₁₀ = 14 p = 0.007
2008	W = 306 N₀₈ = 17 ; N₀₇ = 24 p = 0.007	-	W = 331 N ₀₈ = 26 ; N ₀₉ = 26 p = 0.905	W = 8 N₀₈ = 19 ; N₁₀ = 14 p < 0.001
2009	W = 416 N₀₉ = 24 ; N₀₇ = 24 p = 0.009	W = 293 N ₀₉ = 30 ; N ₀₈ = 23 p = 0.355	-	W = 6 N₀₉ = 19 ; N₁₀ = 14 p < 0.001
2010	W = 368 ; N ₁₀ = 23 ; N ₀₇ = 24 p = 0.051	W = 273 N ₁₀ = 29 ; N ₀₈ = 23 p = 0.269	W = 429 N ₁₀ = 29 ; N ₀₉ = 30 p = 0.934	-

Table A.12. Inter-annual variations of *Cyanea* spp. densities (ind. 100m⁻³) in each region of the Irish Sea.

Wilcoxon rank-sum tests on densities of *Cyanea* spp. from the eastern (top-right diagonal, grey cells) and western (bottom-left diagonal, white cells) half of the Irish Sea (H_0 : no difference between years).

W\E	2007	2008	2009	2010
2007	-	W = 441 N ₀₇ = 27 ; N ₀₈ = 26 p = 0.111	W = 495 N₀₇ = 27 ; N₀₉ = 26 p = 0.011	W = 150 N ₀₇ = 18 ; N ₁₀ = 14 p = 0.377
2008	W = 48 N₀₈ = 17 ; N₀₇ = 24 p < 0.001	-	W = 350.5 N ₀₈ = 26 ; N ₀₉ = 26 p = 0.826	W = 100 N ₀₈ = 19 ; N ₁₀ = 14 p = 0.236
2009	W = 53 N₀₉ = 24 ; N₀₇ = 24 p < 0.001	W = 296 N ₀₉ = 30 ; N ₀₈ = 23 p = 0.384	-	W = 91 N ₀₉ = 19 ; N ₁₀ = 14 p = 0.130
2010	W = 72 ; N₁₀ = 23 ; N₀₇ = 24 p < 0.001	W = 359 N ₁₀ = 29 ; N ₀₈ = 23 p = 0.645	W = 514 N ₁₀ = 29 ; N ₀₉ = 30 p = 0.234	-

APPENDIX B

HAVE JELLYFISH IN THE IRISH SEA BENEFITED FROM CLIMATE CHANGE AND OVERFISHING?

By C.P. Lynam, M.K.S. Lilley, T. Bastian, T.K. Doyle, S.E. Beggs and G.C. Hays

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Have jellyfish in the Irish Sea benefited from climate change and overfishing?

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Keywords

Gadus; Melanogrammus; Sprattus; Clupea; medusae; gelatinous; Aurelia; Cyanea.

Abstract

Climate change and overfishing may lead to ecosystem instability and may benefit non-exploited organisms such as jellyfish. In the Irish Sea, an increase in jellyfish abundance was evident ($r^2 = 0.29$, $p = 0.03$) in a 16-year time-series (1994–2009) collected during juvenile fish surveys. Jellyfish abundance correlated positively with sea surface temperature (SST) over the preceding 18 months ($r = 0.65$, $p_{ACF} < 0.001$) and copepod biomass in the previous year ($r = 0.56$, $p_{ACF} = 0.03$), and negatively with spring (February-May) precipitation ($r = -0.57$, $p_{ACF} = 0.02$). Principal components regression indicated that climatic indices explained 68% of the interannual variability in jellyfish abundance ($p = 0.003$), where the components were based on the North Atlantic Oscillation Index, SST and precipitation. The frequency of cnidarian material present in Continuous Plankton Recorder (CPR) samples has also increased since 1970, with a period of frequent outbreaks between 1982 and 1991. Prior to this period, the herring stock in the northern Irish Sea declined rapidly to a low level, potentially stimulating structural change in the ecosystem. In 1985 there was a step decrease in CPR copepod biomass and in 1989 a step increase in the phytoplankton colour index, suggesting a cascading regime shift during the 1980s. Subsequent overexploitation of gadids, coupled

with warm temperatures and the poor recruitment of cod, led to the rapid decline in cod biomass from 1990. While the biomass of sprats has decreased in the last decade, the herring stock has recovered partially. Reductions in demersal fishing pressure since 2000, intended to stimulate cod recovery, appear to have facilitated further rises in haddock biomass. Since the 1980s regime shift, sea temperatures have increased, the fish community has altered and jellyfish abundance has risen such that jellyfish and haddock may now play an increasingly important role in the ecosystem.

Introduction

There is widespread interest in the consequences for the oceans of global climate change and human actions (e.g. fishing and the accidental introduction of alien species). The past few decades have seen profound changes in the biota of marine systems (Hays *et al.* 2005) with, for example, the removal of top predators (Rogers & Ellis 2000; Myers *et al.* 2007) and major changes in the distribution and phenology of marine plankton (Beaugrand *et al.* 2003; 2008; Edwards & Richardson 2004). Accompanying these changes, there has been widespread concern that the oceans may increasingly be dominated by jellyfish (ctenophores and medusae), because many gelatinous zooplankton species are able to increase in abundance rapidly and adapt to new conditions brought about by ecosystem regime shifts (Bakun & Weeks 2006; Daskalov *et al.* 2007). Hence, there is an increasing awareness of the many negative socio-economic implications of jellyfish-dominated ecosystems (Richardson *et al.* 2009). It has been hypothesised that jellyfish may increase in abundance for at least two different reasons (Purcell 2005; Daskalov *et al.* 2007). Firstly, they may benefit indirectly from commercial “fishing down the food chain”, whereby humans target the largest and most valuable fish species at the apex of the ecological pyramid and, having depleted those stocks, then move down to the next trophic level, and so on. The endpoint of “fishing down the food chain” may be an ocean dominated by jellyfish (Pauly *et al.* 1998, 2002). Secondly, changing environmental conditions (including: temperature, salinity, light availability, current flow and vertical mixing) and climatic fluctuations (wind patterns and air pressure) may be beneficial to jellyfish in certain instances (Purcell 2005, 2007; Molinero *et al.* 2007, 2008; Brodeur *et al.* 2008; Gibbons & Richardson 2009; Purcell *et al.* 2009). Although empirical evidence for these scenarios is limited, jellyfish-dominated ecosystems are often debated because outbreaks of medusae frequently cause clogging of fishing nets and power station intakes, as well as stinging bathers and causing mass mortalities of fish in aquaculture (Purcell *et al.* 2007; Doyle *et al.* 2008). However, perhaps the greatest concern is the proposed self-enhancing feedback loop termed “the never-ending jellyfish joyride” (Richardson *et al.* 2009), wherein jellyfish become established so strongly that it may be impossible for fish abundance to recover to pre-exploitation levels, even if commercial fishing is reduced.

Given such unease about the prevalence of jellyfish, it is perhaps surprising that there are relatively few robust long time-series of jellyfish abundance. This gap in data partly reflects the fact that jellyfish were historically not a focus for research or monitoring. More fundamentally, it can be difficult to gain quantitative estimates of the abundance of a patchily distributed population by scientific surveys, which are all too often restricted in spatial scale and therefore tend to hit or miss hotspots of abundance. Nevertheless, some time-series have shown major changes in jellyfish abundance and statistical links with climatic indices (Lynam *et al.* 2004; Purcell 2005; Brodeur *et al.* 2008; Molinero *et al.* 2008; Gibbons & Richardson 2009). As environmental conditions are changing at unprecedented rates in many ecosystems, e.g. Sea of Japan, Antarctica, and the NE Atlantic (Brander 2007), there is an urgency to understand jellyfish population dynamics in these areas. Indeed, the regional seas of the NE Atlantic have

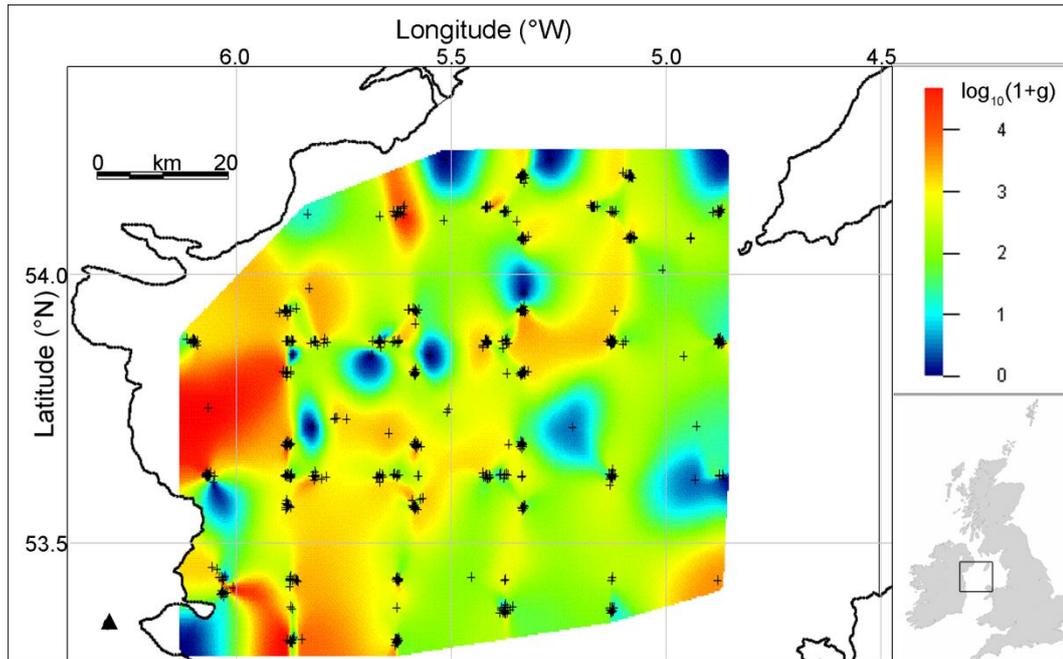


Figure 1. Survey area in the western Irish Sea showing MIK survey haul locations and mean spatial distribution of jellyfish $\log_{10}(1+g)$ where the catch weight per haul is volume standardised. Also shown is the location of rain station (black triangle).

been warming for the past 15 years at a rate not experienced in recent centuries (Hobson *et al.* 2008), yet it is unclear how these changes have impacted upon jellyfish. Here, we analyse a hitherto unexploited dataset on jellyfish abundance collected from extensive fisheries surveys in the Irish Sea. This unique dataset, from a region experiencing such profound environmental changes, offers the potential to provide new insights into how global climate change may impact upon jellyfish.

Material and methods

Jellyfish sampling

Annual surveys for pre-recruit gadid fish in the Irish Sea were conducted by AFBI (Agri-Food and Biosciences Institute, Northern Ireland) using their research vessels MRV *Lough Foyle* (1994–2004) and *Corystes* (2005–2009). Night surveys were conducted using a 5 m² Methot Isaacs Kidd (MIK) frame net with a 5 mm mesh designed to sample juvenile pelagic 0-group gadoids (Methot 1986). The net was towed in a double-oblique profile through the water column to within 4 m of the seabed, with a second double-oblique profile at stations where the depth prevented initial tow durations of >15 min. An impellor flowmeter recorded the volume filtered during each tow. Volume filtered averaged 4113.2 m³ (range 699–11 719 m³). For two tows with non-zero jellyfish catch and where the flow was not recorded, we assumed the mean volume filtered from the other tows. All jellyfish in the catch were separated from fish, crustaceans and ctenophores and then weighed. From 2007, jellyfish were identified to genus where possible and the catch weights for separate taxa were also quantified. Jellyfish catches were dominated by medusae (bell diameter 0.5 to 36 cm) of *Aurelia aurita*, *Cyanea capillata* and *C. lamarckii*. In scarce abundance were *Chrysaora hysoscella* (bell diameter up to 15 cm) and various small hydrozoans (bell diameter <3 cm) including *Cosmetira*, *Leuckartiara* and *Bougainvillia* spp.

The survey was conducted annually between May and June between 53 and 55 °N. The longitudinal range was initially 4.5 – 7 °W (1994–2005), but later this was extended to 3 – 7 °W (2006–2009). To provide comparable data between years, we restricted the analysis to the area well sampled in all years (longitude >4.75 °W, latitude <54.25 °N; Figure 1). Annually, the number of samples from this area averaged 48 (range 13–82). Large catches (many tens of kg) were subsampled quantitatively. For example, if the jellyfish catch filled 20 baskets evenly, then one basket would be weighed and that weight multiplied by 20. For each haul, the total jellyfish weight was volume standardised by multiplying by (volume filtered / mean volume filtered). The sample distributions of the volume-standardised weights were normalised by a $\log_{10}(1 + \text{value})$ transformation and annual means and standard deviations were calculated from the transformed values.

Biological and climate covariate data

Official fisheries catch statistics for the years 1973–2008 and stock and recruitment indices were downloaded from the website of the International Council for the Exploration of the Sea (ICES; www.ices.dk) using the STATLANT and Stock Summary databases respectively. Specifically, data for gadids (cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*) were investigated because the western Irish Sea area is a particularly important spawning area for those stocks (ICES 2009a). Stock assessments for cod are computed using B-ADAPT software and for haddock from single fleet SURBA analysis; there is no currently accepted analytical assessment for whiting (*Merlangius merlangus*) in the Irish Sea (ICES 2009a). The assessment framework for Irish Sea herring is currently being evaluated to address issues of stock identity (i.e. mixing with Celtic Sea fish), so no SSB or recruitment data are available (ICES 2009b). To address the lack of data on planktivores from ICES assessments, we investigated acoustic (38 khz) survey data for the northern Irish Sea (3 to 7 °W and 53.3 to 55 °N, ICES 2009b) for the years 1998 to 2009 conducted annually, between 7 and 18 days in the period 27 August - 29 September by AFBI. The biomass of sprat (*Sprattus sprattus*) was computed from the difference between the total clupeoid biomass detected and the estimated herring (*Clupea harengus*) biomass (all ages) from the same survey.

Plankton data were gathered by the Continuous Plankton Recorder (CPR) and supplied by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) (Batten *et al.* 2003; Reid *et al.* 2003). The CPR sampler is towed at a fixed depth of ~7 m, has a square mouth opening of 1.61 m², and carries silk bands with a mesh of 270 µm with which plankton are filtered and sandwiched before preservation in a solution of borax-buffered formaldehyde (Batten *et al.* 2003). The greenness of the CPR silk (the Phytoplankton Colour Index, PCI) is an accepted measure of the biomass of diatoms and dinoflagellates (Richardson *et al.* 2006). The CPR primarily samples copepods and data for the most abundant copepod species in the Irish Sea (*Acartia* spp., *Para-pseudocalanus*, *Temora longicornus*, *Metridia lucens*, *Calanus finmarchicus*, *C. helgolandicus*, and *Centropages typicus*; Pitois & Fox 2006) were considered for analysis here. The presence of cnidarians on the CPR silk, excluding those siphonophores with rigid bells that are included in the CPR ‘total siphonophores’ category, was determined by SAHFOS through the visual identification of cnidarian tissue and/or nematocysts (Gibbons & Richardson 2009). The resulting index of the frequency of cnidarian occurrence (1971-2008) in CPR samples was used to compare with the shorter jellyfish time-series from the fisheries survey. There are some important caveats with using CPR data in this way: although the presence or absence of cnidarian tissue can be identified from the samples, a more detailed quantification of the amount of material is not possible. Moreover, the CPR samples a relatively small volume, nominally 3 m³ per sample (over ~18.5 km towed), with a small mouth opening and it is likely to undersample large scyphozoan jellyfish, such that the

CPR sampler is likely more indicative of the presence of smaller organisms (i.e. Hydrozoa and Ctenophora, siphonophores without rigid bells and detached tentacles from those siphonophores with rigid bells) (Gibbons & Richardson 2009). Indeed in the North Sea, correlations between CPR frequency of cnidarian occurrence and the abundance of *Aurelia* and *Cyanea* spp. was found to be significant in only one of four regions and for *Aurelia* only (Lynam *et al.* 2010). Nevertheless, visual and genetic analyses have identified the scyphozoan *Pelagia noctiluca* in CPR samples gathered in the Atlantic Ocean to the west of Ireland (Baxter *et al.* 2010; Licandro *et al.* 2010), indicating that scyphozoan medusae are sampled by the CPR among other gelatinous zooplankton. Since it is unclear which species are sampled by the CPR, we use the summer data (May–August) only as this is when scyphozoan medusae such as *Aurelia* and *Cyanea* spp. are abundant.

Raw CPR data collected in the Irish Sea (3 to 7 °W and 52 to 55 °N) between 1961 and 2008 (except cnidarian data which were only available to 2007) were extracted from the CPR database. Following preliminary analysis of the spatial and temporal distribution of the data, the latitudinal range was reduced to 53.25 to 53.75 °N and the year range from 1971 in order to maintain a consistent sampling pattern throughout the time series (Figure S1). Samples were collected further north of 53.75 °N in 1993 to 1995 only, and prior to 1989 samples were taken sporadically further south of 53.25 °N. Each sample within the subset is therefore located between the latitudinal bounds of the fisheries survey area. The sampling effort along the longitudinal gradient was constant throughout, and in order to maintain high sample size the survey area was not restricted further (Figure S1).

The CPR is known to sample zooplankton species with varying efficiency, due largely to differing organism sizes and vertical distributions, and therefore copepod abundance data were compensated for under-sampling by the CPR using conversion factors reported by Pitois & Fox (2006). Copepod abundance data was converted into biomass (mg m^{-3}) using the dry weight values for each species (Pitois & Fox 2006). Monthly means of copepod biomass and phytoplankton colour were calculated and missing monthly means were determined from these using the standard ‘interpolation’ method for CPR data (Richardson *et al.* 2006, and therein Colebrook 1975). The interpolation method is considered robust, i.e. based on an adequate estimate of the seasonal cycle, if ≥ 8 months are sampled. In the data subset, ≥ 8 months were sampled in every year since 1971, with the exception of 1988 when no samples were available and in 1974 and 1979 when only 7 months were sampled. From 1990 onward ≥ 10 months were sampled each year with on average 8 samples per month. The distribution of the monthly mean copepod biomass estimates were normalised by $\log_{10}(1+\text{value})$ transformation prior to calculation of annual means.

Monthly sea surface temperature (SST) values were downloaded from the UK Met Office Hadley Centre’s HadSST2 dataset (<http://hadobs.metoffice.com/hadsst2/>). The data are based on quality-controlled, *in situ* measurements of SST from ships and buoys: data for the period 1850–1997 are taken from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS), and those from 1998 on are from the US National Oceanic and Atmospheric Administration’s (NOAA) National Centers for Environmental Prediction – Global Telecommunications System (NCEP–GTS). SST anomalies were determined by subtraction of the calculated climatology for the period 1970–2000 prior to spatially averaging over a grid of 1×1 or 5×5 degrees (Rayner *et al.* 2006). The station-based winter (December–March) North Atlantic Oscillation Index (NAOI; Hurrell *et al.* 2003) was obtained from the US National Center for Atmospheric Research (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>). The NAO describes an atmospheric pressure dipole, most pronounced in winter, with a high-pressure system in

the south, centred on the Azores, and a low-pressure system over Iceland. The normalised difference between the two pressures recorded at the two stations is an index used to measure the strength of the NAO. When the NAO index is positive, the pressure field results in strong westerly winds blowing warmer air towards northern Europe during winter, warming and mixing Irish Sea surface waters. Any associated increase in precipitation will likely result in increased river flow and increased run-off of nutrients to coastal areas. Monthly rainfall data, recorded at a station at Dublin airport, latitude 53.36 °N, longitude 06.32 °W (Figure 1, triangle) were downloaded from the European Climate Assessment & Dataset (Eca&D) website <http://eca.knmi.nl/> (Klein Tank *et al.* 2002) and considered as a proxy for river flow and salinity in the coastal zone. Precipitation effects on jellyfish have been considered in this way previously by Wilcox *et al.* (2008) and Purcell *et al.* (2009).

Statistical analyses

Sample variability in the annual means of (volume-standardised and log₁₀-normalised) jellyfish catch weights was assessed in terms of Coefficients of Variation ($CV = \text{sample standard deviation} / \text{sample mean}$) and Relative Standard Errors in the mean ($RSE = \text{sample standard deviation} / (\text{sample mean} \times \text{number of samples}^{1/2})$). The RSE were plotted against the number of hauls per year, and a log-linear regression model was fitted in order to determine the number of hauls required to yield a RSE of 5% of the sample mean (Figure 2).

Annual means of jellyfish catch weights ($\log_{10}(1+g)$, volume standardised) were investigated for temporal trend using linear regression analyses. The regression model assumptions of linearity, homogeneity of variance, normality and independence of residuals were tested following procedures outlined in Krzanowski (1998). A cube transformation of the annual values was made to stabilize the spread of the studentised residuals from the regression model (Fox 1997). In addition, the Shapiro–Wilk statistic (Dunn & Clark 1974) was used to test residuals for normality and was assessed at the 0.05 level of significance. Generalised Durbin–Watson statistics and their bootstrapped

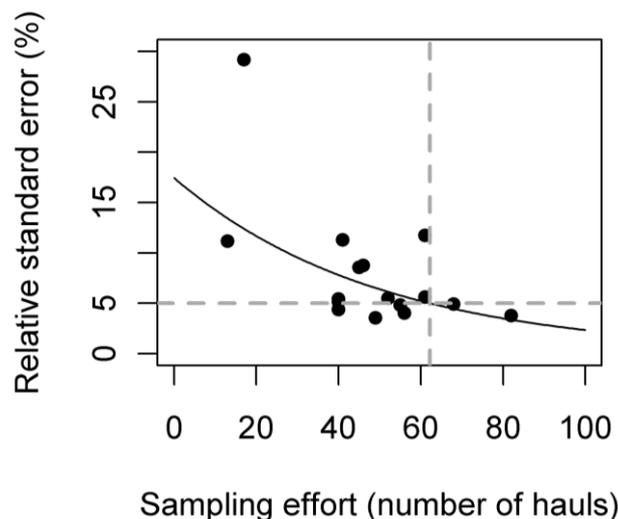


Figure 2. Relative standard error as a function of sampling effort (number of hauls) for mean annual catch weight $\log_{10}(1 + g)$, volume standardised) of jellyfish in the western Irish Sea ($r^2 = 0.38$, $p = 0.011$). The sampling effort at the intersection of the horizontal and vertical lines indicates that 62 hauls are required to reduce the relative standard error to 5%.

significance values were used to assess residual autocorrelations (Fox 1997). Global validations of linear model assumptions were made following the procedures of Pena & Slate (2006). The significance level for each test was chosen to minimise corresponding Type II error (Krzanowski 1998). Significance correction methods, which were developed to aid decision-making, such as the Bonferroni adjustment for multiple tests for significance, were not utilised because application of these methods to statistical inference is controversial (see review by Perneger 1998); we adopt the view of Perneger (1998) that such adjustments are at best unnecessary, and at worst deleterious to sound statistical inference.

Exploratory correlation analyses were made between annual mean jellyfish catch weights and ecosystem and climatic variables (phytoplankton colour, copepod and fish biomass, SST, rainfall and NAOI) in order to determine likely influences on jellyfish populations. For all correlations, the effective degrees of freedom were corrected for autocorrelation using the modified Chelton Method with the Chatfield autocorrelation estimator, and the number of lags to be considered in computing autocorrelation was taken as one-fifth the length of the time-series (Pyper & Peterman 1998); significance values thus corrected for autocorrelation are labelled p_{ACF} . Regime shifts in time-series were investigated using a statistical procedure (supremum F statistic) that identifies, using regression model residuals, whether or not a single change-point has occurred at some unknown location (year), where the null hypothesis was no step change in mean level of the time-series (Zeileis *et al.* 2003). Subsequently, the most parsimonious model (i.e. fewest number of breakpoints required) to minimize the residual sum of squares was chosen using the Bayesian Information Criterion (BIC; Zeileis *et al.* 2003). Fisheries landings and biomass indices were used to explore the hypothesis that a change in the ecosystem instigated by fisheries might alter the abundance of jellyfish. The hypothesis that a change in jellyfish biomass might alter fish recruitment was tested through Ricker stock-recruitment modelling (Chen & Irvine 2001).

Principal components regression (PC regression) was adopted to investigate relationships between jellyfish (where the response variable was annual mean volume-standardised catch weights) and climate and ecosystem indices; whereby Principal Components Analyses (PCA) were conducted to extract the dominant modes of temporal variability from a suite of inter-related variables and the resulting principal components were used as explanatory variables. A notable benefit of such an approach is that stepwise selection of explanatory variables in multiple regression analyses is robust since the independence of the variables is certain and variable selection is unbiased (Graham 2003). Covariate selection for PC regression were made using a backwards stepwise procedure. Two PC regression analyses were conducted; the first using climatic data alone to model jellyfish catch weights and the second including data on climate, plankton and finfish in order to explore potential interactions between finfish (cod and haddock), plankton and jellyfish.

All analyses were made using the R software (R Development Core Team 2009) and additional packages used were: Flexibly reshape data ('reshape'; Wickham 2007), Testing for Structural Change in Linear Regression Models ('strucchange'; Zeileis *et al.* 2002), Global validation of linear models assumptions ('gvlma'; Pena & Slate 2006), Testing Linear Regression Models ('lmtest'; Zeileis & Hothorn 2002) and Companion to Applied Regression ('car'; Fox 2002).

Results

Irish Sea jellyfish

Between 2007 and 2009, the jellyfish catches were dominated by *Aurelia aurita* each year (66%, 92% and 86% by weight respectively). The remainder of the catch comprised *Cyanea* spp. (*C. lamarckii* and *C. capillata*) and other species composed <2% by weight each year. The spatial pattern in jellyfish catch weights is shown in Figure 1. In all samples between 1994 and 2009, the median catch weight of jellyfish was 476 g per haul and the 10th and 90th percentiles were 2 g and 6885 g per haul respectively. The maximum measured catch weight in a haul was 124700 g and five hauls where the jellyfish catch burst the net were assumed to have caught 125000 g of jellyfish. Once volume-standardised the median jellyfish catch was 525 g per haul and the 10th and 90th percentiles were 3 g and 8843 g respectively. The average coefficient of variation (CV) in the annual (volume-standardised and log₁₀ normalised) jellyfish catch weights was 49% (range 25–120%) and the average relative standard error was 7% (range 4%–29%). A log-linear regression model of the relative standard error against the number of hauls per year was significant ($r^2 = 0.38$, $n = 16$, $p = 0.011$) and suggested that 62 hauls were required per year to yield a relative standard error of 5% of the sample mean weight (Figure 2).

Annual means of jellyfish catch weights were investigated for temporal trend using linear regression analyses. An increasing linear trend was evident in annual catch weights ($r^2 = 0.26$, $n = 16$, $p = 0.04$), but a pattern in the studentised residuals of decreasing magnitude vs. fitted values was detected. Once this pattern was stabilised, by a cube transformation of the response variable, all model assumptions were satisfied and the final regression statistics were: $r^2 = 0.29$, $n = 16$, $p = 0.03$ (Figure 3). The inclusion of vessel type as a factor in the regression did not suggest that the increase in jellyfish catch weights was attributable to a step change in 2005 because the term was not significant ($p = 0.48$).

Climatic influences on jellyfish

Fluctuations are common in time-series of jellyfish abundance and inspection of the time-series shows great interannual variability (Figures 3 and 4a). In order to explore potential causes for the underlying mechanism at play, we performed exploratory correlative analyses with climatic data (Figure S2). Various monthly lags of the jellyfish catch weight to the temperature anomaly and total precipitation data were considered to determine the period over which to average the climate data (Figure S3), prior to testing for significance with a correction for autocorrelation (Table 1). The jellyfish catch weight in the sampling period of May-June, correlated positively with SST in those months (mean SST anomaly = +0.70 °C with range -0.39 °C to +1.77 °C) and the preceding 16 months (Figure S3a): the overall mean monthly SST anomaly between 1994 and 2009 was +0.61 °C (minimum -0.84 °C in January 1994 and maximum +2.41 °C in May 2007). Jellyfish catch weights also correlated negatively with precipitation between February and May (i.e. a dry period; mean precipitation 220 mm, range 127 – 335 mm) and positively with precipitation in the previous year between July and December (i.e. a wet period; mean precipitation 431 mm, range 318 – 591 mm) (Figure S3b). The winter (Dec-Mar) NAOI index was positively correlated with SST in the first half of the year (Jan-Jun) suggesting an underlying influence of this atmospheric variable (Table 1). Prior to regression analyses of jellyfish catch weights, a PCA was conducted with the following climatic variables: NAOI with and without a 1-year lead, average SST for the preceding year, SST for January–June of the current year, and average precipitation in the months February–May of the current year (Table 2a). The final model, determined using

backward elimination, included the first, second and third principal components and it explained 68% of the variability in the jellyfish catch weight data (Table 3a, Figure 3).

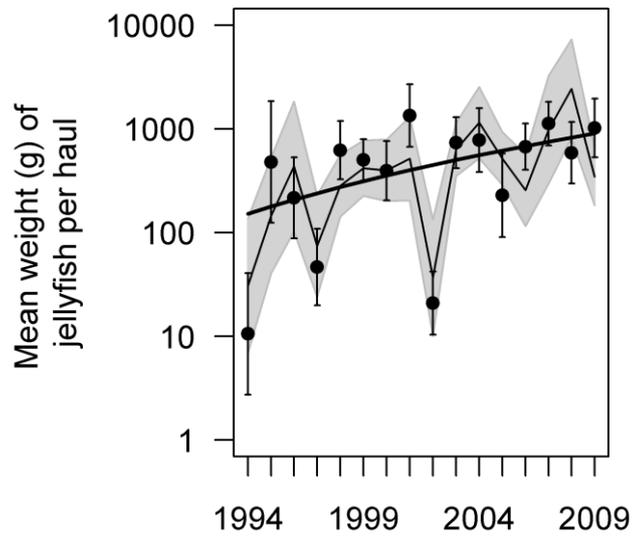


Figure 3. Temporal patterns in mean catch weights per haul of jellyfish in the western Irish Sea (see Figure 1), where black circles with error bars are the back-transformed $\log_{10}(1+g)$ means with 95% confidence intervals. The straight black line shows the regression through the observations (regression equation $y = (1.033x - 2050)^{1/5}$). The solid grey line shows the modelled catch weights and the two grey dashed lines represent the 95% confidence interval from the PC regression.

Table 1. Linear correlation matrix showing R (top right) and p_{ACF} values (bottom left, shaded) determined using the modified Chelton method. Climate (NAOI, SST and Rainfall) data extends over the period 1950-2009. However, correlations with biota are limited to the minimum time-series series length: jellyfish sampling period 1994-2009, copepod biomass and phytoplankton colour index 1971-2008, sprat biomass 1998-2009, cod SSB 1968-2009 and haddock SSB 1992-2009. Entries emboldened if $p_{ACF} < 0.05$. Asterisks also indicate significance: *** if $p_{ACF} < 0.01$, ** if $p_{ACF} < 0.05$, * if $p_{ACF} < 0.1$

$p_{ACF} \setminus R$	Jellyfish weight	Copepod biomass	Phytoplankton Index	Sprat Biomass	Cod SSB	Haddock SSB	NAOI	NAOI year before	SST Jan-Jun	SST (18 months)	Rainfall Feb-May
Jellyfish weight	-	0.23	0.43	-0.55*	-0.68***	0.55**	-0.14	0.26	0.42	0.65***	-0.57**
Copepod biomass	0.421	-	-0.19	-0.67**	0.39	-0.11	-0.06	-0.13	-0.29	-0.30	-0.28*
Phytoplankton Index	0.107	0.503	-	0.18	-0.57	-0.35	0.16	0.04	0.46*	0.50	-0.03
Sprat biomass	0.066	0.024	0.606	-	0.75**	-0.38	0.03	-0.23	-0.09	-0.31	0.33
Cod SSB	0.004	0.275	0.108	0.025	-	-0.68*	0.04	-0.08	-0.41	-0.61	-0.09
Haddock SSB	0.026	0.682	0.170	0.311	0.091	-	-0.45*	-0.27	0.57*	0.86***	-0.36
NAOI	0.601	0.737	0.337	0.932	0.860	0.060	-	0.36*	0.48***	0.29	-0.13
NAOI year before	0.337	0.429	0.807	0.467	0.692	0.274	0.055	-	0.05	0.30	0.03
SST Jan-Jun	0.106	0.266	0.079	0.788	0.236	0.058	0.005	0.786	-	-	-0.09
SST(18 months)	0.006	0.333	0.102	0.356	0.139	0.005	0.148	0.133	-	-	-0.06
Rainfall Feb-May	0.021	0.094	0.864	0.294	0.591	0.144	0.308	0.840	0.492	0.672	-

Table 2. Principal component analysis using (a) climatic data for 1994-2009, (b) climatic and biological data (finfish and plankton) for the period 1994–2008. The PCs are subsequently used as regressors of jellyfish catch weights.

PCA loadings and variability by component	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
(a) Loadings (1994-2009)									
NAOI	-0.15	0.72	-0.45	0.34	-0.38	-	-	-	-
NAOI (1 year lead)	0.37	-0.31	-0.73	0.29	0.39	-	-	-	-
SST (Jan-Jun)	-0.44	-0.62	-0.11	0.36	-0.54	-	-	-	-
SST (1 year lead)	-0.65	0.10	0.12	0.38	0.64	-	-	-	-
Precipitation (Feb-May)	0.48	0.04	0.49	0.72	-0.05	-	-	-	-
<i>Standard deviations</i>	1.44	1.15	1.00	0.73	0.29	-	-	-	-
<i>Proportion of variance</i>	0.41	0.26	0.20	0.11	0.02	-	-	-	-
(b) Loadings (1994-2008)									
NAOI	-0.10	0.61	0.01	0.18	0.00	0.55	-0.46	0.23	-0.10
NAOI (1 year lead)	0.14	0.03	0.76	-0.33	-0.05	0.37	0.15	-0.28	0.23
SST (Jan-Jun)	-0.46	0.07	-0.34	0.07	-0.25	0.22	0.11	-0.72	0.13
SST (1 year lead)	-0.41	-0.37	0.20	-0.08	-0.23	0.21	0.03	0.14	-0.73
Precipitation (Feb-May)	0.37	-0.07	-0.09	0.00	-0.90	0.00	-0.13	0.11	0.10
Phytoplankton colour index	-0.26	0.21	-0.28	-0.81	-0.07	0.01	0.16	0.32	0.14
Copepod biomass	-0.22	0.51	0.24	0.31	-0.22	-0.27	0.62	0.18	-0.05
Cod SSB	0.44	-0.07	-0.34	0.07	0.13	0.56	0.57	0.07	-0.15
Haddock SSB	-0.39	-0.41	0.04	0.29	-0.03	0.27	0.07	0.42	0.58
<i>Standard deviations</i>	1.87	1.46	1.17	0.91	0.78	0.53	0.45	0.29	0.17
<i>Proportion of variance</i>	0.39	0.24	0.15	0.09	0.07	0.03	0.02	0.01	0.00

Table 3. Principal component regression of (a) jellyfish catch weight (1994–2009) on the principal component of climate variables only, (b) jellyfish catch weight (1994–2008) on climatic and biotic data.

(a)	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	2.501	0.100	25.056	0.000
PC1 _{Climate}	-0.219	0.072	-3.045	0.010
PC2 _{Climate}	-0.271	0.090	-3.022	0.011
PC3 _{Climate}	-0.264	0.103	-2.567	0.025
$r^2 = 0.68$; $p = 0.003$				
<i>F</i> statistic: 8.33 on 3 and 12 DF				
(b)	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	2.468	0.118	20.878	<0.001
PC1 _{Climate+biota}	-0.244	0.066	-3.722	0.003
$r^2 = 0.52$; $p = 0.003$				
<i>F</i> statistic: 13.85 on 1 and 13 DF				

PC1 explained 41% of the variance in the climatic indices and the greatest loading on PC1 was SST Jan-Jun (-0.65) followed by precipitation (+0.48). PC2 (26% of variance) largely reflected the NAOI and SST with 1 year lead (loadings = +0.72 and -0.62 respectively). PC3 (20% of variance) was dominated by the NAOI with 1 year lead (-0.73) followed by precipitation (+0.49), (Table 2a). The regression coefficients are all negative (Table 3a) so the model indicates high jellyfish catch weights in warm, dry years (PC1) following a low winter NAOI (PC2) with a high NAOI in the previous year (PC3).

Planktonic interactions with jellyfish, seasonality and long term change

Notably in CPR data, copepod biomass has decreased since 1971, while the phytoplankton colour index and cnidarian frequency of occurrence have increased (Figure 4a-c). Statistical breakpoints analyses suggest a regime shift in the mid-1980s that cascaded through the plankton: structural change tests indicated nonstationarity in mean cnidarian frequency ($\text{sup}(F) = 8.8$, $p = 0.048$) and BIC analysis suggested two breakpoints ($\Delta\text{BIC}_{0 \text{ breaks}} = 9.8$, $\Delta\text{BIC}_{1 \text{ break}} = 8.7$, $\Delta\text{BIC}_{2 \text{ breaks}} = 0$, $\Delta\text{BIC}_{3 \text{ breaks}} = 4.9$), the first a step increase in 1982 (95% confidence interval, CI, 1978-1983) and the second a step decrease in 1990 (CI, 1988-1998) albeit to a higher mean level than during the 1970s; for copepod biomass, a single breakpoint in 1985 (CI, 1982-1992, $\text{sup}(F) = 24.5$, $p < 0.001$; $\Delta\text{BIC}_{0 \text{ breaks}} = 12.4$, $\Delta\text{BIC}_{1 \text{ break}} = 0$, $\Delta\text{BIC}_{2 \text{ breaks}} = 2.8$) was detected and followed by a period of reduced biomass; in phytoplankton colour data, the breakpoint occurred in 1989 (CI, 1985-1994; $\text{sup}(F) = 27.8$, $p < 0.001$; $\Delta\text{BIC}_{0 \text{ breaks}} = 14.4$, $\Delta\text{BIC}_{1 \text{ break}} = 0$, $\Delta\text{BIC}_{2 \text{ breaks}} = 1.0$) and was followed by increased phytoplankton colour scores.

The analysis of seasonality in the frequency of occurrence of cnidarian material on the CPR silk showed that during the mid-period (1983-1990) the index was elevated between May-August, i.e. the typical scyphozoan jellyfish period (Figure 4d). However, no clear changes in the mean seasonal pattern of cnidarians were evident between the differing regimes. The biomass of copepods was elevated between May and September during each regime (pre- and post-1985, Figure 4e). In contrast, the mean seasonal pattern of phytoplankton post-1990 differs from the earlier regime in that the standing stock remained at higher levels during the winter months and the bloom (from March) appears more rapid, sustaining high levels for a longer period (Figure 4f).

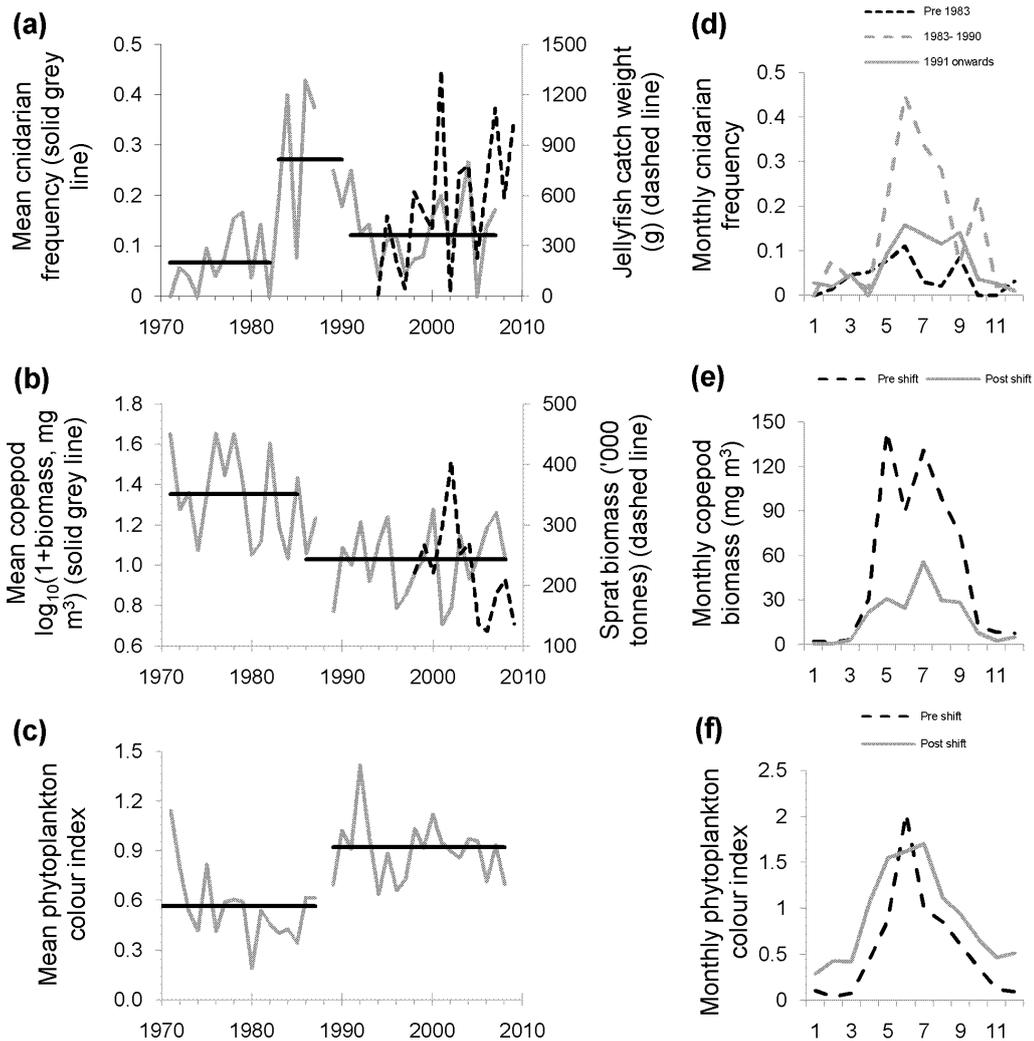


Figure 4. Planktonic regime shift in CPR data with cascading breakpoints in: (a) cnidarian frequency of occurrence; (b) copepod biomass; (c) in phytoplankton colour index and their associated seasonal cycles (d-f). Also shown: jellyfish catch weights (g) back-transformed from the annual means of the $\log_{10}(1+g)$ values (dashed line in a) and sprat biomass determined from the AFBI acoustic survey (dashed line in b).

Jellyfish catch weights per haul (volume corrected, see previous section) correlated positively and significantly with the frequency of occurrence of cnidarian material in CPR samples during May-August (1994-2007; $r = 0.58$, $n = 14$, $p_{ACF} = 0.037$; Figure 4a). Although no relationship was found with either annual phytoplankton colour or copepod biomass without lag, a positive predictive relationship was evident between the annual biomass of copepods and jellyfish catch weights in the following year ($r = 0.56$, $n = 16$, $p_{ACF} = 0.027$, Figure 4ab). Furthermore, a marginal negative correlation between jellyfish abundance and the relative biomass of copepods during the summer (May-August mean / annual mean, 1994-2008) was evident ($r = -0.49$, $n = 15$, $p = 0.082$), suggesting a weak predation effect. Similar correlations, over a longer time period (1971-2007), between the highly variable CPR cnidarian frequency of occurrence index (average $CV = 80\%$) and either annual copepod biomass (with or without 1 year lead) or summer copepod biomass were not significant ($p_{ACF} > 0.05$). However, for a subset of data following the numerous cascading breakpoints in planktonic indices (see above), the CPR cnidarian frequency of occurrence during the summer correlated negatively with the

relative biomass of copepods during the summer (1990-2007, $r = -0.61$, $n = 18$, $p_{ACF} = 0.009$) and positively with the biomass of copepods in the previous year (copepods 1990-2006 versus CPR cnidarian occurrence index 1991-2007: $r = 0.54$, $n = 17$, $p_{ACF} = 0.044$) indicating a potential feedback mechanism between jellyfish and copepods in the recent regime where copepod biomass may be limiting.

Fisheries impacts and interactions between fish and the ecosystem

Fisheries impacts on the Irish Sea ecosystem have been great; official fisheries catch statistics show that annual landings of all finfish and shellfish exceeded >100 thousand tonnes (kt) between 1972 and 1975 and again between 1987 and 1988. During the former period, landings of herring were elevated due to the operation of an industrial fishery on juveniles in the western Irish Sea. Following the decline of herring in the late 1970s and the closure of the industrial fishery in 1978, landings of gadids (mainly cod and whiting) increased until the decrease in the cod stock from 1990 (Figure 5). After which, total landings of finfish and shellfish reduced to ~70 kt within five years and stayed near that level until 2003. Subsequent management action has limited landings of cod and effort by the fleets targeting cod (Figure S4) such that total fish and shellfish landings have stayed <50 kt since 2005. Notably, shellfish landings increased gradually from 1950 and landings of *Nephrops* have been around 9 kt since 1990 making this species the current most landed species.

Acoustic survey estimates during the autumn (August-September) indicate that the biomass of sprats averaged ~250 kt between 1998 and 2005, when herring biomass (all ages) was of the order 10 kt. However, between 2006 and 2009 sprat biomass has averaged 160 kt and herring biomass 30 kt. The biomass of sprat correlates negatively with the annual biomass of copepods between 1998 and 2008 in the recent regime ($r = -0.67$, $n = 10$, $p_{ACF} = 0.024$), indicating predatory effects on secondary production in this period of limited copepod biomass (Figure 4b). Cod biomass decreased dramatically during the 1990s, and recruitment has been below average for the past 17 years (ICES 2009a, Figure 5). In contrast, biomass and recruitment for the haddock stock have trended upward over the period 1992–2009. Jellyfish catch weights correlated significantly with each gadid biomass measure: jellyfish vs. cod: $r = -0.68$, $p_{ACF} = 0.004$; and vs. haddock $r = +0.55$, $p_{ACF} = 0.026$ (for both, $n = 16$, Table 1). The correlation between jellyfish and sprat biomass was weak $r = -0.55$, $p_{ACF} = 0.066$.

No correlative relationship was found between jellyfish catch weights and age-0 survival, $\log(\text{recruitment}/\text{spawning biomass})$, of either haddock or cod. Simple Ricker models of either cod or haddock age-0 survival indicate no significant relationships between spawning stock biomass and survival of either species (both $p > 0.05$). The addition of a jellyfish catch weights term to each Ricker model did not improve the fit and the term was not significant in either case. Annual mean SST (Jan-Jun) did not correlate with the biomass of either fish species ($p_{ACF} > 0.05$), but it did correlate negatively with cod larval survival ($r = -0.49$, $n = 42$, $p_{ACF} = 0.002$). The larval survival of either cod or haddock did not correlate with any other climatic variable and no relationship was evident between survival and annual phytoplankton colour or annual copepod biomass (all $p_{ACF} > 0.05$).

A principal components regression of jellyfish catch weights was made in order to explore the relative predictive strength of climate change and variability in the biota of the Irish Sea (Tables 2b and 3b). The final model, chosen through backward selection, retained only the first principal component (Table 3b) and explained 52% of the variability in jellyfish abundance ($p = 0.003$). In this alternative PCA, PC1 explained 39% of the variance in the 9 time-series (5 climate indices plus 2 measures of fish biomass and

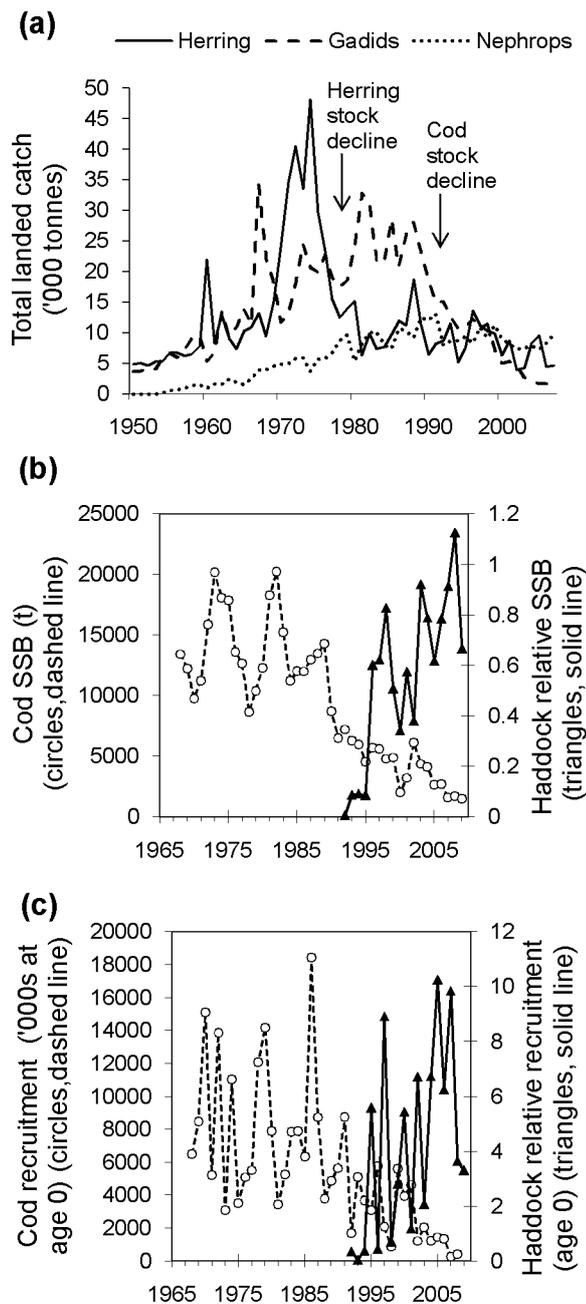


Figure 5. Fish and shellfish in the Irish Sea: (a) landings ('000 t) of the principle species fished: herring, gadids and *Nephrops*. Note the gadids group includes landings of cod, whiting and haddock. There has been a great reduction in herring landings following large annual catches of >30000 t in the early 1970s (peaking at 48000 t in 1974) to <5000 t today. Gadid landings have reached record lows in recent years following the decline of the cod stock. (b) Stock trajectories, and (c) recruitment variability for cod (circles) and haddock (triangles).

2 planktonic indices), and the greatest loading on PC1 was SST(Jan-Jun) (-0.46) followed by cod SSB (+0.44) and SST in the previous year (-0.41) (Table 2b). PC2 (24% of variance) largely reflects the NAOI, copepod biomass and haddock SSB (loadings = +0.61, +0.51 and -0.41 respectively). Climate and biotic relationships on jellyfish were not separated by the model due to the covariance between the variables in the period 1994 to 2008 (e.g. acute angle between arrows representing precipitation and cod biomass and

also between SST and haddock biomass in Figure S5). There was no improvement to the PC regression model fit when including fish and plankton data in the PCA relative to the climate data only PCA (Table 3a vs. 3b). Notably, the SST (Jan-Jun) variable had the greatest loading in each PCA on PC1, a component present in both PC regressions, indicating that this variable is the most predictive of jellyfish catch weights.

Discussion

Monitoring of long term change in jellyfish populations

Our results show strong correspondence between jellyfish abundance (survey catch weights) in the Irish Sea and climate indices, with an increasing trend in jellyfish abundance in recent years (Figure 3). Given the current concern over jellyfish in marine systems it is surprising that relatively few time-series of jellyfish abundance exist. Plankton samplers are not designed to sample large jellyfish and, for this reason, jellyfish collected as bycatch during fisheries surveys provide some of the best jellyfish time-series (Lynam *et al.* 2004; Brodeur *et al.* 2008). Here, for the first time, we analysed jellyfish data collected during fisheries surveys in the Irish Sea. An important initial question regarding plankton sampling is often: how many samples are required for robust estimation of mean abundance? As the variability between samples increases, larger sample sizes are generally required for estimating mean abundance. Planktonic species are particularly challenging to sample because their patchy distribution leads to large intersample variability in abundance. Our analysis suggests that ideally at least 62 MIK samples should be collected annually to maintain the strength of the jellyfish time-series.

We use the reported catch weight of all jellyfish species (largely *Aurelia* and *Cyanea* spp.) combined and show that the time-series agrees with an independent time-series (index of cnidarian occurrence) from the Continuous Plankton Recorder (CPR) sampler (Figure 4a). Therefore, the time-series presented here and the relationships with the climate are considered robust. In terms of long-term change, we can only focus on the CPR index of cnidarian occurrence which, notwithstanding the caveats regarding this data (see methods), indicates that jellyfish outbreaks have been more frequent since 1982: with great outbreaks in 1984 and 1986 and lesser outbreaks in 1991 and 2004. Given the trend in jellyfish catch weights in survey data since 1994 and indications of greater outbreaks historically, might this trend continue? As there were great changes within the plankton during the 1980s, including decreases in secondary production (copepod biomass, Figure 4b), the carrying capacity for jellyfish and finfish may have been reduced in the Irish Sea. Further study and ecosystem modelling may shed light on this important issue.

Gibbons & Richardson (2009) used the large CPR database to assess trends in gelatinous zooplankton abundance in European shelf seas and in the North Atlantic. Gibbons & Richardson (2009) found that SST correlated positively with gelatinous zooplankton abundance in the North Atlantic Ocean, but not in European shelf seas as a whole, potentially because of the amalgamation of many signals from differing ecosystems (including both North and Irish Seas). Attrill *et al.* (2007) and Attrill & Edwards (2008) also studied the CPR frequency of occurrence data for cnidarians in the North Sea and found no relationships to SST, but strong relationships to current inflows into the northern North Sea and weaker positive relationships with the NAOI. Lynam *et al.* (2010) also report that jellyfish abundance, from fisheries survey data, in the north western North Sea was related positively to the NAOI, while jellyfish abundance in the south eastern North Sea was elevated during low NAOI years with particularly cold sea temperatures. So, jellyfish populations appear linked to climatic indices but the processes at play can differ by region.

Possible mechanistic links between the climate and increasing jellyfish catches

In order to understand the processes behind the correlations we must appreciate the complex lifecycle of the true jellyfish (those of the order Scyphozoa). Scyphozoan medusae release planula larvae following the summer feeding period (May-August) and, although some medusae may overwinter, the medusa generally dies in the autumn (Russell 1970). The larvae settle on to hard substrate in coastal waters (including piers and rocks, see Holst & Jarms 2007) and develop into scyphistomae (benthic perennial polyps), which release many ephyrae (young medusoids) during the following spring. Sea temperature is presumably linked to jellyfish reproduction (through the sexual medusa stages, settlement of larvae, and/or the asexual development of the benthic polyp) and this would explain the lagged correlations between medusa abundance and SST (Figure S3a). However, the varied processes that impact on jellyfish reproduction are complex, and the direct effects of temperature can be positive (increased strobilation rates and hence the production of young medusoids) and negative (increased mortality of the benthic polyp, Liu *et al.* 2009). In addition, cold temperature stress will trigger strobilation (e.g. Holst *et al.* 2007; Purcell *et al.* 2009) and a winter minimum threshold may be required to initiate this process, which could impose a thermal limit on the spatial distributions of jellyfish species (Doyle *et al.* 2007).

A likely temperature-stimulated mechanism for retention of jellyfish exists in the Irish Sea in the form of entrainment within the western Irish Sea gyre: a cyclonic, near-surface gyre present annually (Dickey-Collas *et al.* 1997; Horsburgh *et al.* 2000). The gyre forms around a cold, dense pool flanked by strong near-bed density gradients and it is generally present from May until October (Horsburgh *et al.* 2000). The gyre stimulates high phytoplankton and zooplankton abundances and benefits the feeding of *Nephrops* and sprats (Gowen *et al.* 1998; Coombs *et al.* 1992). During June and early July, temperature provides the controlling influence on the density structure in the western Irish Sea. However in April and May, salinity contributes significantly to the density structure as a result of freshwater input along the Irish coast, which in 1995 had its maximum effect on stratification about 40 km offshore (Holt & Proctor 2003). The salinity structure in the western Irish Sea is primarily determined by a competition between river runoff, stimulated by precipitation, and the inflow of more saline water from the Celtic Sea to the south and the Malin shelf to the north (Holt & Proctor 2003). Thus, the correlation between jellyfish catch weights and precipitation can be considered in terms of a direct effect of river runoff on jellyfish and as a proxy for salinity in the coastal zone, where polyp beds of jellyfish are likely to be found. However, given that the greatest monthly correlation between precipitation and jellyfish catch weights was for February (Figure S3b), it is unlikely that the correlation represents an indirect effect on jellyfish via gyre formation. Indeed the greatest precipitation event in February occurred in 2002, a year when jellyfish abundance was particularly low (Figures 3 and S3). At low salinities, strobilation rates and the number of ephyrae produced by the polyps of *Aurelia aurita* (the dominant jellyfish species in the Irish Sea) and *Cyanea lamarckii* may decrease and be delayed (Purcell 2007; Purcell *et al.* 2009). In contrast, *C. capillata* polyps are generally tolerant to a range of salinities (Holst & Jarms 2010). While the gyre may serve to aggregate medusae, strong periodic wind events may disperse medusae through significant flushing of the Irish Sea: an event lasting two days in February 1994 removed 8% of the volume of the Irish Sea through the North Channel, which combined with the series of depressions in that month indicate that ~25% of the volume of the Irish Sea was removed, roughly 4–5 times the typical long-term mean (Young *et al.* 2001). Such great events have the potential to overwhelm the retention effect of the gyre and advect significant numbers of medusae in addition to fish eggs and larvae out of the Irish Sea.

The increasing trend in jellyfish catch weights is unlikely due to phenological change since the CPR index of cnidarian occurrence indicates little change in jellyfish seasonality across the breakpoints in 1982 and 1990 (Figure 4d). Similarly, no change was evident in the seasonality of copepod biomass before and after the breakpoint in 1985. Phenological change has been observed in CPR plankton samples from the North Sea (notably dinoflagellates, meroplankton and copepods; Edwards & Richardson 2004). Despite evidence of seasonal variability in gelatinous zooplankton abundance over time, with a succession of spring-species and autumn-species dominance within communities (Molinero *et al.* 2008), there is, as yet, no clear evidence published for gradual phenological change in any scyphomedusa population. The reduction in copepod biomass in the Irish Sea, together with the increase in SST since 1990, is likely to have contributed to the more rapid increase in the spring phytoplankton bloom in the recent regime (Figure 4f).

Climate influences on fish stocks and interactions with jellyfish

Sea temperature is known to impact on cod physiology and recruitment success (Pörtner *et al.* 2008), but the direction of the relationship changes spatially: from positive in relatively cold waters (such as the Barents Sea) to negative in warmer waters (such as the North and Irish Seas, Drinkwater 2005). Similarly, relationships between jellyfish abundance and climatic indices vary spatially and this is explicable in terms of local processes (Attrill & Edwards 2008; Lynam *et al.* 2010). In contrast to cod, haddock biomass has increased concomitantly with rises in jellyfish catch weights and SST. Unfortunately, given the shortness of the haddock time-series, we cannot say whether or not this increase is partly due to a release from competition with other fish or to reduced predation by adult fish following the dramatic declines in cod and whiting in the Irish Sea (ICES 2009a). Indeed, recent annual egg production estimates of spawning stock biomass (SSB) indicate that haddock SSB (~ 9 kt) in 2008 was greater than that of cod (~5 kt) in the Irish Sea (Armstrong *et al.* 2010). However, the estimates are still low when compared to the historical SSB of cod, which peaked at ~20 kt in 1982 (ICES 2009a). In the North Sea, haddock tend to be found in warmer water than cod, which may indicate that they have a preference for warmer environments (Hedger *et al.* 2004). Haddock typically exhibit greater recruitment variability than cod and this is likely to increase the probability that the haddock stock experiences a strong year class relative to temperature-depressed cod (Fogarty *et al.* 2001). An interaction with jellyfish that may benefit juvenile gadids is that of increased refugia from predation and cannibalisation for young fish that shelter within the jellyfishes umbrella (Lynam & Brierley 2007). In the North Sea, the survival of whiting larvae has been linked to the abundance of *Cyanea* spp. in this way and the spatial distribution of cod, haddock, whiting and Norway pout (*Trisopterus esmarkii*) has been shown to correlate with the abundance of jellyfish in some years but not in others, potentially indicating the transitory nature of such relationships (Hay *et al.* 1990; Lynam & Brierley 2007). Nevertheless, in the northern Benguela upwelling system the bearded goby (*Sufflogobius bibarbatus*) has been found not only to associate with medusae, to avoid predation by piscivorous fish, but also to consume jellyfish (Utne-Palm *et al.* 2010). Jellyfish are also predators of fish eggs and larvae and competitors with juveniles and adult fish for zooplankton resources (Möller 1984; Purcell & Arai 2001). In the western Irish Sea, sprat eggs are spawned between April and June (Coombs *et al.* 1992) and larvae are likely to fall prey to predation by medusae and other predators during the summer. In contrast, larval herring are abundant between October-January and therefore have a temporal refuge from jellyfish predation. Given that jellyfish share similar diets with planktivorous fish, competition between

sprats and jellyfish for copepods is likely (Purcell & Arai 2001; see also Figures 4a and 4b).

Regime shifts and fisheries impacts on the ecosystem

There have clearly been major changes in the fisheries of the Irish Sea (Figures 5a and S4) and fisheries have been proposed to have altered the ecosystem over the course of the 20th century (Rogers & Ellis 2000). The herring fishery was once of great economic importance in the Irish Sea, particularly during the 1970s when the ‘Mornington’ mixed industrial fishery operated in the western Irish Sea: the fishery targeted herring juveniles from the late 1960s and at its peak it caught 10 thousand tonnes of herring per year. However, the fishery was closed due to management concerns in 1978 (ICES 2009b) and restrictions on all fleets targeting herring existed between 1979 and 1981. Although fishing continued during the 1980s, the fishery off the northern Irish coast declined substantially and ceased in the early 1990s. Sprats are currently the dominant planktivore in the Irish Sea (ICES 2009b), and while the biomass of sprats has decreased over the last decade there is evidence of a recent increase in the Irish Sea herring spawning stock biomass.

If an expanded niche in resources were created in the western Irish Sea, through the removal of planktivores (herring and sprat, Figure 5a), jellyfish would be likely candidates to utilise those resources because they are able to grow and reproduce rapidly and consume zooplankton at high rates (Purcell & Arai 2001; Bakun & Weeks 2006). Thus the increase in the CPR cnidarian frequency of occurrence index and its variability after 1982 may be linked indirectly to the overexploitation of herring. Whether or not the great exploitation of the herring stock triggered a regime shift, which through a cascade of events led to a reduction in copepod biomass after 1985 (Figures 4 and 5), we cannot say. Indeed, an exploratory analysis of stock assessment data has indicated a decrease in stock productivity (recruit per spawner ratio and subsequently surplus production) from 1972 onward following high levels during the 1960s (ICES 2007), which could indicate that herring themselves were responding to some environmental influence. Although no data are available for the Irish Sea, we note that copepod biomass to the west of Scotland and west and south of Ireland during the 1960s was elevated relative to the 1970s (Pitois & Fox 2006), which may have improved feeding conditions for adult herring and, if also replicated in the Irish Sea, may have led to improved larval survival there. While jellyfish may have played a predatory role in the depletion of copepods during the 1980s, without an abundance index we cannot say how extensive this would have been. Other planktivorous species such as sprats and also non-commercial species such as Norway pout, poor cod (*Trisopterus minutus*) and lesser spotted dogfish are likely to have played an important role in restructuring the food web.

In the North Sea, outbreaks of *Aurelia aurita* and *Cyanea capillata* occurred following the decline of the herring stock to low levels (Lynam *et al.* 2005) and in the Black Sea, trophic cascades and outbreaks of jellyfish have been reported to have been triggered by overfishing (Daskalov *et al.* 2007). Taken together with this study, we suggest that the decline and collapse of planktivorous stocks is a likely stimulant of structural change in the plankton and may lead indirectly to outbreaks of jellyfish, which can subsequently impact on the structure of the planktonic food web. However, climatic influences and other biological process (e.g. density dependence) will play roles in regulating jellyfish abundance (Purcell 2005; Brodeur *et al.* 2008). We attempted to explore the relative effects of biotic and abiotic factors on the jellyfish catch weights since 1994 and found no improvement to the PC regression model fit when including fish and plankton data in the initial PCA. The net result was to lose the effect of the NAOI

from the model (Table 3a) and replace the term with cod and haddock SSB (Table 3b), which co-vary with the precipitation and SST variables respectively (Figure S5). Thus the NAOI effect may operate on jellyfish catch weights through an indirect pathway, potentially through sea temperature or zooplankton (Table 3b and Figure S5).

Following the cold anomalies in 1986 and 1987, the NAOI has been in a sustained positive phase and sea surface temperature has been rising. This, combined with a reduced predatory impact of copepods following the step decrease in biomass in 1985, is likely to have stimulated the step-increase in the phytoplankton colour index in 1989. Jellyfish populations are known to display ‘boom and bust’ dynamics (Brodeur *et al.* 2008) and the reduction in CPR cnidarian frequency in the Irish Sea from 1990 may be a correction due to an overabundance of jellyfish or, alternatively, a change in the species composition recorded by the CPR. Interestingly, a predatory impact on copepods by sprats and a weak seasonal influence by jellyfish on copepods is only detectable in this later period of reduced copepod biomass. Similarly we have shown that a predictive relationship between copepod biomass and jellyfish in the next year becomes evident after 1990, but not throughout the entire time-series. Thus, a negative feedback loop may exist whereby the jellyfish population is limited through predation on zooplankton prey, for which it must compete with planktivorous fish (such as sprats; Coombs *et al.* 1992). Given that the herring population is currently showing signs of expansion (ICES 2009b), the self-enhancing feedback loop “the never-ending jellyfish joyride” (Richardson *et al.* 2009) may not be strong enough or simply not present in the Irish Sea. Similarly in the North Sea, a negative correlation between *Aurelia aurita* abundance and herring survival was detected, yet the herring stock responded to management action and recovered (Lynam *et al.* 2005). While in the Black Sea, planktivorous fish biomass began to recover following management action despite elevated levels of jellyfish (Daskalov *et al.* 2007).

The decline in the Irish Sea cod stock from 1990 was due largely to overfishing on a stock that experienced low recruitment after 1986, which is due partly to the rise in sea temperature but is likely also due to the shift to reduced biomass of copepods (Figure 4b): a similar mechanism was proposed for North Sea cod by Beaugrand *et al.* (2003). Beaugrand *et al.* (2008) identify an unstable period in the North Sea ecosystem in the 1980s followed by a regime shift in the early 1990s, which was characterised by rising temperatures and poor recruitment of cod. Through causal modelling of CPR data, Kirby & Beaugrand (2009) demonstrate that the North Sea ecosystem, following the regime shift, favours jellyfish in the plankton and decapods and detritivores (echinoderms) in the benthos.

Since 2000, the cod spawning grounds in the western Irish Sea have been closed to groundfish trawling between mid-Feb to the end of April (ICES 2009a), which is unlikely to have had any direct beneficial effect on jellyfish. The directed demersal fishery for *Nephrops* also operates in the western Irish Sea and is particularly intensive in summer when medusae are abundant. The mesh size in use in the fishery varies between 70 mm and 89 mm and can catch larger medusae. Fishermen targeting *Nephrops* have described how their boats (600 horse power) can be slowed down as a result of catching medusae, which clog the net and require the trawl to be emptied to avoid bursting the nets (Ivan Wilde, Pers. Comm. 2010).

Conclusion

In summary, the overexploitation of herring during the late 1970s was followed by a period of ecosystem instability during the 1980s in which the frequency of occurrence of cnidarian material in the CPR sampler rose to high levels, indicating outbreaks of jellyfish. The period of instability stimulated a restructuring of the

ecosystem leading ultimately to a decrease in copepod biomass and an increase in the phytoplankton colour index since 1990. Although overfishing is often held responsible for marine ecosystem degeneration and outbreaks of jellyfish (Daskalov *et al.* 2007), temperature can bring about similar effects (Kirby & Beaugrand 2009) and can explain much of the variability in Irish Sea cod larval survival and in jellyfish catch weight data since 1994. While it is not possible to disentangle completely the specific effect of climate change on the jellyfish population in the Irish Sea from wider ecosystem changes and/or changes in fishing practice, we have explored alternative hypotheses and conclude that it appears that within the current 16-year jellyfish time-series, the strongest driver of long-term changes in jellyfish abundance is climate variation (Table 3a). In contrast, the restructuring of the ecosystem during the 1980s preceded the great rises in temperature (Figures 4 and S2). Whether the processes linking present climate influences to jellyfish are direct (effect on metabolism, growth and/or reproduction), indirect (via ecosystem interactions), or a mixture of both is deserving of further study in experimental and *in situ* conditions. Competition between planktivorous finfish (sprats and herring) and jellyfish would appear likely during the summer when medusae prey upon zooplankton: but given that the herring stock has increased in recent years, jellyfish interactions with herring are not likely to be as important for the stock as the management of fishing mortality is. Nevertheless, the Irish Sea is in a new dynamic regime, with lower copepod biomass, relative to that in existence prior to the decline of the herring stock and the system may not sustain a high biomass of herring and cod in addition to jellyfish, sprats and haddock. Hence, we urge continued monitoring of jellyfish abundance and further work investigating potential interactions with zooplankton and finfish. The move to ecosystem-based fisheries management requires extensive ecological knowledge and an understanding of the risks posed by any indirect effects, such as trophic cascades, of our utilisation of the sea's resources.

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Additional material

Figure S1 to S5 are available online with the published version of the manuscript: 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. doi: 10.1111/j.1365-2486.2010.02352.x

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