UNIVERSITY OF STRATHCLYDE

Modelling the sustainability of overwintering *Mnemiopsis leidyi* populations in the North Sea

by

Ian Gardiner

A thesis submitted in partial fulfillment for the
degree of Master of Philosophy

in the
Faculty of Science
Department of Mathematics and Statistics

2015

Declaration of Authorship

This thesis is the result of the authors original research. It has been composed by the author and has not been previously submitted for examination which has led to the award of a degree.

Signed: ________________________

Date: ________________________

Abstract

Invasive species are widely accepted as one of the leading threats to global biodiversity. The invasive ctenophore *Mnemiopsis leidyi* gained notoriety in the late 1980s when its explosive population growth in the Black Sea – following accidental introduction via ballast water – coincided with a drastic reduction in the stock of the anchovy *Engraulis encrasicolus* in the region. *M. leidyi* has since been found in the coastal waters of many European countries and is a major cause for concern in these areas.

In February 2009, *M. leidyi* was recorded at several offshore locations in the North Sea raising concern among researchers regarding the widely held belief that the winter conditions of the North Sea proper were unsuitable for the survival of the ctenophore. The General Estuarine-Ocean Transport Model (GETM) coupled with the European Regional Seas Ecosystem Model-Biogeochemical Flux Model (ERSEM-BFM) and a Lagrangian particle tracking individual behaviour model (GITM) are used to examine the origin and sustainability of these overwintering *M. leidyi* individuals. The main results of this research are: (i) the model suggests it is possible there exists a UK population of *M. leidyi* somewhere along the English coast that has thus far gone undetected; (ii) *M. leidyi* can survive in the North Sea proper the entire winter until the summer months of July and August when conditions are most favourable for reproduction; (iii) under current climatic conditions the model finds the reproductive capability of *M. leidyi* in the North Sea proper to be minimal due to the relatively low summer temperatures and the consequent high (juvenile) mortality. Theses results are presented with the caveat that there remains substantial uncertainty regarding the model parameterisation which can only be improved with further research on the species. For this reason it is advisable that more effort is dedicated to investigating the factors influencing the rate of transfer between life stages and the mortality rates of *M. leidyi* at lower temperatures.

Acknowledgements

I would like to start by thanking the European Regional Development Fund Interreg IV A, the *Mnemiopsis* Ecology Modelling and Observation (MEMO) project and the Engineering and Physical Sciences Research Council (EPSRC) for making it financially possible for me to complete this thesis. I must also thank my supervisors in the University of Strathclyde, an incredible university that I have enjoyed immensely being part of for the last six years. First Dr. Louise Kelly, my primary supervisor, who always made me feel like I was her priority and provided me with much needed advice, support and encouragement. I am also very thankful to Dr. Douglas Speirs, who always questioned my line of thought and challenged me to fully understand my research. This degree was carried out in collaboration with an industrial partner – the Centre for Environment, Fisheries and Aquaculture Science (Cefas) – and as a result I was fortunate enough to have two additional supervisors to call upon. Thank you to Dr. Sophie Pitois for helping me understand all of the literature and previous research on *Mnemiopsis leidyi* and for always making me feel welcome when I visited the Cefas laboratory in Lowestoft. I am also indebted to Dr. Johan van der Molen who provided me with technical support regarding the models that were used for my research and who was always just a phone call or email away when I needed help.

I must also thank my family who have always been a source of love, advice and support. I am blessed to have such a close knit family and I know I would not be the person I am today without them. A final mention goes to Nicola, who makes me laugh every day and was always understanding during the highs and lows of working towards the final draft of my thesis.

Contents

List of Figures

Dedicated to my friend, colleague and inspiration Professor George Gettinby – Thank you for always believing in me.

Chapter 1

Introduction

1.1 Background information

The introduction of non-native species together with anthropogenic impacts is resulting in the loss of populations and species in almost every ecosystem on the planet (Valdés et al., 2009; Salihoglu et al., 2011). As a result many marine ecosystems across the world have lost their natural populations of large predatory finfish and are now being dominated by a handful of organisms such as prawns, lobster and jellyfish (Howarth et al., 2014). These biological changes are proving to be ecologically and economically damaging (Simberloff et al., 2013). Also, the rate of chemical and physical change in the marine ecosystems induced by climate change is expected to increase in the coming decades in the absence of immediate and dramatic efforts towards climate mitigation (National Research Council, 2011). Rising atmospheric CO_2 levels have increased sea surface temperatures and ocean stratification, reduced subsurface oxygen concentrations and could eventually alter ocean circulation and nutrient dynamics (Keeling et al., 2010). These changes will potentially have dramatic cascading effects on current marine ecosystems, their structure, functioning and biodiversity (Doney et al., 2012).

Many recent publications claim that gelatinous plankton blooms are increasing in both magnitude and frequency (Jackson et al., 2001; Richardson et al., 2009; Costello et al., 2012) which, if true, could have dramatic impacts on commercial fisheries and the tourism industry (Bax et al., 2003). Others however are sceptical of this paradigm shift (Mills, 2001; Condon et al., 2012) and claim historical records show there have always been “bloom and burst” cycles of gelatinous plankton density. Regardless of how accurate these publications are, the media attention they have received cannot be underestimated. In particular they could potentially lead to serious socioeconomic consequences if politicians and other policymakers are influenced by public perception rather than scientific evidence (Condon et al., 2012). Despite this attention however, the currently available information on gelatinous species is at best fragmentary; more fundamental research is required to better understand gelatinous species ecology and their complex life cycles and ecosystem roles.

One particular invasive gelatinous organism which has gained a lot of media attention is *Mnemiopsis leidyi* A. Agassiz, 1865, referred to hereafter as *M. leidyi*. Commonly referred to as the sea walnut, this highly opportunistic ctenophore has a rapid growth rate and high reproduction capabilities under a wide range of environmental conditions. Native to the eastern coastal waters of North and South America, *M. leidyi's* predation on the eggs and larvae of the anchovy *Engraulis encrasicolus* and its competition with the zooplanktivorous fish for food resources (Kideys, 1994) is likely to have contributed to the major collapse of anchovy stocks in the Black Sea in the late 1980s. Whilst there has been some discussion regarding the causative role of *M. leidyi* in the anchovy stock collapse (Bilio and Niermann, 2004) – with overfishing, eutrophication and the lack of a natural predator being cited as other contributing factors – the explosive expansion of *M. leidyi* in the affected region led to the ctenophore being included in the International Union for Conservation of Nature (IUCN) list of 100 world's worst invaders (Lowe et al., 2000) and made the possible introduction in other areas a huge cause for concern.

When occurring in blooms, *M. leidyi* has the potential to cause major pelagic regime shifts in coastal areas which may result in the collapse of commercially important fish populations (Reusch et al., 2010). In 2005 *M. leidyi* was first recorded in the North Sea region (Faasse and Bayha, 2006) and has subsequently been recorded along the North Sea continental coastline from France to Sweden (Antajan et al., 2014; Hansson, 2006). These findings have alarmed the scientific community, especially as these waters are home to of some the world's most commercially important fish stocks and spawning and nursery grounds (Ellis et al., 2012). These fishing grounds also share the depleted state of fish stocks that characterised the Black Sea when *M. leidyi* was introduced

(Boersma et al., 2007) and played a key role in the devastating collapse of anchovy stock (Bilio and Niermann, 2004).

Much of the discussion in the literature regarding *M. leidyi* population dynamics (as reviewed in Costello et al., 2012) is centered around the theory of source-sink dynamics suggesting that much of the North Sea is unsuitable to sustain a year-round population and is therefore annually re-inoculated with *M. leidyi* individuals when conditions become favourable for survival. However, in 2009, the International Bottom Trawl Survey (IBTS, `http://ocean.ices.dk/Project/IBTS`) unexpectedly found surviving *M. leidyi* individuals in open water – and has recorded a similar presence each subsequent winter to date. There has also been research carried out at the Centre for Environment, Fisheries and Aquaculture Science (Cefas) which suggests conditions in large parts of the North Sea may actually be suitable for overwintering *M. leidyi* populations (Collingridge et al., 2014).

The spatial extent of *M. leidyi* populations and bloom periods in the North Sea are unclear. Regular surveys have been conducted in coastal areas, but inadequate sampling and poor conservation techniques may have underestimated the abundance or even overlooked its presence altogether. These recent discoveries in open waters raise questions regarding the current knowledge of the winter survival and distribution of *M. leidyi* in the North Sea region and form the impetus for this thesis.

1.2 Thesis plan

The aim of this thesis is to increase understanding on *M. leidyi* population dynamics by modelling the sustainability of the recorded overwintering *M. leidyi* populations. A three-dimensional hydrodynamical model (GETM: General Estuarine-Ocean Transport Model) coupled with an ecosystem model (ERSEM-BFM: European Regional Seas Ecosystem Model-Biogeochemical Flux Model) is used to provide hydrodynamics and food fields for an offline Lagrangian particle tracking model. A particle tracking individual behaviour model (GITM: General Individuals Tracking Model) – originally designed as an extension to GETM and later modified by Dr. Johan van der Molen at Cefas – is used to: (1) attempt to locate possible origins for the recent open water discoveries; (2) evaluate the possibility that these individuals can survive the winter; (3)

track their future movements and determine whether or not *M. leidyi* individuals from the recorded winter locations can result in the formation of a year-round population. These results will attempt to enhance the understanding of the population dynamics of *M. leidyi* in the North Sea and locate potential risk areas where further monitoring of the species is required. Chapter 2 of this thesis provides a succinct yet thorough review of *M. leidyi*, including its life history, sensitivity to environmental factors, geographic distribution and range expansion as an invasive species. Chapter 3 gives an overview of the hydrographic processes of the North Sea, describes the GETM-ERSEM-BFM model used to generate flow fields and provides a detailed description of the particle tracking individual behaviour model that it implemented for this research. Chapter 4 summarises the sampling procedure used to collect the data which forms the basis of the model runs and presents the results of several model simulations undertaken in an attempt to find the origin and future location of the recent winter discoveries. Chapter 5 provides a detailed discussion of what the results mean in the context of the current *M. leidyi* literature and how this work could be developed upon in the future. Chapter 6 is a conclusion to the thesis and sums up the progress that has been made as a result of this research.

Chapter 2

Mnemiopsis leidyi in a Nutshell

2.1 The autecology of *Mnemiopsis leidyi*

The genus *Mnemiopsis* was previously divided into three species: *M. gardeni* [L. Agassiz, 1860], *M. leidyi* [A. Agassiz, 1865] and *M. mccradyi* [A.G. Mayer, 1900] but since 1994 these three putative species have been reunited as one, *M. leidyi* (Hansson, 2006), with the conclusion that polymorphism is responsible for the differentiation between species found in separate regions.

M. leidyi is a self-fertilising hermaphrodite that is native to temperate and subtropical estuaries and coastal areas along the east coast of the Americas from New England to Argentina. It has been discovered in temperatures ranging from 0 to 32°C and in salinities from <2 to 39 PSU (Costello et al., 2012). This tolerance to a wide range of environmental conditions together with its fast feeding, growth and reproduction rates contribute to the success of *M. leidyi* as an invasive species.

2.1.1 Life stages

Previous research has suggested that the ontogeny of *M. leidyi* can be broken down into four distinct life history stages: egg, cydippid larva, transitional stage and lobate adult (Sullivan and Gifford, 2004; Salihoglu et al., 2011). Spawned eggs develop a thick outer layer within one minute of touching the seawater and embryonic development occurs completely within the egg-envelope (Purcell et al., 2001). Upon hatching, *M. leidyi* round-shaped larvae are released into the water, and have two protruding tentacles (Figure 2.1a). The cydippid larvae then progress into a transitional stage retaining these tentacles whilst growing two small oral lobes (Figure 2.1b). Finally tentacle bulbs resorb the tentacles and the lobate adult stage is reached (Figure 2.1c).

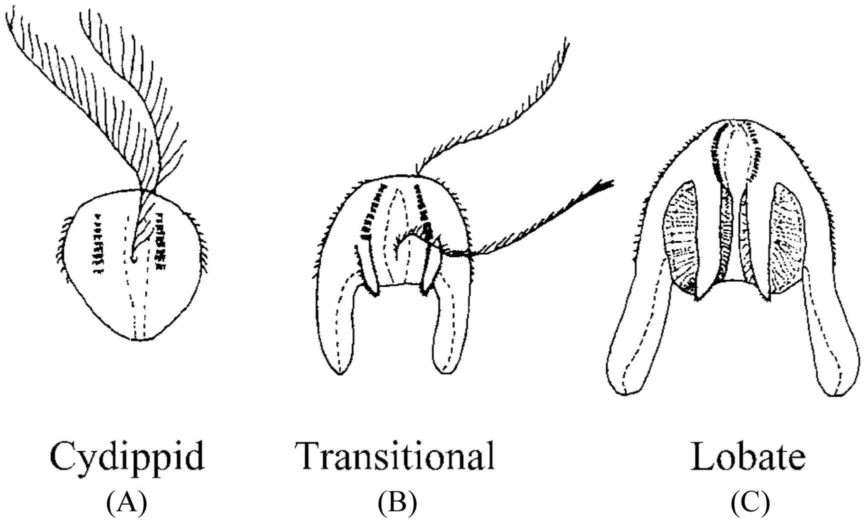

Figure 2.1: Life stages of the ctenophore Mnemiopsis leidyi: (a) cydippid larva, (b) transitional stage between cydippid and lobate form, and (c) lobate adult form. [Obtained from Rapoza et al. (2005)]

2.1.2 Feeding habits

M. leidyi has become well known for its voracious predatory capabilities (Reeve et al., 1978; Rapoza et al., 2005) and the impact it can have on ecosystems both natively and as an invasive species (Shiganova et al., 2001). Historical research claimed that *M. leidyi* was a generalised carnivore; however most of this analysis was based solely on lobate adults (Rapoza et al., 2005) and provided little or no information on larvae dietary requirements – despite the fact that juvenile ctenophores may seasonally dominate overall abundances in native and exotic regions (Kremer and Nixon, 1976; Shiganova et al., 2001). From a functional perspective, the transition from cydippid larva to lobate adult entails a change in prey capture mechanisms (Waggett and Sullivan, 2006). Young larvae rely solely on tentacles containing colloblast cells which, when touched, discharge an adhesive substance which entraps prey. Newly hatched larvae are small and delicate and can be damaged by organisms as small as copepod nauplii (Stanlaw et al., 1981). The larvae are omnivorous and require microplankton prey (20-200 μm) for growth and development (Sullivan and Gifford, 2004). As the larvae grow, consumption rapidly increases and they quickly develop the ability to capture and retain metazoan prey (Rapoza et al., 2005). Once the young ctenophores have progressed into the transitional and lobate adult stages they use cilia to generate a feeding current that continuously entrains large volumes of fluid, yet is virtually undetectable to their prey. It is this trait which has enabled *M. leidyi* to become notoriously successful as an invasive species and led to some labeling the ctenophore "the ultimate hydrodynamically silent predator" (Colin et al., 2010). The feeding rate of adult *M. leidyi* rises with increasing ctenophore size and weight thus, all else being equal, larger ctenophores could catch and digest more food in the same time as smaller ones (Purcell et al., 2001).

2.1.3 Reproduction

M. leidyi has a high reproductive capacity which contributes to its success as an invasive species in European waters. Combined with a short hatching time of approximately 24 hours (Purcell et al., 2001) and high hatching success (60-90%) (Jaspers, 2012) *M. leidyi* can rapidly respond to favourable conditions by spawning. In line with most planktonic ctenophores *M. leidyi* is a self-fertilising hermaphrodite capable of producing viable offspring from a single adult (Planka, 1974). It possesses gonads containing the ovary and spermatophore in their gastrodermis and begins spawning by shedding sperm then quickly releasing oocytes into its own sperm which facilitates external fertilisation. Spawning commences at night typically between 12:00 and 02:00 a.m. and occurs in a wide range of temperatures and salinities. Salihoglu et al. (2011) reported that a full life cycle from egg to adult takes approximately 17 days at a temperature of 25°C but can take considerably longer at lower temperatures (40 days at 15°C) as growth and metabolism are sensitive to temperature (Kremer, 1994; Purcell et al., 2001). Fecundity rises with ctenophore size and egg production has been known to reach 14,000 eggs per day in US waters (Kremer, 1976) and 12,000 eggs per day in the Black Sea (Zaika and Revkov, 1994) but it is important to note that increased fecundity does not always result in increased abundance (McNamara and Lonsdale, 2014). The life span of an egg producing individual can last several months (Costello et al., 2006). The limiting effects of temperature, food availability and salinity on reproduction have been discussed in previous literature (see Section 2.2) and the importance of adequate feeding in particular has divided opinion. Reeve et al. (1989) claim that egg production is highly sensitive to food availability citing the fact that 2-4 days of starvation can result in the termination of egg production.

There is evidence that suggests *M. leidyi* is capable of both paedogenesis (sexual maturity of larvae and juveniles) and dissogony (sexual maturity in two different forms, between which a regression of gonads occurs) (Planka, 1974; Martindale, 1987). *M. leidyi* has the ability to regenerate from fragments larger than one-quarter of an individual (Henry and Martindale, 2000) which also favours rapid population growth.

2.2 Sensitivity to environmental factors

There is no doubt that the flexible physiology of *M. leidyi* is what makes it such a viable candidate to invade many different exotic regions. That is not to say, however, that the distribution of *M. leidyi* and its reproductive capabilities are not influenced by changes in one or more of the environmental factors which are discussed below:

2.2.1 Temperature

M. leidyi has been collected from waters ranging from 0°C in northern native locations in the winter, to 32°C in eastern Mediterranean waters in the summer (Shiganova et al., 2001). This ability to tolerate a wide range of water temperatures allows *M. leidyi* to habituate across a diverse geographical range that includes temperate through tropical marine territories. It is difficult to obtain a global set of survival temperature limits because several abiotic factors interact with one another. For example, *M. leidyi* was collected from waters as cold as -1°C in Narragansett Bay, USA where the salinity level varies between 22 and 33 PSU (Costello et al., 2006), however it is believed *M. leidyi* can not survive below ∼4°C in the Sea of Azov where salinity is between 0 and 14 PSU (Purcell et al., 2001). These reports suggest that low salinity levels can influence the winter survival of *M. leidyi*.

As well as survival temperature limits there is also a threshold at which temperature impacts the reproduction capabilities. Taking into account the various different regions where *M. leidyi* is present egg production is maximised between 15 and 30°C (Purcell et al., 2001). Costello et al. (2012) provide an excellent summary of data from reports carried out at various sampling locations. The results highlight that often there is sampling dates which have adequate temperature levels yet show very little or no evidence of egg production. This demonstrates that optimal temperatures are seen as vital to successful population growth but also emphasises there are other important conditions to be considered such as salinity, food availability and the co-occurrence of a natural predator.

2.2.2 Salinity

M. leidyi has been recorded in conditions close to freshwater in sections of the Sea of Azov and northern Caspian Sea (Shiganova et al., 2001, 2004) and also in hypersaline regions natively at Narragansett Bay and exotically in the Aegean Sea (Kremer, 1976; Shiganova et al., 2004). The phenotypic plasticity of *M. leidyi* is highlighted by its reaction to saline waters. Yazdani Foshtomi et al. (2007) claimed that *M. leidyi* is a hyper-osmoconformer, changing the osmotic concentration of its body fluids to match the extent of its environment. The euryhalinic nature of *M. leidyi* has lead to a perception by some that *M. leidyi* populations are not constrained by salinity variations (Reeve et al., 1989; Kremer, 1994; Purcell and Decker, 2005). Despite this notion, low salinities can lead to smaller maximum body size (Purcell et al., 2001) and can also reduce the winter survival of *M. leidyi.* Jaspers et al. (2011) claim areas with high salinity levels such as the Kattegat appear to act as source regions for the *M. leidyi* population in the central Baltic Sea, however this may be an unlikely assumption as the Baltic Sea generally exports water and only sporadically imports water from the Kattegat (Burchard et al., 2009). It is more likely that in fact, contrary to the findings of Jaspers et al. (2011), *M. leidyi* does persist all year round in the Baltic Sea. Experiments have shown that egg production rates decrease significantly with decreasing salinity. Reproduction rates at a salinity resembling the conditions in the Kattegat (30 PSU) were over 20 times higher than those in a salinity resembling the central Baltic Sea (6 PSU) (Jaspers et al., 2011). In contrast, Lehtiniemi et al. (2012) claim that at salinities of 30 PSU the rate of reproduction was negligible. These results suggest that salinity could be an important explanatory variable when modelling the reproduction rates of *M. leidyi* and highlight the need for further research into the relationship between reproduction and salinity in combination with temperature – in particular to investigate the presence of an upper limit on reproduction in high saline waters. Only once a well-understood causal relationship is established can salinity be meaningfully included in reproduction modelling.

2.2.3 Prey abundance

Whilst it is true that *M. leidyi* is a generalist predator capable of exerting strong regulatory control on the zooplankton community (Purcell et al., 2001), it is important to recognise that the dietary breadth of this ctenophore is life-stage dependent. Early cydippid larvae feed almost exclusively on microzooplankton and protozoa whereas lobate forms feed primarily on mesozooplankton such as copepods, mollusc larvae, eggs and young fish larvae (Sullivan and Gifford, 2004). The availability of microzooplankton can determine the magnitude of larval survivorship, growth and their subsequent recruitment into mesozooplankton-feeding adults (McNamara et al., 2013). Field data from McNamara et al. (2013) conveyed a strong top-down control of microplankton and mesozooplankton during peak abundances of larval and adult *M. leidyi*, respectively. Furthermore, a significant reduction of mesozooplankton by adult *M. leidyi* released certain microplanktonic taxa from predation pressure which resulted in a cascading effect on microplankton abundances, enhancing prey conditions for larval ctenophores.

Understanding the different nutritional requirements of each stage may have important ecological consequences. Population models should acknowledge the fact that overall growth can be curtailed if cydippid larvae have an inadequate supply of prey available, irrespective of the abundance of lobate prey.

Despite recent research by Rowshantabari et al. (2012) showing that the quantity of food digested by *M. leidyi* at 27°C was twice the quantity recorded at 12°C, Salihoglu et al. (2011) and Anninskii and Abolmasova (2000) agree that high growth rates under high temperatures can only be reached if the food sources of both larval and adult *M. leidyi* are not limited (i.e. 25mg Cm^{-3} and 90mg Cm^{-3} mesozooplankton and microplankton respectively). Only, therefore, when growth conditions are favourable for all stages are the high overall population growth rates associated with population blooms likely to be found.

2.2.4 Predation

The abundance of *M. leidyi* can also be regulated by influential predators. There is a broad selection of predators known to consume *M. leidyi*, including vertebrate and gelatinous predators (Mianzan et al., 1996; Purcell et al., 2001). *Beroe ovata* is a pelagic ctenophore that shares a native region with *M. leidyi* in Chesapeake Bay, USA. *B. ovata* can strongly influence *M. leidyi* abundance patterns and its accidental introduction to the Black Sea is thought to have had a regulatory effect on the expanding *M. leidyi* population which had devastated fish stocks in the region (Shiganova et al., 2001). Despite the rapid population growth potential of *M. leidyi*, predators such as *B. ovata* and the carnivorous jellyfish *Chrysaora quinquecirrha* have the ability to reduce *M. leidyi* biomass in native waters in even the most favourable food and temperature conditions for the ctenophore (Condon and Steinberg, 2008).

Much of the literature appears to focus on the predation by gelatinous species (Purcell and Cowan, 1996; Purcell and Decker, 2005; Condon and Steinberg, 2008) but there is some evidence of fish also preying on *M. leidyi.* Oviatt and Kremer (1977) hypothesised that the predation by the butterfish *Peprilus triacanthus* may account for the autumn decline of the *M. leidyi* population in Narragansett Bay. The interactions between ctenophores and fish can have positive and negative effects on commercially important fish populations. Whilst *M. leidyi* has been known to predate on fish eggs and larvae and provide potential competition for food, there are also records of other ctenophores having a commensal relationship with young fish (Purcell and Arai, 2001). These results suggest that there is a need for fish-stomach research in areas with known *M. leidyi* abundance to improve knowledge on predation.

M. leidyi invasions have caused particular devastation in regions without other gelatinous predators such as the Black and Caspian Seas (Purcell et al., 2001). The situation was partly alleviated following the introduction of *B. ovata* and it is believed that native predators such as *Pelagia noctiluca*, *Cyanea capillata*, *Beroe gracilis* and *Beroe cucumis* in the North and Baltic Seas are important in controlling the invasive ctenophore (Hosia and Titelman, 2010). *P. noctiluca* is potentially an important predator of *M. leidyi* in the northwest Mediterranean as it has been known to consume other gelatinous species and forms blooms at the same time as *M. leidyi* (Tilves et al., 2013).

2.3 Geographic distribution

Temperate and subtropical coastal regions have seasonal temperature fluctuations which can dramatically effect *M. leidyi* populations. The entire life cycle of *M. leidyi* is planktonic and does not include any specialised overwintering or benthic stages (Costello et al., 2006). This means that in native and invaded regions when temperatures fall and *M. leidyi* reproduction decreases, there is no way to replace the losses by advective flows to open water where flushing rates may be higher (Abdelrhman, 2005) and water temperatures are lower. This in turn leads to the local disappearance of *M. leidyi* in the non-reproductive winter months. Furthermore, because ctenophores are holoplanktonic, survival of larvae directly influences the population dynamics of adult *M. leidyi* blooms. There are, however, low advection regions in invaded waters where overwintering *M. leidyi* persist all year round (Kube et al., 2007; Viitasalo et al., 2008). These sub-populations are often referred to as source regions. By contrast, the areas which repeat the annual cycle of local population elimination in the winter months followed by re-inoculation in the warmer months are known as sinks (Costello et al., 2012). Local circulation currents provide the delivery method from source to sink regions and *M. leidyi* is able to re-establish itself when conditions promote growth and reproduction.

Source-sink dynamics are vital to the persistence of *M. leidyi* in both its native and invaded habitats (Purcell et al., 2001; Costello et al., 2006). In Narragansett Bay it was found that *M. leidyi* was present in inshore waters all year round (Costello et al., 2006). These interior waters have long hydrographic retention periods (Abdelrhman, 2005) and serve as a refuge for overwintering populations until temperature and prey conditions become favourable for reproduction (Beaulieu et al., 2013). The high reproductive capability of *M. leidyi* then leads to seasonal recolonisation as the species propagates throughout the entire bay. Temperature appears to be of overriding importance in determining conditions suitable for the population increase and expansion of *M. leidyi* (Huwer et al., 2008).

Reusch et al. (2010) found that the *M. leidyi* populations recorded in Eurasia are the result of at least two distinct invasions. It is believed those found in the Baltic and North Seas were introduced directly from native regions and are independent of those recorded earlier in the Black Sea and surrounding areas – this is illustrated by the transport routes in Figure 2.2. The entire Southern European metapopulation is of Gulf of Mexico origin and can be grouped together in one genetic cluster (Bolte et al., 2013). Furthermore, the greater allelic richness in populations from the Black Sea compared to those from the Caspian and Mediterranean Seas suggests the Black Sea is the source region from which a stepping-stone scenario has lead to local populations being established in the surrounding areas.

Genetic analysis has also been used to demonstrate the dynamics of the Northern European populations. The stable genetic diversity over a number of years between the populations in the North Sea and western Baltic Sea indicate successful recruitment took place in both regions and both populations are self-sustaining (Bolte et al., 2013), however an alternative hypothesis may be that the species have evolved to adopt to the varying conditions in which they are found. The former argument is backed up by the findings of Antajan et al. (2014) which suggest there were multiple and simultaneous introductions of *M. leidyi* in the main harbours of Northern Europe, most likely by means of ballast water transport.

2.4 Vertical distribution

Despite its considerable ecological importance, the research on spatial distribution patterns of *M.leidyi* is still in its infancy. In particular, the vertical distribution patterns of established *M. leidyi* populations are seldom described and when mentioned the factors determining the distribution are not well defined. The overall vertical distribution pattern of *M. leidyi* was described as “somewhat confusing” when reviewed by Mianzan et al. (2010). Often there are several factors impacting the organism’s distribution simultaneously which makes it difficult to determine what exactly is causing the organism to vertically migrate. Water depth and degree of vertical stratification not only appear to be influential (Purcell et al., 2001), but may also reflect a range of behavioural responses within local populations (Mianzan et al., 2010). In the Black Sea the majority of *M. leidyi* are located above the pycnocline across the entire day but evidence of vertical migration within the perceptible upper water layers has been recorded (Mutlu, 1999). In shallow, vertically stratified waters, such as the native Chesapeake Bay, *M. leidyi* was also found above the pycnocline both night and day (Purcell et al., 1994). In vertically homogeneous habitats such as the Pamlico Sound (USA), *M. leidyi* was dispersed throughout the water column during the night but aggregated near surface during the day (Miller, 1974). *M. leidyi* can dramatically alter their vertical position over a period of less than an hour (Costello and Mianzan, 2003). Miller (1974) observed that *M. leidyi* retreated from surface layers during periods with high surface winds and choppy sea conditions. Subsequent research by Mianzan et al. (2010) suggest low vertical sheer levels represent a necessary, but not sufficient, condition for high concentrations of *M. leidyi* to occur in surface waters.

Haraldsson et al. (2014) reported some cases in the Baltic Sea where small and medium sized *M. leidyi* migrated upwards an average distance of over 10m per day whilst the largest individuals seemed to remain in deeper water without migrating. Theoretical models for other planktivorous species suggest different optimal strategies between growth and survival depending on life stage, where small individuals tolerate high predation risk in shallow and more illuminated waters in order to achieve sufficient feeding and growth rates (Giske and Aksnes, 1992; Rosland and Giske, 1997). As fecundity increases with ctenophore body size, perhaps *M. leidyi* reaches a size whereby optimum population expansion is achieved solely by reproduction at deeper water levels, where higher salinities and slightly lower temperatures are found, without risking predation at the surface. The fact that the same diel vertical migration was not detected by Haraldsson et al. (2014) at some of the other sampling locations suggests that vertical distribution is controlled by more than one factor.

The influence of light sensitivity on ctenophore migration divides opinion as light sensing organs have not been identified within the phylum (Graham et al., 2001). Despite this, spawning of *M. leidyi* does occur a few hours after sunset so it it may be unwise to completely rule out sensitivity to light as a factor governing diel vertical migration in *M. leidyi.* It may be the case that light sensitivity is a confounding factor and the perceived avoidance of light is actually a reflection of predator avoidance. There is evidence in both native and exotic waters that predator presence appears to alter *M. leidyi's* swimming direction and speed (Kreps et al., 1997; Titelman et al., 2012).

During winter and spring in the Baltic Sea when the species was found in low densities and a high proportion of adults were present, the bulk of the population was concentrated in bottom waters (Javidpour et al., 2009a). Afterwards, with the rising temperatures and the slight development of vertical stratification, the population grew and was dominated by a higher proportion of larval stages, and the bulk of the population shifted towards the upper layers. This may concur with the earlier hypothesis that young, smaller ctenophores are more inclined to risk predation in the upper water layers as they seek maximum growth potential however whether or not this result stems from the fact the adult *M.leidyi* migrated downwards or that simply those in the upper layer died off is not clear.

Kube et al. (2007) found that *M. leidyi* occurred in the central Baltic Sea during the winter months below the permanent halocline, where temperatures do not fall below 4°C. It is possible that the stratification of the water column in the Baltic Sea due to salinity and temperature differences in the surface and bottom water layers might provide an overwintering refuge for *M. leidyi.* Mianzan et al. (2010) also claimed vertically stratified waters appear to contain higher abundances than unstratified ones. Conversely Huwer et al. (2008) found that low salinity was a major factor limiting the population expansion in the Baltic Sea. Strong stratification may therefore act as a physical barrier which restricts population growth (Haraldsson et al., 2014). *M. leidyi* has shown a great tolerance to low dissolved oxygen concentrations (Purcell et al., 2001) and so the threat of hypoxia is probably not a major restriction on population expansion. In some instances when dissolved oxygen concentrations are not lethally low, they can allow *M. leidyi* to feed better than other organisms with which it competes for food resources because it is able to withstand the low dissolved concentration levels and consume planktonic prey in hypoxic waters that others may avoid (Purcell et al., 2014).

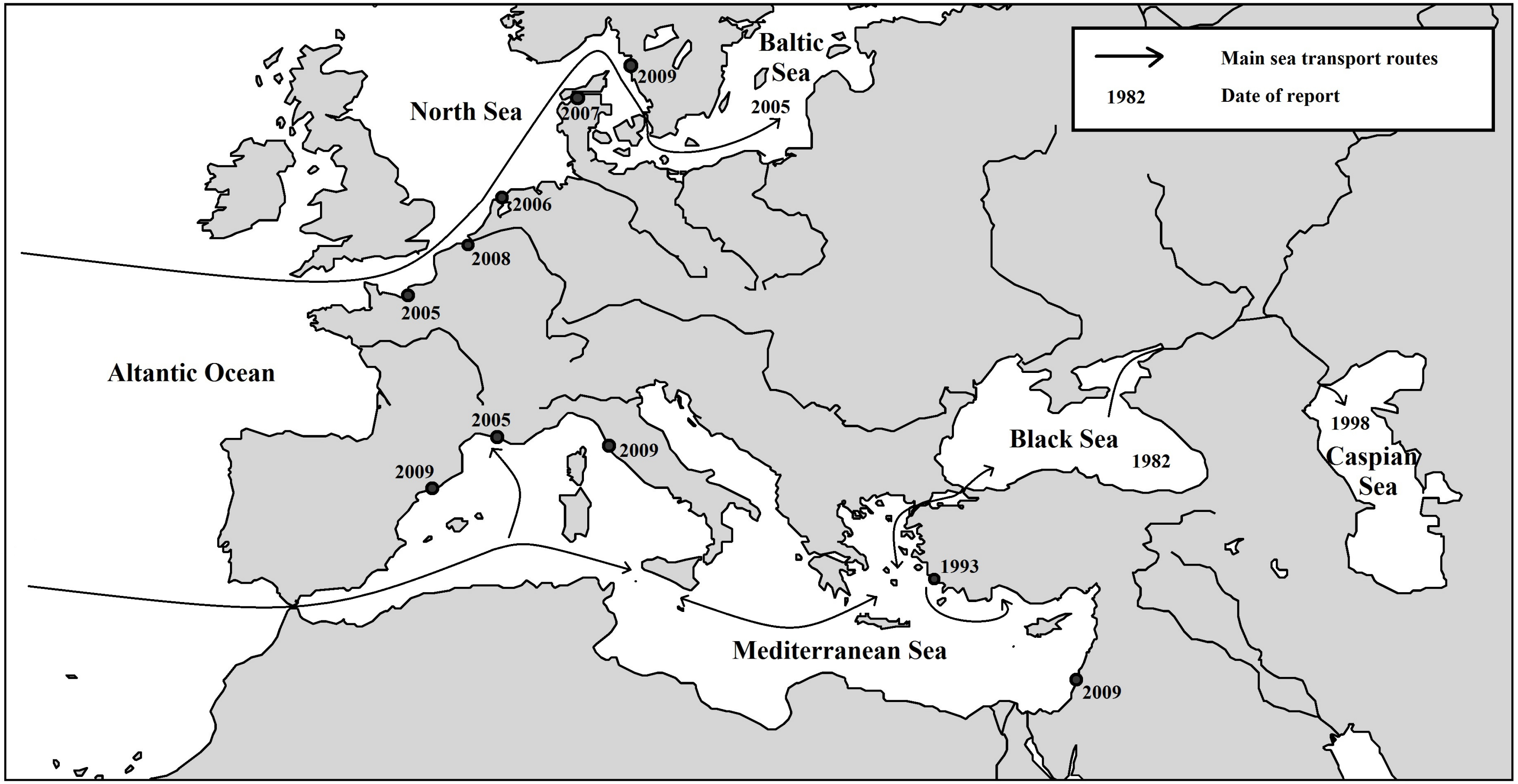

Figure 2.2: The spread of *Mnemiopsis leidyi* through European seas 1980-2010. The dates indicate when the ctenophore was first reported and the arrows indicate the main sea transport routes.

2.5 The range expansion of *Mnemiopsis leidyi* in European shelf seas

M. leidyi was first located in Europe in inshore waters of the Black Sea in 1982 (Pereladov, 1988). It wasn't until 1988 that it began to encompass much more of this area (Vinogradov et al., 1989) and by autumn 1989 it reached peak abundance with a density of 304 individuals m^{-3} (Purcell et al., 2001). There was then a steady decrease in numbers and biomass until the summer of 1993. Another peak in abundance was recorded in the autumn of 1994. Although the second outbreak did not reach the levels of the original one, greater biomasses were recorded in inshore waters compared to those in 1989. A third peak was measured in 1998 which led Purcell et al. (2001) to claim a marked inter-annual variation in the abundance of *M. leidyi* in the Black Sea as a result of environmental factors and food availability (Shiganova, 1998). In its native environment *M. leidyi* populations exhibit long term fluctuations in their density and Kremer (1994) noted that the pattern of varying year to year abundance in the Black Sea appeared to resemble this. In native waters, this interannual variation in population size has been attributed to interannual variation in spring-time temperatures (Purcell et al., 2001), variations in zooplankton biomass (also linked to temperature) (Kremer, 1994) and predator abundance (Kremer and Nixon, 1976).

During the late 1980's *M. leidyi* from the Black Sea moved into the adjacent basins (Figure 2.2). It was first detected in the Sea of Azov in the summer of 1988 and has bloomed there every year since between summer and early autumn. *M. leidyi* was first found in the southern area neighbouring the Kerch Strait and later it spread through the Sea of Azov and reached peak biomass around August/September. It is believed the organism cannot survive the low temperatures observed in the Sea of Azov during the winter months and therefore must be re-introduced annually through the Kerch Strait (Purcell et al., 2001). The year-to-year fluctuations in the timing and extent of the dispersion into the Sea of Azov depends on wind driven currents (Volovik et al., 1993). Despite having the potential to achieve substantial population biomass, *M. leidyi* remained relatively small (1.5-2.5cm) in the Sea of Azov (Purcell et al., 2001). This may be due to the constant re-introduction of new young organisms as the population dies out during the winter months or may be a consequence of the organisms allocating resources to reproduction as a more efficient means of sustainability than growth.

In 1989, *M. leidyi* spread to the Sea of Marmara via the Bosporus Strait where, unlike the Sea of Azov, it occurs all year round in the upper water layer. The following year it advanced to the Mediterranean Sea where it was first identified in the Aegean Sea (Shiganova, 1998). *M. leidyi* has been recorded in low densities in the spring, summer and autumn months. Conditions in the spring and autumn seem favourable for *M. leidyi* with temperatures not exceeding 26°C but more noteworthy is that it has been detected during the summer months when temperatures are much greater and salinity is consistently around 39 PSU. Today a wide distribution of M. leidyi across these waters remains and indicates established permanent populations throughout southern Europe.

More recently there has been a series of discoveries in northerly European waters. In November 2005, *M. leidyi* was first recorded in the Baltic Sea and is now thought to be widespread there (Javidpour et al., 2009b). The first records of its occurrence in the North Sea were in 2006 when Faasse and Bayha (2006) confirmed via genetic analysis the presence of *M. leidyi* in two different estuarine regions along the Dutch coast. (Faasse and Bayha, 2006) claim there is a high possibility *M.leidyi* was present in these waters for more than ten years before this discovery but had been misidentified as *Bolinopsis infundibulum.* This cold water lobate ctenophore had recorded unusually high numbers in the summer months in warm waters since 1992 (Holsteijn, 2002) and it is now thought these blooms may have been *M. leidyi.* These large populations in the southern North Sea are possibly the source for the *M. leidyi* discoveries in the Skagerrak (Hansson, 2006). The first record of *M. leidyi* in French waters (Le Harve Harbour, 2005) coincided with the initial discovery in the northern part of the North Sea (Antajan et al., 2014), however it wasn't until September 2009 that the species was actually recorded in French North Sea water.

By the end of 2006, *M. leidyi* had spread to the coastal waters north and south of Denmark (Tendal et al., 2007). It was first observed in Limfjorden (Denmark) in 2007 and is believed to have been transported there by ballast water from the North Sea via the Thybøron Kanal. The mass occurrence recorded in the late summer of 2007 (Riisgård et al., 2007) showed densities reaching more than 800 individuals m^{-3} in the innermost parts of Limfjorden (Riisgård et al., 2011) – greater than the peak abundances recorded in the Black Sea at the time of the anchovy collapse.

In 2009, weekly measurements were taken in the western Dutch Wadden Sea and it was discovered that *M. leidyi* was present all year round in these waters (van Walraven et al., 2013). In contrast to the single peak in abundance usually recorded around September in its native range, *M. leidyi* saw several peaks throughout the year in the Wadden Sea – all of which were dominated by small (<20mm) ctenophores – suggesting the Wadden Sea may be a sink region (Costello et al., 2012) which is continually re-inoculated by waters along the Dutch coast.

In a study of the Belgian part of the North Sea *M. leidyi* was recorded continuously between June 2010 and March 2011 despite water temperatures becoming as low as 2°C (Van Ginderdeuren et al., 2012). *M. leidyi* was also found in high numbers in some of the Zeeland estuaries as part of the Interreg MEMO (*Mnemiopsis* Ecology and Modelling: Observation of an invasive comb jelly in the North Sea) project, in October 2012 (L. van Walraven, pers.com.). It is thought the presence of *M. leidyi* could have a substantial negative effect on the abundance of sole which spawns from April to September (Munk and Nielsen, 2005) due to the overlap between the *M. leidyi* blooms and the sole larvae in the water column. There are also concerns that the species could have a detrimental effect on the economically important oyster farm in the Sluice Dock at Ostend as it competes with oysters for planktonic food resources.

Since 2009, blooms of *M. leidyi* have also been identified in the waters of Israel (Galil et al., 2009), Italy (Boero et al., 2009), Spain (Fuentes et al., 2010) and Sweden (Hosia and Titelman, 2010) and is now a great cause for concern for most European countries.

2.6 Mathematical models of *Mnemiopsis leidyi* populations

A first attempt at developing a predictive spatial model was undertaken by Siapatis et al. (2008) to identify areas in the Greek seas and the entire Mediterranean basin that could serve as a potential habitat for the species. General additive models (GAM) with a binary presence/absence response variable were applied to *M. leidyi* presence data and satellite environmental data from the Aegean Sea. The results showed a high degree of interannual variability in the northern Aegean Sea – similar to the earlier findings from the Black Sea (Purcell et al., 2001). The results also showed that river outflows influenced by human impact resulted in increased nutrients and a subsequent increase in zooplankton populations which benefited *M. leidyi* population expansion.

There was a higher probability of *M. leidyi* in warmer more stratified waters and a contrasting spatial occupation of *M. leidyi* and anchovy eggs. The potential of similar predator-prey overlapping in northern European waters is what makes *M. leidyi* such a concern in these regions.

The population abundance of *M. leidyi* recorded at the beginning of the year is highly dependent on the environmental conditions of the preceding winter and not on the numbers recorded the previous year (Knowler, 2005). To fully appreciate the importance of these environmental factors and attempt to disentangle the interplay between them it is necessary to construct a suitable population model. A good illustration of how each factor in isolation can not possibly tell the full story is provided by Costello et al. (2012). In the summer at Chesapeake Bay, the low and high saline waters serve as a refuge to *M. leidyi* from predation by *C. quinquecirrha*, which prefers salinities of 10-25 PSU. In this case the ctenophore benefits from its wide tolerance to salinity and can be abundant in lower salinities than what are regarded as optimal conditions.

At the time of writing it is believed there is currently only one available individual based population dynamics model of *M. leidyi* available for review (Salihoglu et al., 2011). This deterministic simulation model was designed with a view to analyze the influence of temperature and food availability on *M. leidyi* reproduction and blooms in the Black Sea. The stage resolving model considers detailed mass and population growth dynamics of four stages of model-ctenophore. The model is stage-dependent – incorporating the different growth characteristics of egg, juvenile, transitional and adult stages – as a consequence of research by Sullivan and Gifford (2004) who highlight three distinct life stages in the development of larvae. Given the vastly differing feeding habits of cydippid and lobate forms discussed in Section 2.1.2, the stage resolving aspect of this model is a necessity. A detailed overview of the parameterisation of this stage resolving life cycle model is provided in Salihoglu et al. (2011). The results imply a strong temperature control on the biomass of all life stages and also the strong capability of mesozooplankton abundance to control the adult ctenophore biomass.

Following research from Kremer (1976) and Kremer and Reeve (1989), the feeding rate of adult *M. leidyi* – unlike many plankton-feeding animals – is independent of prey concentration and is instead modelled as a function of temperature and organism size. The feeding rate equation contains a negative exponential coefficient to incorporate the trend of decreasing weight-specific clearance rate (amount of water cleared per individual per unit time) with size and another coefficient to convey the increased feeding rates at higher temperatures. Kremer and Reeve (1989) highlighted a considerable effect of prey concentration on the clearance rate of smaller ctenophores (<1 mg C) so for transitional stage ctenophores that are less than 1 mg C in biomass, the adult clearance rate is adjusted empirically to reflect this effect. The juvenile clearance rate is estimated by a linear relationship developed by Sullivan and Gifford (2004) that incorporates the length of the ctenophore. Grazing rates define the amount of ingested food per day in relation to the biomass of an individual ctenophore of any stage. Grazing rates are stage-dependent and related to food concentration and the time taken for transfer to the next stage is then linked to this grazing rate. Egg production increases with ctenophore size (Purcell et al., 2001) and for this reason adult reproduction rates are dependent on ctenophore mass together with temperature and food concentrations.

The assimilation efficiency rate of 72% used in the grazing rate equations was originally determined for adult *M. mccradyi* – subsequently defined to be the same species as *M. leidyi* – at “ecologically reasonable food levels” (Kremer, 1976). Kremer and Reeve (1989) found that if the ctenophores continue to feed at high prey concentrations, incoming food is only partially digested and the assimilation efficiency decreases substantially. For this reason the adult assimilation efficiency is assumed to vary with food concentration. The assimilation efficiency of juvenile ctenophores is not known and could be the source of some empirical research in the future. In this model it is set to a constant rate of 75%. Sensitivity analysis later finds that a small change (±10%) in the assimilation efficiency can have a dramatic effect on the biomass levels that are produced by the model – suggesting this parameter requires future targeted research.

The model assumes that all adults can reproduce and that immediately after transfer from the transitional stage only 1% of unmetabolised assimilation is designated to reproduction. As the ctenophore grows, this fraction increases exponentially, reaching 100% when the maximum size attainable in the growth model is achieved. This relationship is questionable as there is a known *M. leidyi* population in the Sea of Azov with no ctenophores large enough to be considered adults. More targeted research into the allocation of resources between growth and reproduction may shed some light on this issue.

Augustine et al. (2014) found that physiological rates start to deviate from the Arrhenius relationship around 12°C. This agreed with previous research which showed the rate of change in clearance rate as a consequence of increasing the temperature (Q_{10} coefficient) in the range from 12-20°C was higher than that between 20-27°C, suggesting the relationship across the scale is not strictly linear (Rowshantabari et al., 2012). Thus using a constant Q_{10} coefficient is not the best method to use when comparing growth rates spanning large temperature ranges.

Observations on mortality of different life stages of *M. leidyi* are very limited and as a result the model of Salihoglu et al. (2011) assumes constant mortality rates for eggs (99% per day), juveniles (95% per day), transitional stage ctenophores (30% per day) and adults (2% per day). It is questionable, however, that these mortalities are reported correctly in the paper, as an attempt to reproduce the results of the reference run in Salihoglu et al. (2011) with a simplified version of the model required mortality settings of 70% per day for eggs, and 22% per day for juveniles (van der Molen et al., 2015).

Mortality is a key aspect of population modelling and can be broken down into three main components: starvation induced mortality, advection based mortality and predation based mortality. As the model is zero-dimensional, any potential lack of habitat connectivity and losses as a result of drifting to unfavourable regions are unaccounted for. Predator-based mortality will vary depending on the region being investigated and also the time of year. More empirical research is required on known predators of *M. leidyi* to facilitate the development of novel approaches to estimate predator-prey overlaps and the threats posed to *M. leidyi.*

In the North Sea, temperature and salinity are not usually considered constraints on survival due to the high tolerance of *M. leidyi* to environmental factors however (Collingridge et al., 2014) found that its distribution is limited by winter temperatures in some places. That being said, the results showed that food availability was the key factor which limited winter survival and restricted the overwintering population. Finenko et al. (2014) found that water temperature and individual body weight have a minor effect on feeding intensity in the Black Sea and that the abundance of prey is the limiting factor affecting the quantity of consumed food. *M. leidyi* has only been found where mesozooplankton concentrations exceed 3mg Cm^{-3} (Fuentes et al., 2010), so this value was used when modelling the suitability of conditions for *M. leidyi* survival. Given that there is evidence of *M. leidyi* withstanding starvation (Purcell et al., 2001;

Oliveira et al., 2007), it may well be the case that the ctenophore can survive at food levels below this threshold. To date, no experiments have investigated the survival of *M. leidyi* at very low food concentrations but slowed metabolism at lower winter temperatures means food requirements are likely to be lower (Purcell et al., 2001). If *M. leidyi* could survive at lower food concentrations for longer periods then the sensitivity analysis carried out by Collingridge et al. (2014) suggests the suitable overwintering area of the North Sea would be increased.

Knowler (2005) claims that *M. leidyi* ingests its prey in an approximately linear proportion to prey abundance over a wide range of population densities. Observations regarding density dependence are very limited and this may also be an area for future research. No previous research to date explores the possibility of population density being a limiting factor but it may well be worth confirming that this condition can be excluded from any future models. There has been some very recent research using Dynamic Energy Budget (DEB) theory showing that, because *M. leidyi* has a low reserve capacity, one day of starvation will affect different sizes of ctenophore very differently. The belief is the impact of one day of starvation on a large individual is much greater than the comparable effect on a small individual (Augustine et al., 2014). This hypothesis suggests that smaller individuals may be more likely to overwinter.

A cohort experiment by Jaspers (2012) found that in the early stages of development energy is primarily allocated towards growth. This trend continues until the larvae enter the transitional phase and begin to form lobes. At this point the growth rate is significantly reduced and energy allocation is focused more towards egg production. These findings suggest the transfer of allocation happens earlier than what is suggested by the Salihoglu et al. (2011) model. According to Augustine et al. (2014), *M. leidyi* appears to undergo a so-called metabolic acceleration after hatching. In some cases the onset of this acceleration appeared to be delayed but there is no evidence yet as to why this might be the case. One hypothesis is that the onset of metabolic acceleration might be triggered by an environmental factor and that delaying it until food and temperature conditions are more favourable could help surviving periods without much food. This would be a highly ecologically relevant feature as the results appear to show that small larvae can last a very long time at low food levels and more effort should be dedicated to understanding energy allocation.

In order to monitor and predict the invasion success of *M. leidyi* it is important to have an individual behaviour model that simulates the life-cycle of *M. leidyi* as accurately as possible. This model can then be coupled with ecosystem and hydrodynamical models to effectively assess potential impacts on the marine environment. It is therefore vital that hydrodynamics of the area in which this model will be run – in this case the North Sea – are fully understood in order to make sense of the results obtained from the individual behaviour model. For this reason Chapter 3 provides an overview of the North Sea hydrography and then describes the biogeochemical model which is used to simulate the hydrography and plankton dynamics of the study area.

Chapter 3

How The North Sea and *Mnemiopsis leidyi* are Modelled

In order to effectively simulate *M. leidyi* populations in the North Sea it is important to understand both the hydrography of the subject area and the underlying processes of the physical and individual behaviour models used. Section 3.1 of this chapter provides an brief summary of the North Sea hydrography and an overview of the hydrodynamical model used in this study. Section 3.2 provides a detailed description of the particle tracking individual behaviour model (GITM) that was implemented for this research with particular focus on the biological extension and how it enables populations of *M. leidyi* to be simulated over time and space.

3.1 Hydrographic processes of the North Sea

3.1.1 Overview of the North Sea hydrography

The North Sea is a shallow shelf sea adjacent to the North Atlantic that borders Norway, Denmark, Sweden, Germany, Netherlands, Belgium, France, England and Scotland. It is one of the most intensely investigated sea areas in the world largely due to its importance for marine shipping, fishing, oil and gas extraction and tourism (Paramor et al., 2009). More recently it has also become an important area for renewable installations such as wind farms.

The North Sea is more than 970km from north to south and 580km from east to west, with a surface area of roughly 750,000km^2. The majority of the North Sea is shallower than 200m – the mean depth is around 80m (Sündermann and Pohlmann, 2011) – although it also contains the Norwegian Trench and the Skagerrak Strait at the southern end of Norway which have depths of up to 400m and 700m respectively (Rodhe, 1987). One of the most prominent features of the North Sea is the Dogger Bank, which has a water depth of 30m and is separated from the Norfolk Banks to the southwest by the Silver Pit (van der Molen et al., 2015). The Oyster Grounds, with depths of 40-50m, are situated southeast of the Dogger Bank. The Southern Bight is situated further south, and consists of a deep channel in the west (around 50m) and a shallow area (typically less than 30m) in the east (Figure 3.1).

Brown et al. (1999) provides a synopsis of the surface currents of the North Sea and concludes that a large anti-clockwise gyre rotates around the basin and influences the entire region. There are three northerly oceanic inflows to the North Sea: the Fair Isle Current, the East Shetland Atlantic Inflow (ESAI) and the North Atlantic Current which flows down the western slope of the Norwegian Trench and provides the main inflow into the North Sea (Turrell et al., 1996). There is also a smaller, warmer and more saline inflow in the southwest via the Strait of Dover which originates from the Atlantic Ocean and passes through the English Channel (Paramor et al., 2009). Water primarily leaves the North Sea northwards via the Norwegian Coastal Current. The source and volume of water entering the North Sea is highly variable between seasons and years (Paramor et al., 2009). Precipitation influences the salinity of the North Sea and its seasonal variability both directly and via continental discharge (Sündermann and Pohlmann, 2011).

FIGURE 3.1: Map of the North Sea region. [Obtained from Halava (2010)]

Temperature and salinity determine the density of the sea water and the structure of the water masses. The dominant physical division of the North Sea is conveyed by classifying three key regions:

1. **Southern Bight** (51-54°N) with water depths of less than 40m;
2. **Central North Sea** (54-57°N) with water depths of 40-100m – except for the shallow areas on the Dogger Bank and along the western coast of Denmark;
3. **Northern North Sea** (north of 57°N) including an area of shelf water 100-200m deep, and the Norwegian Channel with water depths from 200-700m in the Skagerrak between Denmark and Norway.

A thermal stratification occurs in the deeper northern and central parts of the North Sea during the calmer, warmer months of summer (from May until October) when the heating of surface water causes a two-layer system with a sharp interface, the thermocline, which remains until early autumn (Brown et al., 1999). In autumn and winter this stratification breaks down as a consequence of reduced surface heating and tidal, wind and wave induced mixing. The two-layer system then reduces to a vertically well mixed water column of uniform temperature. Under stratified conditions, a subsurface jet induced by density differences transports water around the north, east and southeast slopes of the Dogger Bank into the Oyster Grounds (Brown et al., 1999; Hill et al., 2008). Conversely, with the exception of coastal regions of fresh water influence, the shallow southern North Sea is permanently vertically mixed as a result of strong tidal currents flowing through the relatively shallow water (Sündermann and Pohlmann, 2011).

Salinity ranges from approximately 29 PSU in the southeastern North Sea, where a large volume of fresh water runs off the continental land mass, to more than 35 PSU in the north-west, where oceanic Atlantic water enters the North Sea (Mackinson and Daskalov, 2007). The average temperature range for waters in the North Sea in winter is 3-8°C. In the summer the average temperature range for the northern and central North Sea is 6-10°C for bottom waters and 12-14°C for surface waters. In the well mixed southern North Sea both surface and bottom summer water temperatures are 16-19°C. The sea surface temperatures in the North Sea follow a strong annual cycle. They are primarily affected by heating by the sun and heating/cooling through contact with the air, which is accentuated during high wind conditions. They are also influenced by the mixing of surface water with deep water caused by wind or tidal currents in shallow areas; by the inflow of freshwater, in particular cold water following the spring melting of ice and snow; and by the temperature of water entering from the Atlantic and Channel (Paramor et al., 2009).

The temperature of bottom waters (those near or on the sea bed) tends to be more stable than that on the surface. It is largely affected by the water bodies entering the North Sea from the Atlantic Ocean. Cold water flows into the northern North Sea and remains below the surface mixed layer. In the southern North Sea warmer water enters the southern basin via the English Channel. The shallow nature of the southern basin and the English Channel and the strong tidal flows mean that this region is well mixed and bottom water temperatures follow those of the surface waters. The temperature of surface waters varies more than the temperature of deeper waters as they are exposed to atmospheric forcing. This means that there is more 'disturbance' in these areas and the organisms need to be tolerant of a wide range of temperatures.

One of the most spatially complete surveys of North Sea temperature undertaken in 1976 found evidence of a pool of cold, dense bottom water north of the Dogger Bank in summer, with August surface to bottom temperature differences of 12°C (Harding and Nichols, 1987). A later survey reported by Gmitrowicz and Brown (1993) revealed surface to bottom temperature differences of 7°C which correspond more closely to the long term average in the area. Interestingly, salinity varied at most by 0.62 PSU across the entire Dogger Bank region indicating that variations in the density field in the North Sea are controlled almost exclusively by temperature (Brown et al., 1999). A similar baroclinic feature, the Dooley Current, is found in the northern North Sea where a geostrophic jet driven by density differences follows a 100m contour around the Fladen Ground (Turrell et al., 1992; Brown et al., 1999).

These baroclinic features are critical to the understanding of North Sea hydrography and must therefore be represented by a hydrodynamic model in order to allow us to simulate the transport, connectivity and population dynamics of *M. leidyi* at the scale of the North Sea.

3.1.2 Coupled hydro-biogeochemical model (GETM-ERSEM-BFM)

The General Estuarine Transport Model (GETM, see `www.getm.eu`) is coupled with the European Regional Seas Ecosystem Model - Biogeochemical Flux Model (ERSEM-BFM, see `www.nioz.nl/northsea_model`) to produce hydrodynamics and food fields which are used to drive an offline particle tracking model. This hydro-biogeochemical model generates fields which are saved every hour, recording physical parameters (such as temperature and salinity), currents data, sea surface elevations and plankton dynamics which allow the creation of food fields.

GETM is a public domain, three-dimensional finite difference hydrodynamical model which solves three-dimensional partial differential equations for conservation of mass, momentum, salt and heat. GETM incorporates the General Ocean Turbulence Model (GOTM, see `www.gotm.net`) which is a one-dimensional model that provides vertical turbulence structure. The geographical domain of the model extends between 48.5°-60.0°N latitude and 5.15°W-16.2°E longitude. Spherical coordinates are used in the horizontal plane, while general coordinates are used in the vertical (equidistant in shallow water and contracted near the surface and the seabed in deep water). The model grid is 6 nautical miles (approximately 10km) in the horizontal and 25 sigma layers are used in the vertical.

The model can implement the inflow of fresh water and describes the development of stratification in the domain both as a result of salinity and temperature gradients. Regions of Freshwater Influence (ROFI) are noticeable along the Dutch, German and Danish coasts due to riverine inflow. Some freshwater outflow out of the Skagerrak and along the Norwegian coast is also visible. Open model boundaries are located to the north (between the North Sea and North Atlantic), the south (at the English Channel), and to the east (where the Kattegat meets the Baltic Sea). The shallow water equations are solved on an Arakawa C-grid whilst lateral boundary conditions are represented by a land mask on the horizontal numerical grid. Elevations and currents, derived from a shelf-wide barotropic model driven by Topex-Poseidon satellite altimetry data, are prescribed at the open boundaries using a Flather boundary condition.

The ERSEM-BFM version used in this thesis is a development of the model ERSEM III and describes the dynamics of the biogeochemical fluxes within the pelagic and benthic environment. The ERSEM-BFM model simulates the cycles of nitrogen, phosphorus, silica, carbon, and oxygen and allows for variable internal nutrient ratios inside organisms, based on external availability and physiological status. Plankton dynamics are parameterized by considering a number of plankton functional groups, each representing a class of taxa. These plankton functional groups are sub-divided into producers (phytoplankton), consumers (zooplankton), and decomposers (bacteria). These broad functional classifications are further partitioned into functional subgroups to create a planktonic food web (e.g. diatoms, picophytoplankton, microzooplankton, etc.). From a mathematical point of view, the BFM is a set of ordinary differential equations describing the time rate of change of a number of biogeochemically active tracers. The BFM structure is flexible and modular, so that the number, type and properties of the functional groups can be easily modified and different model configurations can be used to focus on different aspects.

For more information on GETM see Burchard and Bolding (2002) and `www.getmeu`. For details on ERSEM-BFM see Vichi et al. (2007) and `www.nioz.nl/northsea_model` and for recent applications see Lenhart et al. (2010), van Leeuwen et al. (2013) and van der Molen et al. (2013). This coupled model produces flow fields and food fields which facilitate the use of a particle tracking model to monitor populations of *M. leidyi* in the North Sea.

3.2 Particle tracking individual behaviour model (GITM)

3.2.1 Model overview

In physical oceanography, a tracer is a substance such as a dye or radioactive isotope that can be used to track movement in a mean flow field. Since the 1970s, tracer methods have made significant contributions to the understanding of the ocean circulation and internal water mass structures. Furthermore, numerical simulations of tracer transport are a valuable tool to estimate the dispersion of pollutants, such as oil or sewage disposals, in the ocean for the research of long-term effects and the development of effective counter-active measures.

The General Individuals Tracking Model (GITM) is a three-dimensional off-line particle tracking model designed as an extension of the hydrodynamic model GETM to include the advective and diffusive transport of passive Lagrangian tracers. The original code of GITM was developed as an on-line version by Frank Wolk (Wolk, 2003) and re-written off-line by Hide Yamazaki. Cefas obtained a version of this code from Karsten Bolding in 2005 and developed it further to include modules which allow for biological development and migration behaviour. GITM describes the motion of a number of discrete particles through a three-dimensional velocity field. It is important to model a sufficient number of particles to ensure the transport patterns observed are representative of all particle movement from the sources.

3.2.2 Eulerian vs. Lagrangian perspective

There are two frames of reference from which to describe the motion of a fluid and its associated properties (temperature, salinity, concentration of a substance, etc.) – Eulerian and Lagrangian. The Eulerian approach identifies a certain fixed location in the flow field and follows the change in its properties as different materials pass through that location. This perspective can be visualized as sitting on the bank of a river and watching the water pass your fixed location. With the Lagrangian approach, spatial position is not a fixed reference but another variable of the particle. The Lagrangian approach identifies a material of the fluid, follows it, and monitors the changes in its properties. The flow variables are written with respect to time t and a single initial reference point e.g. a particle's position $x(x_0, t)$ and it's velocity $v(x_0, t)$ with x_0 the initial particle position at $t = 0$ (see Wolk, 2003, Section 2.2.4). This approach can be visualized as sitting in a boat and drifting down a river.

A Lagrangian method was chosen for this model because it is extremely beneficial to the task of modelling the far-field fate of passive biological particles, giving both qualitative and quantitative information about the position of the particles in a timely, accurate manner. Within the Lagrangian framework, particle pathways (trajectories) are readily identified. Also, in Lagrangian models the computational effort is concentrated on regions where most particles are located, while in Eulerian models all regions of the domain are treated equally in terms of computational effort.

3.2.3 Modelling the physical processes

The transport of particles is described in the model as a combination of advection and diffusion. Advection is the transport associated with the mean flow of a fluid while diffusion is associated with random motions of molecules, turbulence and eddies within a fluid that are not resolved by the computational mesh. Molecular diffusion – the net flux of molecules from a region of higher concentration to one of lower concentration – alone is entirely insufficient to produce the rate of mixing observed in natural waters. The difference between the observed rate of diffusion and the rate expected from molecular diffusion is the result of turbulent diffusion caused by random and chaotic time dependent motions (e.g. wave induced mixing).

The advection-diffusion elements of GITM are based on a re-coded version of the semi-analytical advection-diffusion method developed by Wolk (2003) which employs the Runge-Kutta 4th order advection algorithm and takes into account both molecular and turbulent diffusion. First, the analytical solution of the Lagrangian advection equation (Duwe, 1988) ensures the that particles follow stream lines exactly. Secondly, a random walk method with advective correction (Visser, 1997) is included to simulate diffusion (Hunter et al., 1993). This method uses a constant diffusion coefficient in the horizontal direction and temporally and spatially varying diffusion coefficients – obtained from the turbulence closure model in GETM – to compute the vertical motion (see Wolk, 2003, section 2.2.2). Finally, the principle of superposition allows these processes to be added together because advection and diffusion are linearly independent. For all simulations a time step of 10 seconds is chosen to ensure the accuracy of the tracer model. More detailed information about GITM can be found in Wolk (2003). The combined hydrodynamics model (GETM) and particle tracking model (GITM) were applied recently to simulate the transport of plaice larvae in the North Sea (Tiessen et al., 2014).

3.2.4 Biological extension

This model was recently expanded upon at Cefas with modules to allow for biological development and behaviour methods based on earlier work presented in van der Molen et al. (2007). The model can be used to study the fate of marine fish, eggs and larvae and in particular the influence of development and larvae behaviour on dispersal routes. It is coded in a general way with an extensive set of switches which can be to be used to define species-specific behavioural and development features. Each particle can have an egg phase and a larval phase, each of which can be subdivided into any number of stages with different characteristics such as growth rate and vertical migration behaviour. These features can result in changes in a particle's position in addition to passive advection and diffusion by the hydrodynamics. As this migration behaviour can change over time as particles develop and grow, development can indirectly affect the particle's trajectory. However, some of these mechanisms were not used for this research. Instead the model was modified to include a simplified version of the reproduction mechanism suggested by Salihoglu et al. (2011), elements of which originate from the model of Kremer (1976) (see van der Molen et al., 2015, for more detail).

At this point it is useful to define two concepts that are used throughout the description of this model and the subsequent results. For the purposes of this work, a 'super-individual' is defined as a particle which represents a prescribed number of adult individuals of average mass. Due to the underlying structure of the particle tracking model, the total number of particles in the run must be prescribed beforehand and this number cannot change throughout the simulation. To get around this, the fluctuation in individual numbers – either by mortality or reproduction – is expressed by the change in the weighting provided to each super-individual. By using this method, a run becomes much more efficient as one particle in the model can be used to represent an arbitrary number of *M. leidyi* individuals which significantly reduces computational time. This method of course has its limitations as the entire super-individual will follow exactly the same trajectory as one real particle would instead of each of the represented particles possibly being dispersed in different directions by advection and diffusion.

The second phrase that requires explanation is 'instantaneous adulthood'. In order to allow the super-individual to represent a number of adults of average mass, but at the same time include reproduction, the egg and juvenile stages need to be infinitely short in 'model time'. This means that the number of surviving young adults produced by reproduction is added instantaneously to the overall number associated with any particular super-individual. However, in terms of the mortality applied to the egg and juvenile stages, the model does take into account the entire 'real time' duration. This means that the actual number of surviving young adults from reproduction does reflect the time taken to mature and the associated daily mortality rates of eggs and juveniles along the way. The downside of this simplification is that any offspring that reach adulthood are immediately reproductive on the day they are spawned and not after the time taken to mature which could have serious implications for the population dynamics (see Section 5.2). Food stocks in the model are also assumed not to be impacted upon by the feeding of *M. leidyi.* As a result, the resulting survival and reproductive success of individuals simulated by the present model implementation should be considered an over-estimate.

This simplified reproduction mechanism was developed by van der Molen et al. (2015) and is described as follows.

Although genetic evidence suggests there are differences between northern and southern European populations (Reusch et al., 2010), there has been no corresponding evidence found in the literature for differences in physiological response to temperature. It is therefore assumed, unless specified otherwise, that the parameter values suggested by Salihoglu et al. (2011) are a reasonable first approximation for populations in the North Sea. See Appendix A for a complete table of the parameter estimates used for the model simulations.

Eggs are only produced if temperature and salinity are above the thresholds of 12°C and 10 PSU, respectively (Lehtiniemi et al., 2012, however, see Section 5.3). The number of eggs produced per time step (n_e) depends on food availability:

$$n_\mathrm{e} = \frac{f F_\mathrm{a}}{w_\mathrm{e}} \tag{3.1}$$

where F_a is the food assimilation of the adult population represented by the super-individual [$mg\ C\ timestep^{-1}$], w_e is the average mass of an egg [$\mu g\ C$], and f the proportion of food turned into eggs. The adult food assimilation is calculated as:

$$F_\mathrm{a} = n_\mathrm{a}\,\frac{f_\mathrm{a}}{1000} c_\mathrm{cd}\, w_\mathrm{a}\, G_\mathrm{a}\, A_\mathrm{a}\, \frac{\mathrm{d}t}{24 \times 3600} \tag{3.2}$$

where n_a is the number of adults represented by the super-individual, f_a is the adult food concentration [$mg\ C\ m^{-3}$] (taken here as mesozooplankton from the GETM-ERSEM-BFM model, see Section 3.1.2), w_a is the average mass of an adult [mgC], $\mathrm{d}t$ is the time step(s), c_{cd} is a factor to convert carbon weight to dry weight $[mg\, mg^{-1}\, C]$ and A_{a} is the adult assimilation efficiency. Following previous research by Kremer (1976) and Kremer and Reeve (1989), G_{a}, the adult clearance rate $[L\, mg^{-1}\ dry\ weight\ day^{-1}]$ is estimated by:

$$G_{\mathrm{a}} = a_0 \left[\left(\frac{w_{\mathrm{a}}}{c_{\mathrm{w2c}}} \right)^{-b} \right] e^{\mathrm{kT}} \tag{3.3}$$

where a_0 is an empirical constant $[L\, mg^{-1}\, d^{-1}]$, b is a power, k is a decay coefficient $[{}^{\circ}C^{-1}]$, c_{w2c} is a conversion factor of wet weight to carbon weight $[mg\, C\, mg^{-1}]$ and T is the temperature $[{}^{\circ}C]$.

In equation (3.1) the proportion of food turned into eggs (f) is calculated as:

$$f = 0.01\, T_{\mathrm{f}}\, e^{c_{\mathrm{f}}(w_{\mathrm{a}}/c_{\mathrm{w2c}})} \tag{3.4}$$

where c_{f} is an empirical constant and T_{f} is a temperature function given by:

$$T_{\mathrm{f}} = \max(T_{\mathrm{f,\ min}}, a_{\mathrm{T}}\, e^{b_{\mathrm{T}} T}) \tag{3.5}$$

where $T_{\mathrm{f,\ min}}$ is a minimum function introduced here to prevent negative values, and a_{T} and b_{T} are empirical constants. Of the three functions suggested by Salihoglu et al. (2011) this one is chosen over the linear function preferred by the authors, which has a cut-off at a rather high temperature of approximately 14°C. In the reference run example of Salihoglu et al. (2011), the order of magnitude of the number of eggs (several hundreds) produced using these equations corresponded with the observations for small individuals presented by Kremer (1976) and Reeve et al. (1989). Note that a direct comparison is impossible because the conditions of the observations, as far as reported, cannot be fully represented with the current model.

Subsequently, the number of eggs calculated in equation (3.1) is subject to egg and juvenile mortality. The number of surviving eggs (n_{es}) is calculated by applying constant fractional mortality per day (m_{e}) and assuming an egg phase duration of 1 day:

$$n_{\mathrm{es}} = (1 - m_{\mathrm{e}})\, n_{\mathrm{e}} \tag{3.6}$$

Juvenile mortality is calculated as a combination of daily background mortality (m_{j}) and food availability. The fractional egg and juvenile daily mortalities used here were calibrated by van der Molen et al. (2015) in an attempt to reproduce the results of the reference run example by Salihoglu et al. (2011). The surviving juveniles (n_{js}) after application of the background mortality is given by:

$$n_{\mathrm{js}} = (1 - m_{\mathrm{j}})^{D_{\mathrm{j}}}\, n_{\mathrm{es}} \tag{3.7}$$

where D_{j} is a temperature-driven duration of the juvenile stage in days given by:

$$D_{\mathrm{j}} = a_{\mathrm{d}} + b_{\mathrm{d}}\, T \tag{3.8}$$

with a_{d} and b_{d} empirical constants based on the graphs presented by Salihoglu et al. (2011).

Juvenile starvation is implemented by comparing the daily food intake (F_{j}) with the average daily weight gain (w_{g}) required to reach w_{aj} – the mass at the end of the transitional stage. This is given by:

$$w_{\mathrm{g}} = \frac{w_{\mathrm{aj}} - w_{\mathrm{j}}}{D_{\mathrm{j}}} \tag{3.9}$$

where w_{j} is the average mass of a juvenile. The daily juvenile food intake is calculated as:

$$F_{\mathrm{j}} = \frac{f_{\mathrm{j}}}{1000}\, c_{\mathrm{cd}}\, w_{\mathrm{j}}\, G_{\mathrm{j}}\, A_{\mathrm{j}}\, (1 - L_{\mathrm{j}}) \tag{3.10}$$

where f_j is the juvenile food concentration $[mg C\, m^{-3}]$ (taken here as microzooplankton from the GETM-ERSEM-BFM model, see Section 3.1.2), A_j is the juvenile assimilation rate and L_j is a metabolic loss fraction. Empirical evidence by Kremer (1976) and Sullivan and Gifford (2004) is combined to develop G_j, the juvenile ingestion rate $[L\, mg^{-1}\; day^{-1}]$ calculated as:

$$G_\mathrm{j} = c_1 \times c_2 \times \left(\frac{w_\mathrm{j}}{c_\mathrm{w2c}}\right)^{c_3} + c_4 \tag{3.11}$$

where c_1, c_2, c_3 and c_4 are empirical constants.

Then finally, by combining the results of equations (3.7), (3.9) and (3.10), the number of new adults recruited to the existing population (n_ar) in the time step under consideration (i.e. assuming infinitely short egg and juvenile duration in 'model time', but including mortality calculated over their 'real time' duration) is calculated as:

$$n_\mathrm{ar} = \min\left(1, \frac{F_\mathrm{j}}{w_\mathrm{g}}\right) n_\mathrm{js} \tag{3.12}$$

Adults are assumed not to survive temperatures less than 2°C and thus for temperatures this low there is no reproduction in the model. As the maturation in the model is artificially compacted into a single time step, strictly speaking there are no juveniles in the model and so a similar rule for juvenile mortality is not required. For temperatures above 2°C, a background mortality of 2% is imposed for completeness, following Salihoglu et al. (2011). There is evidence to suggest *M. leidyi* can survive at temperatures below this threshold (Costello et al., 2006) so this element of the model may be refined. However, as offshore water temperatures in the southwestern North Sea only very rarely fall to such low levels, the results presented here are not expected to change if such a refinement was implemented. There is also a daily starvation mortality rate of 13% for food concentrations less than 3 $mg\; C\; m^{-3}$ – the lowest concentration of zooplankton at which *M. leidyi* has been found in the field (Kremer, 1994) – based on the observation that *M. leidyi* can survive for up to 17 days without food (Oliveira et al., 2007). This daily starvation mortality rate results in approximately 10% of the population surviving after 17 days.

3.2.5 Model structure and visualisation

3.2.5.1 Initial requirements and model setup

The model setup centres around the experiment definition file. This file contains a series of information including the run identification, the prescribed start and stop times for the run, input and output file directories and some general settings for the particle tracking model. The model is forced by pre-simulated velocity fields provided by the hydrodynamic model and so the reliability of this process is guaranteed via the GETM validation. For the simulations done here, the forcing files also need to contain food fields for juvenile and adult *M. leidyi*. These were obtained from the biogeochemical model ERSEM-BFM coupled to GETM (see Section 3.1.2 for more detail). As well as the simulated flow field, the associated topography and grid information, the model also requires two other key input files in order to run – a species-definition file and a spawning file. The species-definition file contains all the settings that define biological particle development and movement (some of which are not used in this model due to the simplifications explained in Section 3.2.4). This file contains a matrix of general settings where each column defines the development and behaviour of a single egg or larval stage. The rows contain the list of general settings which allow the choice of mortality rate (constant daily vs. temperature dependent), growth rate, development type (no growth vs. continuous vs. temperature dependent), etc. The spawning definition file prescribes the number of particles to be included in the run and also where and when they are to be released on the model grid. Each particle is provided with a unique particle number, a release date and time, a release longitude, a release latitude and a vertical position of release with respect to the mean sea level. If particles are specified at a depth greater than the sea depth at a particular location they will be released just above the sea bed. The particles are also each provided with a super-individual weighting that is reduced/increased during the simulation to reflect mortality/reproduction.

3.2.5.2 General internal procedure

First initial particle positions are determined for a time step. This is accomplished either by using the spawning file or (after the first time step) through output from the previous time step. Flow calculations interpolate the local flow spatially at the particles location. The trajectory integration determines the position of the particle at the end of the time step using the advection-diffusion routine discussed previously. Each particle position is checked for violation of boundary conditions before finally the update particle positions are produced. These newly calculated positions are the input for the next iteration and the process is repeated. The particle position and the associated conditions from each time step are used by the biological module to update the particle weighting depending on the reproductive capability and mortality at that location.

3.2.5.3 Output and visualisation

The output of GITM is the trajectories (tracks), i.e. the positions of the particles – in this case passive *M. leidyi* individuals – over time. The model stores the results from each of the iterations in a NetCDF file. This file records a time series of each particle's position. The time series also documents the temperature, salinity and food concentrations experienced by each particle along its trajectory and includes the variable weight factor which reflects the mortality and reproductive capability of the super-individual at each time step.

Python scripts are used to post-process these NetCDF files in order to visualise and interpret the trajectories of the particles over time. This graphical output can be in the form of particle tracks over time, particle positions or particle densities at prescribed moments in time. There is also the possibility of plotting the time series of the temperature or salinity experienced by a particular particle.

Chapter 4

Modelling Overwintering Populations of *Mnemiopsis leidyi* in the North Sea

4.1 Data gathered from offshore North Sea monitoring

The North Sea and English Channel are sampled annually in the first quarter by the International Bottom Trawl Survey Research Programme (IBTS) (ICES, 2009). This European programme – coordinated by the International Council for the Exploration of the Sea (ICES) – is fundamentally dedicated to gathering data which helps to produce abundance indices for the main fish species of commercial interest in the North Sea region. The survey also includes station observations of hydrochemical measurements which has resulted in a very comprehensive dataset of the area being formed.

More recently the French Research Institute for Exploration of the Sea (Ifremer) have worked in collaboration with this survey to extend their winter sampling of plankton with a particular focus on gelatinous species. This scientific campaign is conducted on board the R/V Thalassa simultaneously with the IBTS programme and as such records are taken only at the designated IBTS sampling stations.

The data used in this study were collected by Ifremer in January and February 2009 using a Midwater Ring Net with a 2m ring diameter, 1.6mm mesh size and a flowmeter attached (ICES, 2013). The trawls were conducted using an oblique tow and all gelatinous species sampled were sorted, identified and measured live on board to avoid any potential issues which may arise due to preservation. Temperature and salinity profiles were recorded at each station using a SBE-19plus CTD recorder and Niskin bottles. Temperature ranged from 1.6°C to 6.8°C and salinity between 27.5 and 35.5 PSU at stations where *M. leidyi* was present.

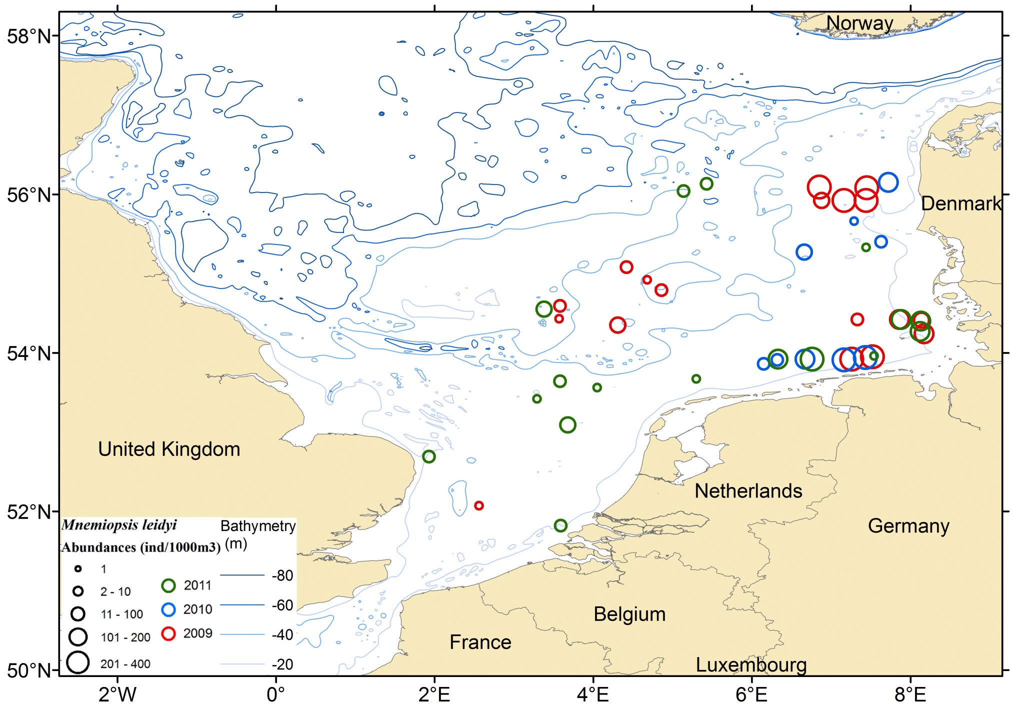

Figure 4.1: *Mnemiopsis leidyi* discoveries in the North Sea 2009-2011. The data was collected by Ifremer whilst on board the IBTS cruise in January and February of each year. [Obtained from David et al. (2014, in Revision)]

Since 2009, the IBTS surveys have recorded *M. leidyi* each winter in open waters. Between 2009-2011, recurrent patches of *M.leidyi* were recorded off the coasts of Denmark, Germany and the Netherlands. This study focuses on the 2009 discoveries – in particular the clusters of findings (1) off the Danish coast; (2) in the German Bight; and (3) in the Dogger Bank region (Figure 4.1). Three polygons are generated by the Lagrangian particle tracking individual behaviour model to schematically represent the three main areas where *M. leidyi* individuals were discovered during the 2009 IBTS cruise – i.e. the three clusters of red circles which can be observed in Figure 4.1. The first polygon represents the findings around 50 miles off the coast of Denmark (blue), the second represents the cluster of findings in the German Bight (green) and the third represents the findings in the Dogger Bank region (red).

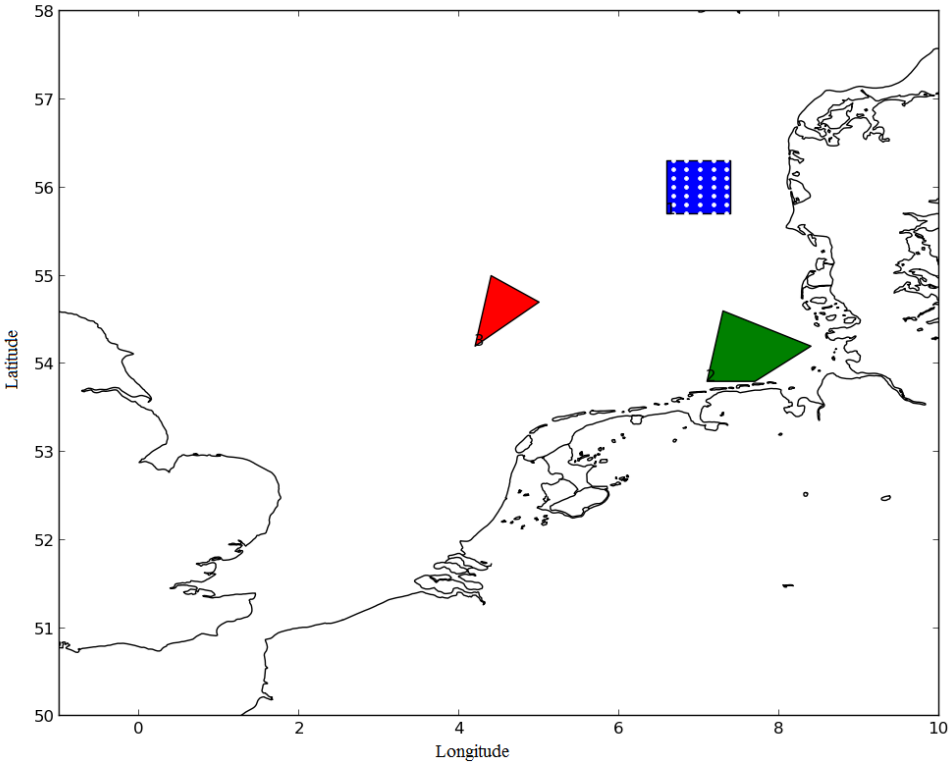

FIGURE 4.2: A schematic representation of the three main regions where *M. leidyi* was found to be overwintering in the North Sea in 2009 following the IBTS cruise in January and February of that year.

4.2 Locating possible source regions of observed offshore populations

4.2.1 Set-up of model run

For the first part of this research, the particle tracking model was run for 208 days from 21 July 2008 until 14 February 2009, with 6,000 particles released between 21 July 2008 and 10 August 2008. These particles were spread uniformly across the entire model grid (Figure 4.3) with each being released from the centre of a model grid cell. The particles were introduced daily at 01:00 – the approximate time *M. leidyi* is believed to spawn (Purcell et al., 2001) – at a depth of 0.5m below the sea surface. The three week period chosen to release the particles corresponds with peak North Sea water temperatures and the expected *M. leidyi* bloom times (e.g. Collingridge et al., 2014). The end of the run corresponds with the date of the IBTS cruise on which the data were collected. The particles being released uniformly over latitude and longitude allows for more flexibility in the interpretation of the results as no prior information on spawning grounds is included. The particles were assumed to be passive tracers and, upon release, each was assumed to represent 1,000 adult *M. leidyi* individuals.

4.2.2 Results

At the end of the particle tracking simulations on 14 February 2009 the trajectories of the particles present in each of the 3 previously defined polygons (Figure 4.2) were analysed in an attempt to shed some light on potential spawning regions for *M. leidyi* in the North Sea area. It is important to note that a *M. leidyi* individual could have originated (spawned) at any point along a particle trajectory depicted in the plots and not necessarily on the same date that the particle was spawned for this model simulation.

The trajectories of those particles located in the first polygon of interest (Figure 4.4) – around 50 miles east of the Danish coast and northwards of the North Frisian Islands – encompass much of the Southern Bight and Central North Sea and thus do not provide much meaningful insight regarding particular areas of interest within this region. The model suggests that the *M. leidyi* individuals found off the Danish coast in January

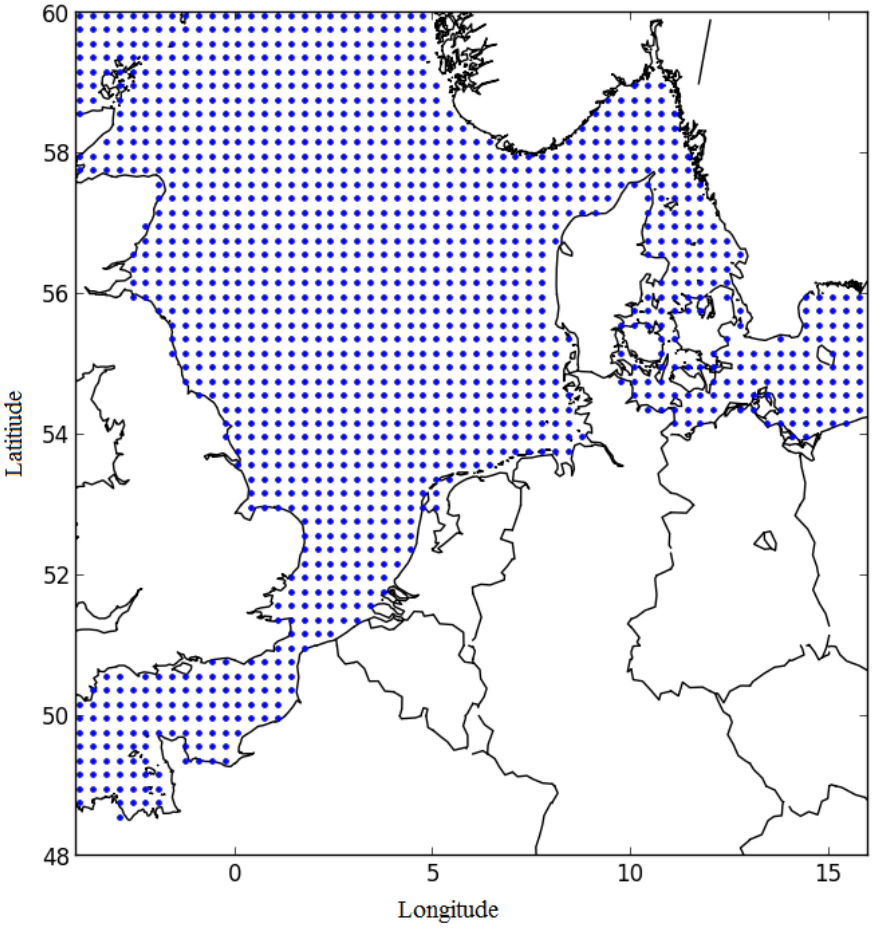

Figure 4.3: Spawning map showing how particles were released uniformly across the entire model grid.

and February 2009 could have originated from almost anywhere from the Straight of Dover northwards along the continental coast. There is also the possibility that these individuals originated from the Thames Estuary and on the East Anglian coast of England. The simulations do not highlight any possible source regions from Scottish waters or indeed any UK waters at all northwards of East Anglia in England. The same can be said for any regions north of the Danish coastal discoveries, most notably the Norwegian trench and Skagerrak.

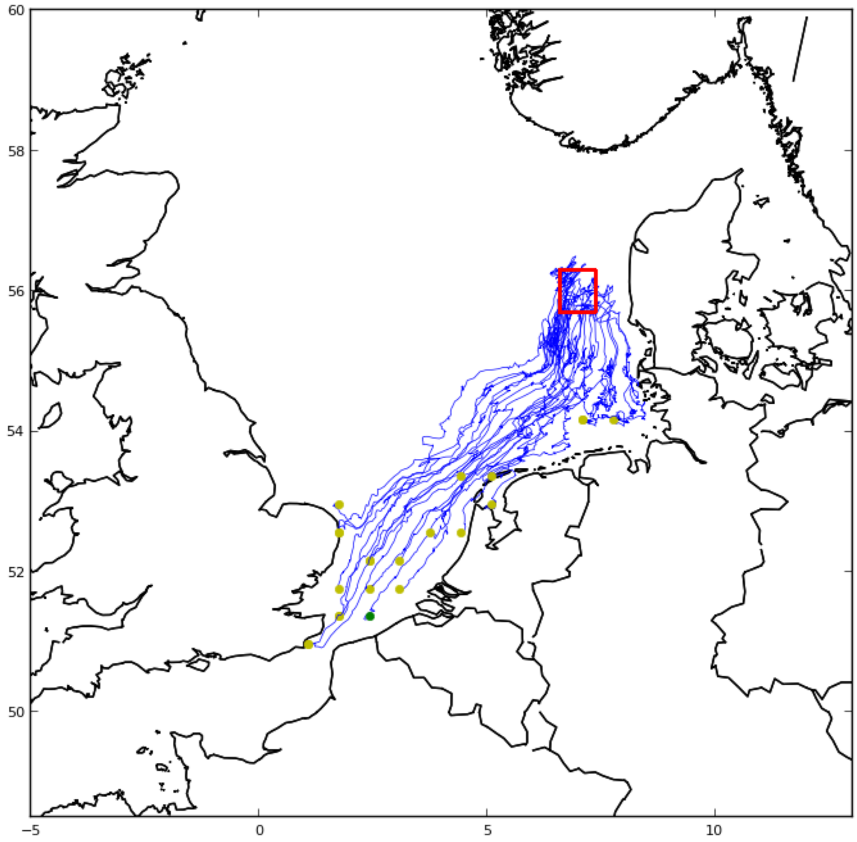

FIGURE 4.4: Particle trajectories of all particles found in the Danish coast region (Polygon 1) at the end of the model simulation (14 February 2009).

The trajectories of those particles found in the German Bight region (Figure 4.5) show that a proportion of the particles found here may have originated from the German Bight or the nearby East Frisian Islands region, despite being spawned over 6 months previously in the model run. This is indicative of a hydrographic retention area that could perhaps be capable of retaining a sustained year round population if conditions were favourable. The trajectories also suggest it is possible that these particles originated along the continental coast from as far south as the English Chanel and the coast of France near Calais and Dunkirk. Interestingly, the particle tracks from the German Bight region appear to follow the coastline more tightly than those in Figure 4.4 which cross through the Oyster Grounds in the central North Sea. As with Figure 4.4, the strong anti-clockwise gyre in the North Sea is conveyed by the particle trajectories as there is no indication of particles drifting southwards to the German Bight from the coast of Denmark, the Skagerrak or the Norwegian trench.

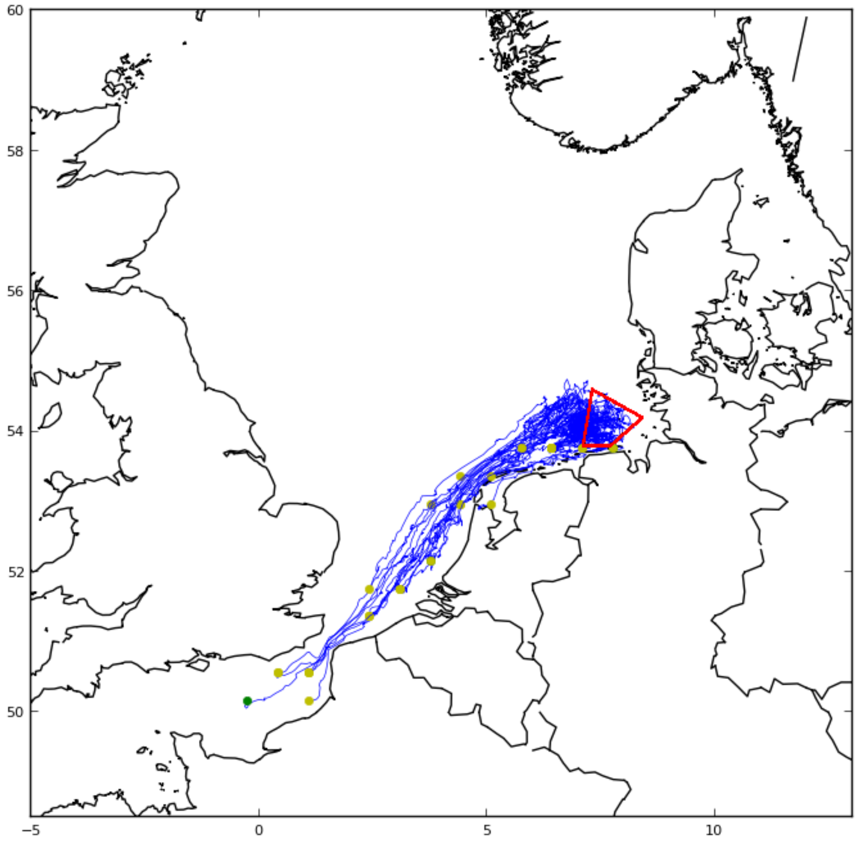

Figure 4.5: Particle trajectories of all particles found in the German Bight region (Polygon 2) at the end of the model simulation (14 February 2009).

The trajectories of those particles which finished up in the third polygon of interest (Dogger Bank region) tell quite a different story (Figure 4.6). The model suggests that it is unlikely that the individuals discovered in the Dogger Bank region in the winter of 2009 originated from anywhere along the continental coast of Europe. Indeed the particle tracks in question all originate from UK waters. As was the case with

Figure 4.4, some of the particles originate from the English Chanel, Thames Estuary and the East Anglian coast of England. In addition, there are also trajectories from particles spawned in The Wash, the Inner Silver Pit and even as far northwards as the coast of Middlesbrough and the River Tees. This result suggests there is very limited connectivity between the continental coast and UK waters and that the 2009 winter discoveries in the Dogger Bank region must have originated from somewhere along the eastern coast of England.

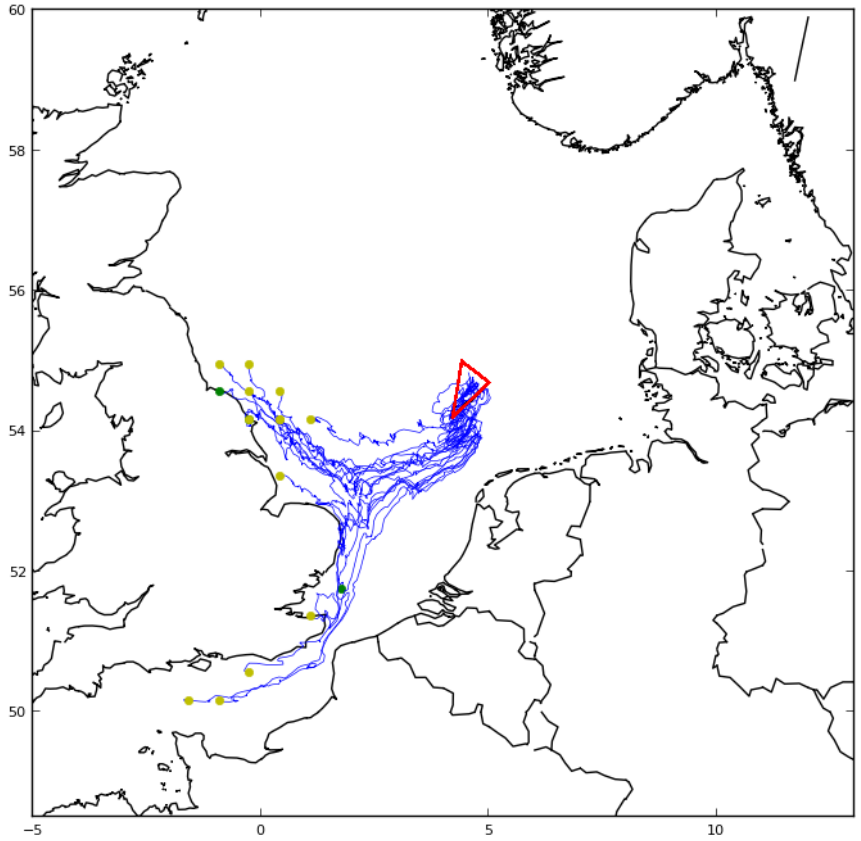

Figure 4.6: Particle trajectories of all particles found in the Dogger Bank region (Polygon 3) at the end of the model simulation (14 February 2009).

4.3 Modelling the potential fate of observed offshore populations

4.3.1 Set-up of model run

For the second part of this research, the particle tracking model was run for 393 days from 1 February 2009 until 28 February 2010. A total of 20,000 particles were released between 1 February 2009 and 17 February 2009, corresponding to the dates the data were gathered on the IBTS cruise. As before, the particles were assumed to be passive tracers and, upon release, each was assumed to represent 1,000 *M. leidyi* individuals. The particles were released daily at 01:00 from the grid points within three prescribed 'polygons' (depicted in Figure 4.2). The 20,000 particles in the model run were divided into the three polygons proportionally depending on the the number of grid points within each polygon. Approximately 6,000 particles were introduced via the first polygon (Danish coastal region), 7,500 from the second polygon (German Bight region) and 5,500 introduced via the third polygon (Dogger Bank region). The average depth of the discoveries included in the polygons ranged from 22.5m in the German Bight to 45m in the Dogger Bank region however in each case the findings were close to the seabed. Because the model corrects for particles spawned below the seabed – instead spawning them at a depth just above the seabed at that particular location – the decision was taken to spawn all particles at 45m to produce the most realistic initial conditions possible for the run.

4.3.2 Results

Whilst the first portion of model simulations shed light on the potential origins of the winter discoveries of 2009, it is also useful to understand their movements going forward and assess their potential to contribute blooms the following summer. To do this, particles were released from each of the 3 previously defined polygons (Figure 4.2) on 1 February 2009 – the approximate date the discoveries were made – and simulations were carried out until the 28 February 2010, 13 months later. Initially this section looks solely at particle numbers (i.e. excluding the effects of reproduction/mortality) and then later interprets the affect the biological extension has on these results by modelling the weighted density of *M. leidyi* individuals.

The particles released from the first polygon (Danish coast) in February 2009 drifted northwards, with the majority of particles found in the Norwegian Trench as early as May 2009 (Figure 4.7b). There is however a high density of particles found in the Jutland Bank region, and near the Thybøron Kanal and Limfjorden in northern Denmark. By the middle of August (Figure 4.7c) the particles had been further dispersed throughout the Norwegian Trench with particles drifting northwesterly around the coast of Sweden. Particles had also drifted east as far as the the coast of Aalborg in the northernmost Kattegat. Interestingly, by the middle of August the previous high density of particles near Limfjorden had completely separated from the Danish coast. The varying particle density in the Norwegian Trench over the course of the simulations is perhaps a model artifact related to the coarse model resolution in this area combined with the proximity of the open boundary. In reality particles should stay fairly close to the coast and be transported along the coast to the north. That being said, some particles do leak northwesterly towards the Fladen Ground and the Orkney and Shetland islands. As the model simulation continues, particles are also found drifting southwards deep into the Kattegat and can be found in low densities as far south as Odense (Figure 4.7e) – at a similar latitude as the particles were originally released 13 months previously – on the other side of the Jutland Peninsula .

The particles released from German Bight region in February 2009 (Figure 4.8) drifted northwards as a plume tight to the German and Danish coasts. By May 2009 the vast majority of particles were found to be in and around the North Frisian Islands just off the coast of northern Germany and the southeastern Danish coast (Figure 4.8b). No particles had yet reached the Norwegian Trench and only low densities were recorded near the Thybøron Kanal. By August 2009 there was still a significant number of particles retained in the Helgoland region at the mouth of the River Elbe. Many particles had also spread up the entire east coast of Denmark and into the Skagerrak. Over 6 months since the model simulation began, only a very low number of particles had made their way to the Norwegian Trench (Figure 4.8c). By November 2009 this was no longer the case. Despite a band of particles remaining along the entire German and Danish coasts, a substantial proportion of particles had now made their way to the Norwegian Trench and Skagerrak regions (Figure 4.8d). By February 2010, some particles had continued in low densities southwards from the Skagerrak and deep into the Kattegat. There was also a very limited spread of particles southwards down the continental coast towards the West Frisian Islands and into Dutch waters. The vast majority of particles however were either in the Norwegian Trench/Skagerrak region or had drifted northwards off the model grid (Figure 4.8e).

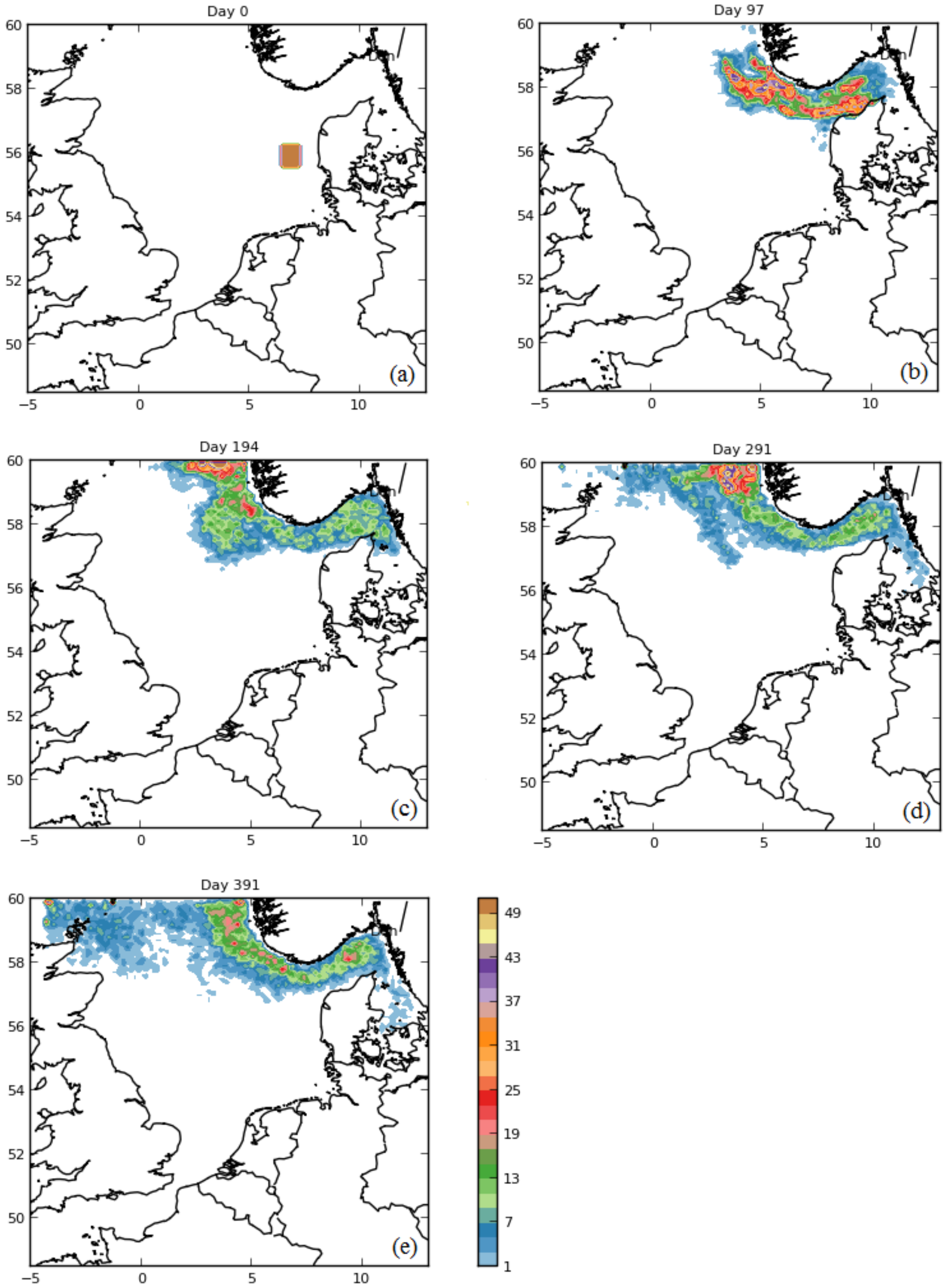

FIGURE 4.7: Density of the simulated particles on the model grid [number of particles per grid cell] on (a) day 1 of the simulation (1 February 2009); (b) day 97 of the simulation (9 May 2009); (c) day 194 of the simulation (14 August 2009); (d) day 291 of the simulation (19 November 2009); (e) day 391 of the simulation (28 February 2010).

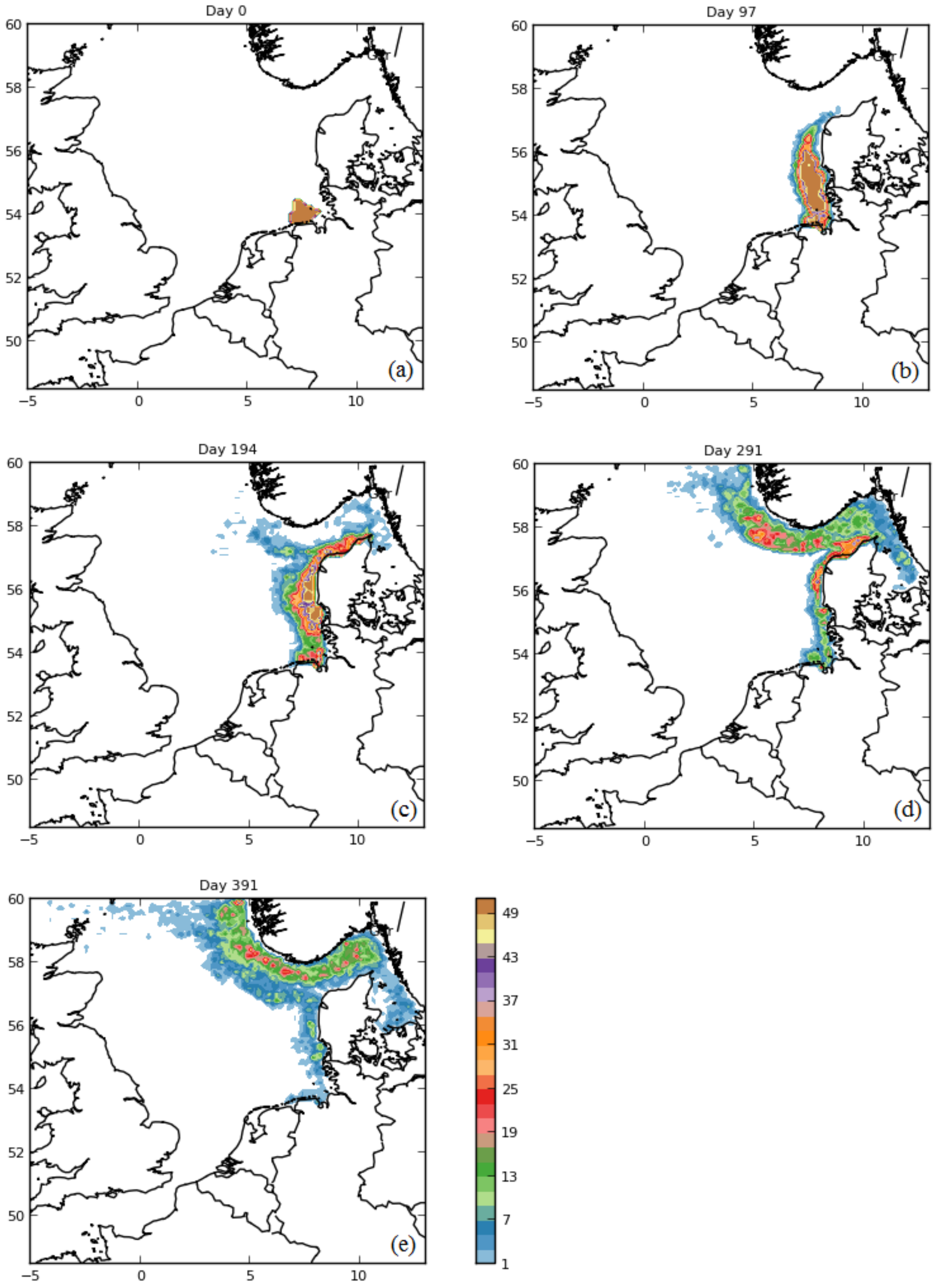

FIGURE 4.8: Density of the simulated particles on the model grid [number of particles per grid cell] on (a) day 1 of the simulation (1 February 2009); (b) day 97 of the simulation (9 May 2009); (c) day 194 of the simulation (14 August 2009); (d) day 291 of the simulation (19 November 2009); (e) day 391 of the simulation (28 February 2010).

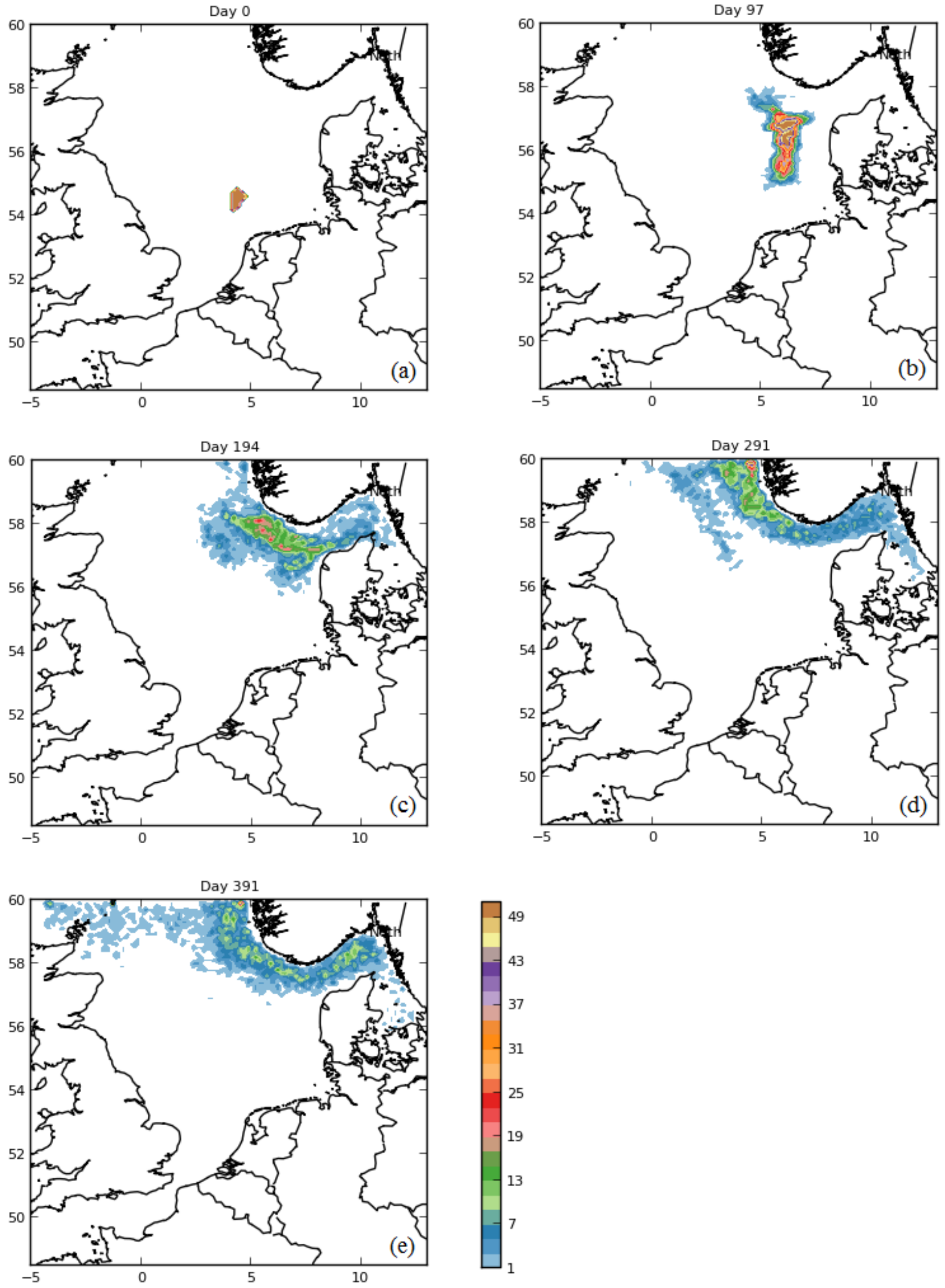

FIGURE 4.9: Density of the simulated particles on the model grid [number of particles per grid cell] on (a) day 1 of the simulation (1 February 2009); (b) day 97 of the simulation (9 May 2009); (c) day 194 of the simulation (14 August 2009); (d) day 291 of the simulation (19 November 2009); (e) day 391 of the simulation (28 February 2010).

The particles released in the Dogger Bank region in February 2009 (Figure 4.9) showed no sign of reaching the coasts of the Netherlands, Belgium or Germany. By May 2009 the particles had all drifted northeasterly but remained in the North Sea proper to the west of the Jutland Bank. By August 2009 these particles had drifted mainly to the Norwegian Trench although some particles were recorded in the Skagerrak and at the very north of the Jutland Peninsula (Figure 4.9c). By November 2009 these particles were now almost entirely in the Norwegian Trench, the Skagerrak or the Fladen Grounds between Scotland and Sweden. By February 2010 the low densities remaining solely in the Northern North Sea suggested that many of the particles had drifted northwards off the model grid and thus out of the North Sea entirely (Figure 4.9e).

Figure 4.10 introduces the use of the biological extension to the particle tracking model used thus far. As was explained in detail in Section 3.2.4, this extension explores the introduction of a simplified reproduction mechanism to the previous particle tracking results. Notice that in the consequent density plots the scale is now in weighted *M. leidyi* numbers and not simply particle numbers. The total number of *M. leidyi* individuals increased rapidly throughout February as particles were released into the model run and then declined sharply in March as the introduction of new particles ceased and starvation set in (Figure 4.10a). Food abundance began at low winter values for both juveniles and adults until April when food levels for both juveniles and adults increased and remained high before falling again at the beginning of October (Figures 4.10b and 4.10c). The average temperature experienced by particles in the North Sea rose steadily from March 2009 and peaked at 15°C in August before declining back to winter values between 4-6°C (Figure 4.10h). Average salinity increased slightly over the course of the model run but ranged less than 2 PSU throughout the entire 13 months of model simulation (Figure 4.10i). The reason for the distribution of population numbers provided by the model is two-fold. First, the food levels at the beginning of the run (i.e. in the winter months of February and March) are too low to sustain the number of *M. leidyi* individuals represented in the model so numbers fall dramatically to a much reduced level. Second, despite producing over 175 eggs per hour for a continuous three month period (July-September, Figure 4.10d), the reduced population failed to add many new adults to the population (Figure 4.10g) which is primarily due to juvenile mortality (Figure 4.10f). Previous sensitivity analysis (van der Molen et al., 2015) found that, given the way juvenile mortality is implemented in this model, lower temperatures – like those experienced in much of the North Sea proper even in the height of summer – lead to a prolonging of the juvenile stage duration which ultimately results in strongly reduced overall survival when daily mortality is taken into account.

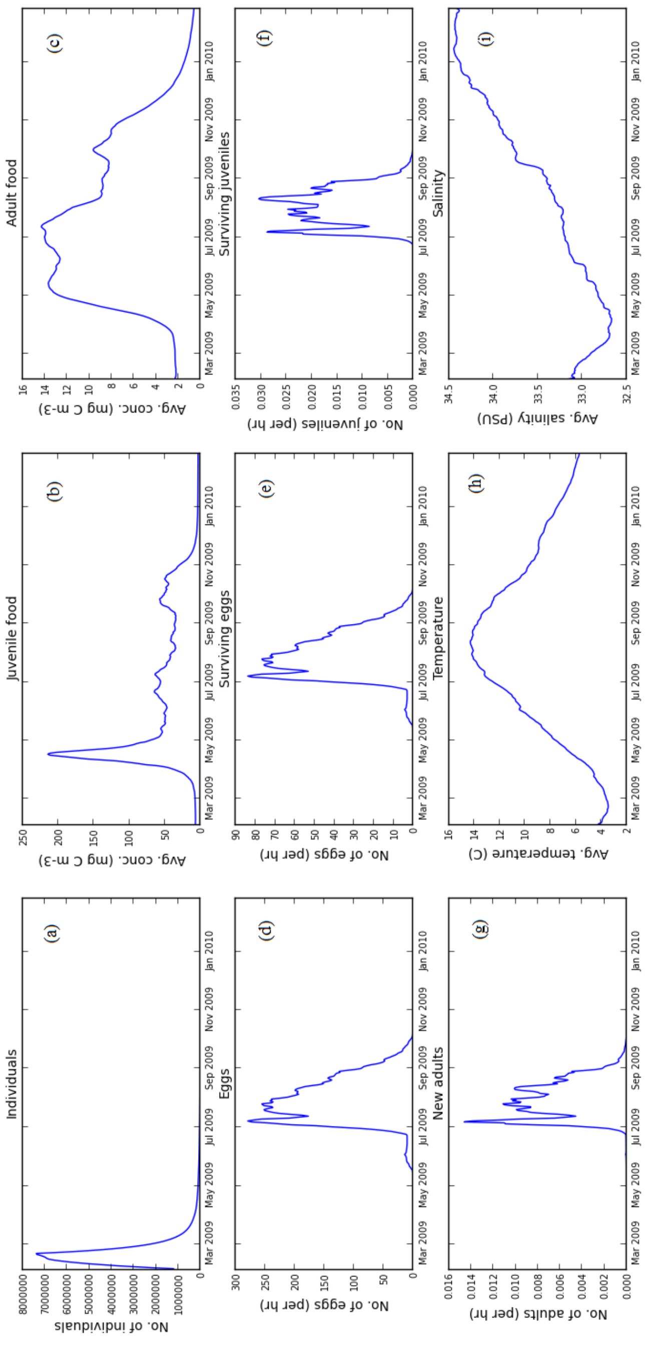

FIGURE 4.10: Cumulative results over all particles as a function of time for the model simulation: (a) simulated number of *M. leidyi* individuals; (b) average juvenile food concentration available to particles [$mg\,C\,m^{-3}$]; (c) average adult food concentration available to particles [$mg\,C\,m^{-3}$]; (d) total number of eggs released per hour; (e) total number of surviving eggs per hour; (f) total number of surviving juveniles per hour; (g) total number of adults added to the population through reproduction per hour; (h) average temperature experienced by the particles; (i) average salinity experienced by the particles.

In order to assess how the inclusion of the biological extension to the particle tracking model affects the results the surviving weighted density of *M. leidyi* individuals released into the model was plotted. Each of the 20,000 particles released in the model simulation was given an initial weighting of 1,000 *M. leidyi* individuals and therefore there was a total of 20,000,000 *M. leidyi* individuals represented when the model simulation was initiated. With numbers such as these it may be anticipated that the scale on the associated density plots would be significantly higher than what was required for particle density, however the substantial reduction in surviving adults by March (as a result of starvation) meant that a scale half of that used for the particle density (25 vs 50) was required to convey any meaningful results at all on the plots.

Looking at Figure 4.7 the model suggests that the simulated *M. leidyi* individuals released from the first polygon (Danish coast) in February 2009 drifted northwards towards the Norwegian Trench and the top of the Jutland Peninsula on the coast of northern Denmark. It can be seen from the model simulations which take into account the biological extension that by May 2009 (Figure 4.11b) the surviving *M. leidyi* individuals have greatly reduced in numbers. There is a patchy distribution of surviving *M. leidyi* individuals in the Norwegian Trench, around the Jutland Bank region and near the Thybøron Kanal. The highest density of *M. leidyi* individuals is found off the coast of Lokken and Hirtshals at the northernmost point of Denmark. By August 2009, virtually no simulated *M. leidyi* individuals had survived with only a few individuals found in the Norwegian Trench and Skagerrak regions (Figure 4.11c). This suggests that although some individuals released off the Danish coast (Polygon 1) may survive the winter, they will not survive long enough until temperatures rise and conditions become favourable for reproduction.

From Figure 4.8 it has been shown the simulated *M. leidyi* individuals released from the second polygon (German Bight) in February 2009 drifted northwards as a plume tight to the German and Danish coasts. By August 2009, with the biology taken into account, there remained a high weighted density of *M. leidyi* in and around the North Frisian Islands just off the coast of northern Germany and the southeastern Danish coast (Figure 4.12c). A high density of *M. leidyi* individuals were also present in the Helgoland region at the mouth of the River Elbe – not far from where the simulated *M. leidyi* individuals were spawned 6 months previously. Some *M. leidyi* individuals had also made their way to the Thybøron Kanal and as far north as the top of the

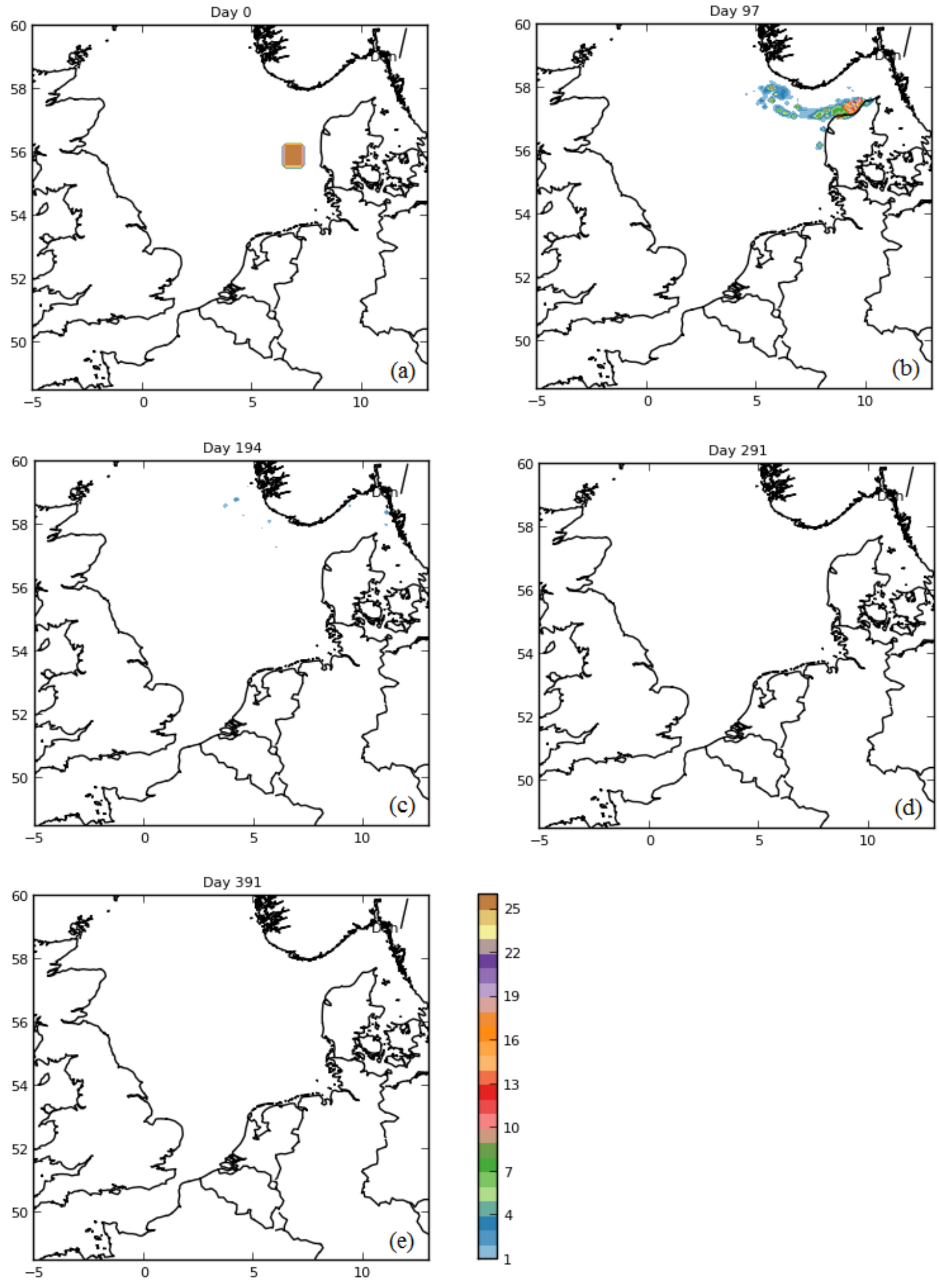

FIGURE 4.11: Density of the simulated *M. leidyi* individuals on the model grid [number of individuals per grid cell] on (a) day 1 of the simulation (1 February 2009); (b) day 97 of the simulation (9 May 2009); (c) day 194 of the simulation (14 August 2009); (d) day 291 of the simulation (19 November 2009); (e) day 391 of the simulation (28 February 2010).

Jutland Peninsula. This result suggests that those overwintering *M. leidyi* individuals discovered in the German Bight region can survive long enough to be the source for reproductive blooms further northwards along the continental coasts of Germany and Denmark. By November 2009 the density of surviving *M. leidyi* individuals had greatly reduced (Figure 4.12d) and by February 2010 no *M. leidyi* individuals remained. This suggests that whilst the individuals discovered in the German Bight region in February 2009 had the ability to survive the winter of 2009 and contribute to reproductive blooms further up the continental coast when conditions become favourable, it is unlikely that the discoveries from February 2010 off the Danish coast or in the German Bight (see Figure 4.1, blue circles) were from the same sustained population as those individuals recorded in these regions the previous year.

From Figure 4.9 it can be seen the simulated *M. leidyi* individuals released from the Dogger Bank region in February 2009 drifted northeasterly but but remained in the North Sea proper to the west of the Jutland Bank By May 2009. By August 2009, with biological mortality taken into account, a significant weighted density of *M. leidyi* had survived and reached the Norwegian Trench and the Jutland Bank region(Figure 4.13c). This result suggests that the *M. leidyi* individuals discovered in the Dogger Bank region cans survive long enough to be the potential source of a possible bloom recorded in the Jutland Bank region the following summer although it is important to note the model does not convey much reproductive power from the surviving population as a whole. By November 2009 a patchy distribution of surviving *M. leidyi* individuals was all that remained (Figure 4.13d) and by February 2010 all individuals had died off or drifted northwards off the model grid and thus out of the North Sea entirely (Figure 4.13e). It is therefore unlikely that any of the findings from February 2010 (see Figure 4.1, blue circles) were from the same sustained population as those found in the Dogger Bank region the previous year.

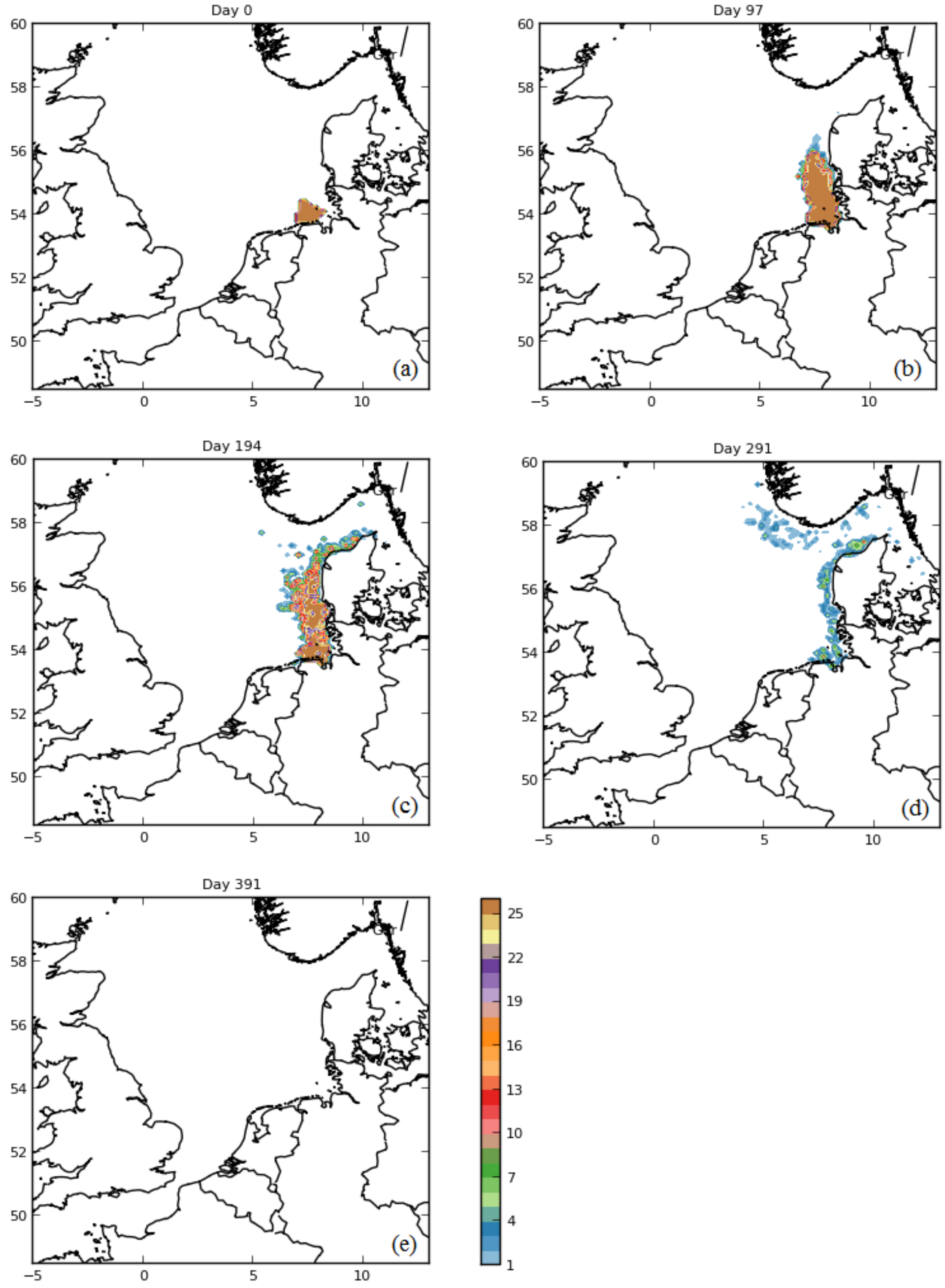

FIGURE 4.12: Density of the simulated *M. leidyi* individuals on the model grid [number of individuals per grid cell] on (a) day 1 of the simulation (1 February 2009); (b) day 97 of the simulation (9 May 2009); (c) day 194 of the simulation (14 August 2009); (d) day 291 of the simulation (19 November 2009); (e) day 391 of the simulation (28 February 2010).

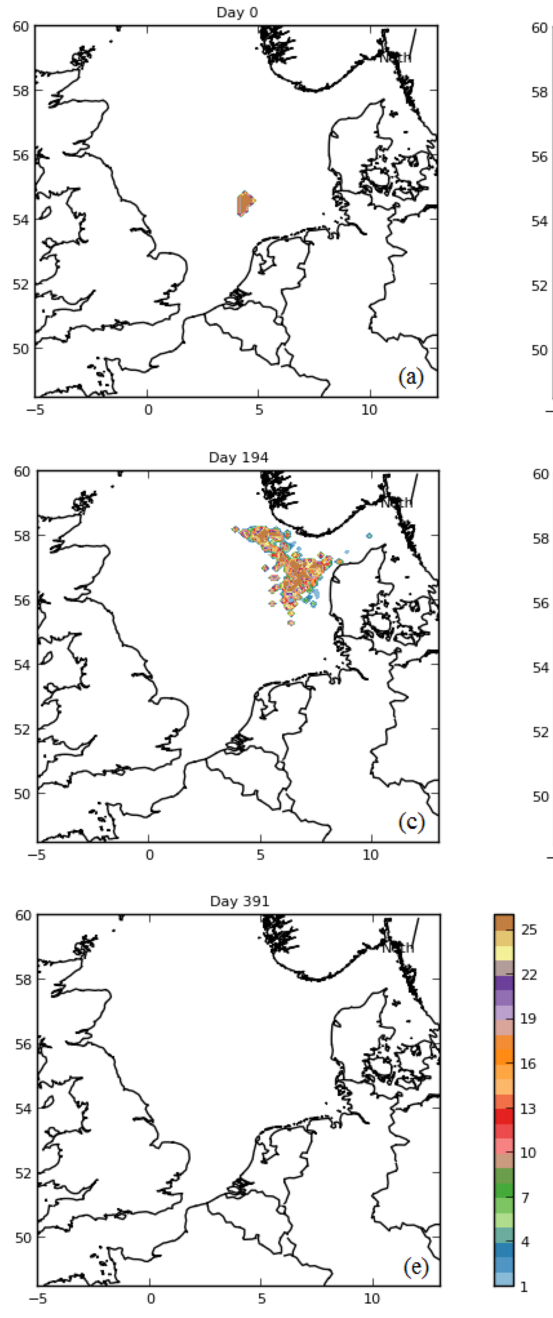

FIGURE 4.13: Density of the simulated *M. leidyi* individuals on the model grid [number of individuals per grid cell] on (a) day 1 of the simulation (1 February 2009); (b) day 97 of the simulation (9 May 2009); (c) day 194 of the simulation (14 August 2009); (d) day 291 of the simulation (19 November 2009); (e) day 391 of the simulation (28 February 2010).

Chapter 5

Discussion

5.1 Locating possible source regions of observed offshore populations

Ever since *M. leidyi* was first recorded in North Sea waters in 2005 (Faasse and Bayha, 2006), large blooms have been frequently observed in estuaries along the coastal regions of the eastern and southern North Sea. Most of these observations have occurred in coastal areas during the months of summer and autumn when water temperatures average between 10-23°C and reproduction potential is maximised, leading to some researchers claiming that winter conditions in the North Sea proper may not favour *M. leidyi* survival (Boersma et al., 2007) even in the shallow waters of the southern North Sea (Riisgård et al., 2011). In truth *M. leidyi* has often been described as a coastal and estuarine species, both in native and invasive waters and thus it was a huge surprise when in January 2009, the IBTS cruise unexpectedly found surviving *M. leidyi* individuals in open water. This winter presence of *M. leidyi* in the North Sea proper raised questions regarding the spatial and temporal limits of the species and also its ability to overwinter in the North Sea.

The model results in Section 4.2 suggest that individuals follow a general south to north transport along the continental coast. The *M. leidyi* individuals recorded in January off the coast of Denmark (Polygon 1) and in the German Bight (Polygon 2) may have originated anywhere southwards along the continental coastline from as far south as the Straight of Dover. This pathway encompasses many regions where *M. leidyi* has been found – France, Antajan et al. (2014); the Netherlands, Faasse and Bayha (2006); Belgium, Van Ginderdeuren et al. (2012); Germany, Boersma et al. (2007) – and it is possible that all of these regions may have contributed to the populations of overwintering *M. leidyi* individuals discovered in 2009. Most interestingly, the individuals found in the Dogger Bank region (Polygon 3) appear to have originated from UK waters. The particles were released uniformly over latitude and longitude to ensure there was no bias to specific regions in the model simulations when locating possible spawning grounds for the *M. leidyi* individuals. That being said, the model suggests it is very unlikely that the individuals discovered in the Dogger Bank region in the winter of 2009 originated from anywhere along the continental coast of Europe – in fact all of the associated particle trajectories for this region originated from UK waters. Of course it is important to note the model simulations do not take into account the potential effect vertical migration may have on the distribution of *M. leidyi* in North Sea waters.

To date there have been no *M. leidyi* discoveries on the English coast. However this may be down to a lack of continued sampling in the region. There is a monitoring programme carried out by EDF Energy near Sizewell (Suffolk, England) where monthly plankton samples are analysed but as yet no *M. leidyi* has been identified and other than this only a few sporadic plankton surveys off the East Anglian coast have actively searched for the ctenophore (S. Pitois, pers.com.). The model suggests the individuals found in the Dogger Bank region may have originated from as far south as English Chanel and as far north as the River Tees. Included in this range are two key areas of interest, the East Anglian coast and the Thames Estuary. In a recent study by Collingridge et al. (2014), the entire North Sea was modelled to discover which areas of the North Sea may have conditions suitable for overwintering *M. leidyi* populations. Despite *M. leidyi* being close to the limits of its occurrence in the North Sea (considering the winter water temperatures) the research indicated that together with the Norwegian Trench and the Skagerrak, the East Anglian coast was one of the most suitable regions for year-round survival. Furthermore, the Thames Estuary was found to be suitable for *M. leidyi* reproduction for a large portion of the year (Collingridge et al., 2014). The results indicate that both of these regions are potential areas of invasion for *M. leidyi* and if the model is to believed and the individuals discovered in the Dogger Bank region could not have originated from continental populations, it may well be the case that this species is already present in UK waters and has simply not been discovered yet either due to inadequate sampling or poor conservation techniques. Given that *M. leidyi* has been known to cause major ecological regime shifts from a pelagic system dominated by planktivorous fish to one dominated by gelatinous plankton (Reusch et al., 2010) – not least the total collapse of pelagic fisheries in the Black Sea in the late 1980s – the potential to impact plankton and fisheries in these regions is considerable and a close monitoring of UK waters – in particular the Thames Estuary and East Anglian Coast – is strongly advisable.

5.2 Modelling the potential fate of observed offshore populations

The unexpected discovery of *M. leidyi* individuals in the North Sea proper in January and February of 2009 led to researchers seeking answers to many new questions. Could these individuals survive an entire winter and reproduce when conditions became favourable for egg production? If so, where would these individuals be transported to by the summer and autumn months when reproduction is most favourable? Could these individuals perhaps even form a sustainable offshore population in the North Sea? The model results in Section 4.3 are an attempt to understand the mechanisms involved and are presented here to help answer these questions. According to the individual behaviour particle tracking model (GITM) it is abundantly clear that the average food levels in winter months are much too low to sustain a large population of *M. leidyi* individuals in the North Sea proper. The vastly reduced populations that were modelled, however, do show signs of successful survival and even limited reproductive capabilities. Importantly, this research couples a version of the Salihoglu et al. (2011) model with a particle tracking model which can account for any losses to advective flows – a key aspect of mortality that is overlooked by the zero-dimensional Salihoglu et al. (2011) model.

By August 2009 – when temperatures are highest and the potential to reproduce is believed to be maximised (Kremer, 1994; Purcell et al., 2001) – virtually none of the individuals released off the coast of Denmark the previous February had survived. In contrast, many of the individuals released in the German Bight region in February 2009 did survive until August with some drifting northwards as plume near to the German and Danish coasts and the rest remaining in the German Bight/Helgoland region. Some simulated *M. leidyi* individuals traveled as far North as the Thybøron Kanal in Denmark which leads to Limfjorden – an important refuge hosting year-round populations of *M. leidyi* that act as a source for the Baltic Sea (Riisgård et al., 2011). It is possible that these individuals propagate into Limfjorden and add to the sustained population that already exists in this area.

Despite a significant number of individuals surviving until conditions became favourable for reproduction, by November 2009 the number of simulated *M. leidyi* individuals in the model had actually fallen significantly, suggesting that the mortality rate for *M. leidyi* outweighed the reproductive rate of the ctenophore. The model predicts that even at peak North Sea temperatures the juvenile stage duration remains very long and because the daily juvenile mortality rate removes a certain amount of individuals per day, the extended application of this rate ultimately results in almost all young *M. leidyi* individuals dying before they are able to develop and be added to the simulated adult population. *M. leidyi* is a holoplanktonic species and the survival rate of larvae and juveniles directly influences the population dynamics of adult *M. leidyi* blooms (Costello et al., 2006). These results agree with previous research which also found temperature to be of overriding importance in determining conditions suitable for populations to bloom and expand (Huwer et al., 2008). By instantaneously adding surviving juveniles to the adult population, any surviving offspring become reproductive on the day they are spawned in the model. This makes the model oversensitive to producing blooms which could have potentially significant implications for the population dynamics. Despite this, the fact that the model does not show any such blooms in the North Sea adds confidence to the conclusion that a self-sustaining offshore population is unlikely to occur.

The model simulations show that there is potential for passive particles to remain in the Helgoland region for up to a year but the biological extension indicates that survival for a *M. leidyi* individual for this length of time may prove more difficult. Marine species can only exist in geographic locations within which there can be continuity in the life cycle (Tiessen et al., 2014); i.e. in a geographical setting within which retention of the population (including reproduction) balances losses (either to advective flows or mortality) in some integrated sense for the life cycle as a whole. Therefore, despite the retentive characteristics of the German Bight/Helgoland region, the model suggests it remains unlikely a sustained population life cycle can form in the North Sea proper due to a lack of new *M. leidyi* individuals being added to the population via reproduction to replace those lost to advective flows or mortality.

A sensitivity analysis by van der Molen et al. (2015) increased the temperature of the North Sea artificially by a factor of 1.3 so that a temperature of 20°C became 26°C. This change made the temperature more similar to Black Sea conditions and consequently many more eggs were produced. Additionally there was a much increased juvenile survival due to the shortening of the juvenile stage duration (which is driven by temperature) and so blooms were replicated by the model similar to what is expected in the Black Sea. This gives confidence to the hypothesis that the North Sea provides *M. leidyi* with only limited reproductive capability.

Despite this apparent inability to sustain a year long population, the IBTS surveys in subsequent years recorded *M. leidyi* individuals in similar areas of the North Sea. Costello et al. (2006) describes how in Narragansett Bay *M. leidyi* is found year round but only at inshore locations that have long hydrographic retention periods. These low advection areas (source regions) serve as a refuge for overwintering populations until temperature and prey conditions become favourable for reproduction (Beaulieu et al., 2013) at which point local circulation currents provide the delivery method and *M. leidyi* is able to re-establish itself throughout the entire bay.

It is believed that source-sink dynamics are just as vital to the persistence of *M. leidyi* in its invaded habitats (Purcell et al., 2001; Costello et al., 2006). According to van der Molen et al. (2015) an estuary or harbour in the North Sea containing an established *M. leidyi* population can, within one year, act as a source area for other estuaries and harbours along the coast to the north up to hundreds of kilometres away. This added to the fact there are very limited reproductive capabilities in the North Sea proper suggests that the overwintering *M. leidyi* being discovered year on year by the IBTS cruise may be the result of individuals from harbours and estuaries along the European coast being annually flushed out into open waters by advective flows.

5.3 Research limitations and recommendations for further work

It should first be noted that subsequent research has found that the temperature threshold of 12°C applied in this research as a baseline for reproduction was artificially established by Lehtiniemi et al. (2012) and should not be used in future modelling. That being said, this oversight should not have any meaningful influence on the model results presented here, as a previous sensitivity analysis by van der Molen et al. (2015) found that egg production in this model falls to very low levels (in response to reductions in food-availability and temperature-driven reductions in feeding and egg-production efficiency) before the average temperature experienced by the super-individual drops to 12°C. Given that the increase in population numbers due to reproduction is negligible even in the height of summer, it would not make any meaningful difference to the findings if egg production commenced earlier in the year.

There is a balance in this model between temperature and juvenile mortality that determines whether or not adults are added to the overall population. The problem with this is that, particularly at low temperatures, very little is known about *M. leidyi* mortality and so the results are subject to considerable uncertainty. Also there is a fixed summer metabolism assumed in the model which may overstate the mortality experienced in winter months when food concentrations are low. It seems contrary to Darwinian evolution theory that *M. leidyi* would continue to produce eggs when temperatures are too low for juvenile survival. It is believed as a result of the research of Jaspers (2012) that energy is primarily allocated by *M. leidyi* to growth until development occurs and the lobate form is reached. At this point *M. leidyi* switches its energy allocation to egg production. One hypothesis may be that the ctenophore is able to switch its energy allocation back towards growth when conditions are unsuitable for reproduction. Recent dynamic energy budget (DEB) research has found that *M. leidyi* appears to undergo a so called metabolic acceleration after hatching which can be delayed under certain circumstances (Augustine et al., 2014). There is no evidence to suggest why this delay occurs but it could be that the ctenophore is able to delay it until food and temperature conditions are more favourable. In order to substantiate any of these hypotheses more effort should be dedicated to understanding energy allocation which will in turn enable researchers to better formulate and parameterise the model going forward. It is possible the current model simulations are understating the potential for survival and connectivity in the North Sea due to the lack of understanding surrounding metabolic energy allocation.

Given that juvenile ctenophores can seasonally dominate overall abundances during peak bloom times (Shiganova et al., 2001) it may also be useful in the future to incorporate stage structure into the model where juveniles and adults can co-exist. Due to the current model structure all individuals in the model are assumed to be adults of average size. Augustine et al. (2014) provides evidence that larger individuals are more sensitive to a drop in food availability. The results appear to show that small larvae can last a very long time at low food levels which may undermine the survival threshold of 3mg Cm^{-3}. To date no other experiments have investigated the survival of *M. leidyi* at very low food concentrations but a slowed metabolism at lower winter temperatures would mean food requirements are likely to be lower (Purcell et al., 2001) and smaller *M. leidyi* individuals may be able to overwinter until conditions became favourable for growth and reproduction. Again this may mean the current results are understating the true potential for *M. leidyi* to overwinter in the North Sea.

Because of the euryhalinic nature of *M. leidyi* – observed by its phenotypic plasticity in a wide range of conditions – more effort should be made to understand and report on the influence of salinity on this ctenophore and its population dynamics. Purcell et al. (2001) highlight a potential positive relationship between increasing salinity and ctenophore survival. This hypothesis stems from the fact that *M. leidyi* has been found in high saline native waters at temperature around 0°C but cannot survive in the less saline Sea of Azov below 4°C. This conclusion relates only to the low end of the temperature range, however, and in future the whole two-dimensional temperature-salinity parameter space should be investigated.

Given the diffusive (random walk) aspect of the particle tracking model and the relatively small number of particles used in the model runs presented in this thesis, the results may be influenced by stochastic variability. Consequently, in the future it would be a good idea to substantiate these conclusions by using either a much larger number of particles released across the entire grid or similar numbers concentrated in the suspected source areas as indicated by the initial model runs.

Overall there is a need for continued research on this species – particularly its early life stages – as there is still much that is not yet fully understood. Going forward research must be dedicated to investigating the hypothesis that *M. leidyi* has a reduced metabolism at lower temperatures. It would also be hugely beneficial to gain more of an understanding on mortality rates and if they are proportional to the size of the ctenophore. By increasing the knowledge on the growth physiology of *M. leidyi* and the factors influencing the rate of transfer between life stages, model parameterisation will be improved and more confidence can be placed on the results presented from this model.

Chapter 6

Conclusions

Recent observations have shown than *M. leidyi* can survive in the North Sea proper for extended periods of time – even during winter when temperatures are as low as 2°C. These winter offshore discoveries of *M. leidyi* have raised many new questions throughout the scientific community. The results presented in this thesis provide a new insight into *M. leidyi* population dynamics in the North Sea and highlight the necessity for further dedicated research in this area of study. The results suggest a population of *M. leidyi* may exist in UK waters which has thus far gone undetected. Indeed the model highlights the Thames Estuary and the East Anglian coast as two key areas of interest where close monitoring for *M. leidyi* is strongly advised. Taking into account the notorious history of *M. leidyi* in its native and invaded waters, it is vital the future spread and bloom events of this invasive species are carefully examined. The most recent findings from the 2015 IBTS survey show *M. leidyi* is being identified in waters much closer to the UK than ever before (S. Pitois, pers.com.). The question remains whether *M. leidyi* is spreading east from established populations in the North Sea proper or if in fact there does exist an undiscovered population of *M. leidyi* in UK waters; only with increased monitoring of UK waters will the answer to this question become clearer.

The results also imply that individuals discovered in the North Sea proper can survive the entire winter and spring period until the month of August when water temperatures are at their peak and conditions are most favourable for reproduction. The reproductive capability of these individuals, however, is minimal because of the relatively low summer temperatures in the North Sea and the consequent high (juvenile) mortality rate. There is of course substantial uncertainty surrounding the mortality of this veracious ctenophore and it is vital that more time is spent researching the metabolism and mortality rates of *M. leidyi*, particularly at lower temperatures. At present the model indicates that the individuals found overwintering offshore each year since 2009 in the North Sea proper are most likely being annually flushed out into open waters by advective flows from populations which are present in the surrounding harbours and estuaries, and not as a result of a self-sustaining offshore population.

Overall there is a need for continued research on this species – particularly its early life stages – as there is still much that is not yet fully understood. Going forward research must be dedicated to investigating the hypothesis that *M. leidyi* has a greatly reduced metabolism at lower temperatures. It would also be hugely beneficial to determine whether or not mortality rates are proportional the size of the ctenophore. By increasing the knowledge on the growth physiology of *M. leidyi* and the factors influencing the rate of transfer between life stages, model parameterisation will be improved and more confidence can be placed on the results presented from such a model.

Evidence suggests that due to the link between climate change and biological invasions the trend of increasing gelatinous blooms is likely to continue (Butchart et al., 2010). Climate change has already led to the earlier warming of inshore waters during spring months which in turn has reduced the annual duration of the overwintering period in temperate waters (Costello et al., 2012). The result of this trend is that *M. leidyi* population growth can begin earlier and persist longer in temperate coastal regions than it could in the past. As well as an increase in the number of days per year available for growth and reproduction, species have also been shown to expand their current distribution range (Condon and Steinberg, 2008). Even if the magnitude of blooms does not change over time, the synergistic effects of eutrophication, overfishing, climate change and decreased biodiversity could result in gelatinous zooplanktivores having a greater influence on ecosystem functioning than ever before (Condon et al., 2012). If climate warming can increase the average water temperatures in the North Sea then the reproductive capability of *M. leidyi* in this region could increase significantly. This spatiotemporal expansion and the potential ecological impacts associated with *M. leidyi* highlight the importance of the continuing monitoring of this species.

Appendix A

Model parameterisation

Table A.1: Definitions and and units of variables and parameters used in the equations that describe the dynamics of the *M. leidyi* life cycle

Symbol	Definition	Value	Origin
w_{e}	Average mass of an egg $[\mu g\, C]$	0.1	Salihoglu et al. (2011)
w_{j}	Average mass of an juvenile $[mg\, C]$	0.13	Salihoglu et al. (2011)
w_{aj}	Mass at the end of the transitional stage $[mg\, C]$	1.5	Salihoglu et al. (2011)
w_{a}	Average mass of an adult $[mg\, C]$	2.8	Salihoglu et al. (2011)
c_{cd}	Conversion factor of carbon weight to dry weight $[mg\, mg^{-1}\, C]$	73	Kremer (1976)
c_{w2c}	Conversion factor of wet weight to carbon weight $[mg\, C\, mg^{-1}]$	0.574	Salihoglu et al. (2011)
A_{j}	Juvenile assimilation efficiency	0.75	Salihoglu et al. (2011)
A_{a}	Adult assimilation efficiency	0.72	Salihoglu et al. (2011)
m_{e}	Egg mortality rate $[d^{-1}]$	0.70	van der Molen et al. (2015)
m_{j}	Juvenile mortality rate $[d^{-1}]$	0.27	van der Molen et al. (2015)
b	Exponential term that represents the decrease of clearing rate with size	0.5	Kremer (1976)
a_0	Adult stage basal increase of clearing rate with temperature $[L\, mg^{-1}\, d^{-1}]$	0.09	Salihoglu et al. (2011)
k	Exponential term that represents the increase of clearing rate with temperature $[^{\circ}C^{-1}]$	0.05	Salihoglu et al. (2011)
c_{f}	Coefficient of exponential increase of transfer $[mg^{-1}]$	0.115	Salihoglu et al. (2011)
$T_{\mathrm{f,\ min}}$	Minimum introduced to prevent negative values	0.01	van der Molen et al. (2015)

a_{T}	Constant of a non-linear empirical temperature function	0.03	Salihoglu et al. (2011)
b_{T}	Exponential term of a non-linear empirical temperature function	0.14	Salihoglu et al. (2011)
a_{d}	Constant term that represents the juvenile stage duration when temperature is zero	76.0	van der Molen et al. (2015)
b_{d}	Constant term that represents the decrease of juvenile stage duration with temperature	-2.4	van der Molen et al. (2015)
L_{j}	Constant metabolic loss function	0.06	van der Molen et al. (2015)
c_1	Coefficient of a linear clearance rate function $[L\,mg^{-1}\,d^{-1}\,mm^{-1}]$	0.4	Sullivan and Gifford (2004)
c_2	Coefficient of a weight function $[L\,mg^{-1}\,d^{-1}]$	12.3	Kremer (1976)
c_3	Exponential term of a weight relationship	0.574	Kremer (1976)
c_4	Constant of a linear clearance rate function $[mm\,mg^{-1}]$	0.1	Sullivan and Gifford (2004)

Bibliography

Abdelrhman, M. A. (2005), 'Simplified modeling of flushing and residence times in 42 embayments in new england, usa, with special attention to greenwich bay, rhode island', *Estuarine, Coastal and Shelf Science* **62**(1), 339–351.

Anninskii, B. E. and Abolmasova, G. I. (2000), 'Temperature as a factor influencing the intensity of the metabolism and mass development of the ctenophore *Mnemiopsis leidyi* in the black sea', *Okeanologiia* **40**(5), 686–692.

Antajan, E., Bastian, T., Raud, T. et al. (2014), 'The invasive ctenophore *Mnemiopsis leidyi* a. agassiz, 1865 along the english channel and the north sea french coasts: another introduction pathway in northern european waters?', *Aquatic Invasions* **9**(2), 167–173.

Augustine, S., Jaspers, C., Kooijman, S. A. and Cothers (2014), 'Mechanisms behind the metabolic flexibility of an invasive comb jelly', *Journal of Sea Research* .

Bax, N., Williamson, A., Aguero, M. et al. (2003), 'Marine invasive alien species: a threat to global biodiversity', *Marine policy* **27**(4), 313–323.

Beaulieu, W. T., Costello, J. H., Klein-Macphee, G. and Sullivan, B. K. (2013), 'Seasonality of the ctenophore *Mnemiopsis leidyi* in narragansett bay, rhode island', *Journal of plankton research* **35**, 785–791.

Bilio, M. and Niermann, U. (2004), 'Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the caspian sea', *Marine Ecology Progress Series* **269**, 173–183.

Boero, F., Putti, M., Trainito, E. et al. (2009), 'First records of *Mnemiopsis leidyi* (ctenophora) from the ligurian, thyrrhenian and ionian seas (western mediterranean) and first record of *Phyllorhiza punctata* (cnidaria) from the western mediterranean', *Aquatic Invasions* **4**(4), 675–680.

Boersma, M., Malzahn, A. M., Greve, W. and Javidpour, J. (2007), 'The first occurrence of the ctenophore *Mnemiopsis leidyi* in the north sea', *Helgoland Marine Research* **61**(2), 153–155.

Bolte, S., Fuentes, V., Haslob, H. et al. (2013), 'Population genetics of the invasive ctenophore *Mnemiopsis leidyi* in europe reveal source-sink dynamics and secondary dispersal to the mediterranean sea', *Marine Ecology Progress Series* **485**, 25–36.

Brown, J., Hill, A. E., Fernand, L. and Horsburgh, K. J. (1999), 'Observations of a seasonal jet-like circulation at the central north sea cold pool margin', *Estuarine, Coastal and Shelf Science* **48**(3), 343–355.

Burchard, H. and Bolding, K. (2002), *GETM: A General Estuarine Transport Model; Scientific Documentation*, European Commission, Joint Research Centre, Institute for Environment and Sustainability, Italy.

Burchard, H., Janssen, F., Bolding, K., Umlauf, L. and Rennau, H. (2009), 'Model simulations of dense bottom currents in the western baltic sea', *Continental Shelf Research* **29**(1), 205–220.

Butchart, S. H. M., Walpole, M., Collen, B. et al. (2010), 'Global biodiversity: indicators of recent declines', *Science* **328**(5982), 1164–1168.

Colin, S. P., Costello, J. H., Hansson, L. J., Titelman, J. and Dabiri, J. O. (2010), 'Stealth predation and the predatory success of the invasive ctenophore *Mnemiopsis leidyi*', *Proceedings of the National Academy of Sciences* **107**(40), 17223–17227.

Collingridge, K., van der Molen, J. and Pitois, S. (2014), 'Modelling risk areas in the north sea for blooms of the invasive comb jelly *Mnemiopsis leidyi* a. agassiz, 1865', *Aquatic Invasions* **9**(1), 21–36.

Condon, R. H., Graham, W. M., Duarte, C. M. et al. (2012), 'Questioning the rise of gelatinous zooplankton in the world's oceans', *Bioscience* **62**(2), 160–169.

Condon, R. H. and Steinberg, D. K. (2008), 'Development, biological regulation, and fate of ctenophore blooms in the york river estuary, chesapeake bay', *Marine Ecology Progress Series* **369**, 153–168.

Costello, J. H., Bayha, K. M., Mianzan, H. W. et al. (2012), 'Transitions of *Mnemiopsis leidyi* (ctenophora: Lobata) from a native to an exotic species: a review', *Hydrobiologia* **690**(1), 21–46.

Costello, J. H. and Mianzan, H. W. (2003), 'Sampling field distributions of *Mnemiopsis leidyi* (ctenophora, lobata): planktonic or benthic methods?', *Journal of Plankton Research* **25**(4), 455–459.

Costello, J. H., Sullivan, B. K., Gifford, D. J. et al. (2006), 'Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in narragansett bay, rhode island', *Limnology and Oceanography* **51**(4), 1819–1831.

David, C., Vaz, S., Loots, C. et al. (2014), 'Understanding winter distribution and transport pathways of the invasive ctenophore *Mnemiopsis leidyi* in the north sea: coupling habitat and dispersal modelling approaches', *Biological Invasions* . (in Revision).

Doney, S. C., Ruckelshaus, M., Duffy, J. E. et al. (2012), 'Climate change impacts on marine ecosystems', *Marine Science* **4**, 11–37.

Duwe, K. (1988), Modellierung der Brackwasserdynamik eines Tideästuars am Beispiel der Unterelbe, Phd dissertation, Department of Geosciences, University of Hamburg, Hamburg, Germany.

Ellis, J. R., Milligan, S. P., Readdy, L. et al. (2012), 'Spawning and nursery grounds of selected fish species in uk waters', *CEFAS Science Series Technical Report* **147**, 56.

Faasse, M. A. and Bayha, K. M. (2006), 'The ctenophore *Mnemiopsis leidyi* a. agassiz 1865 in coastal waters of the netherlands: an unrecognized invasion', *Aquatic Invasions* **1**(4), 270–277.

Finenko, G. A., Abolmasova, G. I., Datsyk, N. A. et al. (2014), 'Effect of food composition and temperature on in situ feeding rates of ctenophore invader *Mnemiopsis leidyi* a. agassiz', *Russian Journal of Biological Invasions* **5**(1), 49–55.

Fuentes, V. L., Angel, D. L., Bayha, K. M. et al. (2010), 'Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the mediterranean sea in 2009', *Hydrobiologia* **645**(1), 23–37.

Galil, B. S., Kress, N., Shiganova, T. A. et al. (2009), 'First record of *Mnemiopsis leidyi* a. agassiz, 1865 (ctenophora; lobata; mnemiidae) off the mediterranean coast of israel', *Aquatic Invasions* **4**(2), 356–362.

Giske, J. and Aksnes, D. L. (1992), 'Ontogeny, season and trade-offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri*', *Sarsia* **77**(3-4), 253–261.

Gmitrowicz, E. M. and Brown, J. (1993), 'The variability and forcing of currents within a frontal region off the northeast coast of england', *Continental Shelf Research* **13**(8), 863–890.

Graham, W. M., Pagès, F. and Hamner, W. M. (2001), 'A physical context for gelatinous zooplankton aggregations: a review', *Hydrobiologia* **451**(1-3), 199–212.

Halava (2010), '*Map of the North Sea* [online]'. Available at: `http://commons.wikimedia.org/wiki/File:North_Sea_map-en.png` [Accessed: 27/11/14].

Hansson, H. G. (2006), 'Ctenophores of the baltic and adjacent seas – the invader *Mnemiopsis* is here', *Aquatic invasions* **1**(4), 295–298.

Haraldsson, M., Båmstedt, U., Tiselius, P. et al. (2014), 'Evidence of diel vertical migration in *Mnemiopsis leidyi*', *PloS one* **9**(1), e86595.

Harding, D. and Nichols, J. H. (1987), 'Plankton surveys off the north-east coast of england in 1976: an introductory report and summary of the results', *Fisheries Research Technical Report* **85**, 56.

Henry, J. Q. and Martindale, M. Q. (2000), 'Regulation and regeneration in the ctenophore *Mnemiopsis leidyi*', *Developmental biology* **227**(2), 720–733.

Hill, A. E., Brown, J., Fernand, L. et al. (2008), 'Thermohaline circulation of shallow tidal seas', *Geophysical Research Letters* **35**(11).

Holsteijn, H. (2002), 'Toch nog een beetje nieuw: *Bolinopsis infundibulum* (müller, 1776) en *Beroe cucumis* (fabricius, 1780) aan onze kust', *Het Zeepaard* **62**(5), 142–150. (in Dutch).

Hosia, A. and Titelman, J. (2010), 'Interactions between native and alien ctenophores: *Beroe gracilis* and *Mnemiopsis leidyi* in gullmarsfjorden', *Marine Ecology, Progress Series* **422**, 129–138.

Howarth, L. M., Roberts, C. M., Thurstan, R. H. and Stewart, B. D. (2014), ‘The unintended consequences of simplifying the sea: making the case for complexity’, *Fish and Fisheries* **15**, 690–711.

Hunter, J. R., Craig, P. D. and Phillips, H. E. (1993), ‘On the use of random walk models with spatially variable diffusivity’, *Journal of Computational Physics* **106**(2), 366–376.

Huwer, B., Storr-Paulsen, M., Riisgard, H. and Haslob, H. (2008), ‘Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central baltic sea, november 2007’, *Aquatic Invasions* **3**(2), 113–124.

ICES (2009), *Report of the International Bottom Trawl Survey Working Group(IBTSWG)*, ICES CM 2009, Bergen, Norway.

ICES (2013), *Manual for the Midwater Ring Net sampling during IBTS Q1. Series of ICES Survey Protocols SISP 2-MIK 2*, International Council for the Exploration of the Sea, Copenhagen, Denmark.

Jackson, J. B., Kirby, M. X., Berger, W. H. et al. (2001), ‘Historical overfishing and the recent collapse of coastal ecosystems’, *Science* **293**(5530), 629–637.

Jaspers, C. (2012), Ecology of gelatinous plankton. With emphasis on feeding interactions, distribution patterns and reproduction biology of *Mnemiopsis leidyi* in the Baltic Sea, Phd thesis, Technical University of Denmark, Copenhagen.

Jaspers, C., Møller, L. F. and Kiørboe, T. (2011), ‘Salinity gradient of the baltic sea limits the reproduction and population expansion of the newly invaded comb jelly *Mnemiopsis leidyi*’, *PLoS one* **6**(8), e24065.

Javidpour, J., Molinero, J. C., Lehmann, A. et al. (2009b), ‘Annual assessment of the predation of *Mnemiopsis leidyi* in a new invaded environment, the kiel fjord (western baltic sea): a matter of concern?’, *Journal of Plankton Research* **31**(7), 729–738.

Javidpour, J., Molinero, J. C., Peschutter, J. and Sommer, U. (2009a), ‘Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the kiel fjord, western baltic sea’, *Biological Invasions* **11**(4), 873–882.

Keeling, R. F., Körtzinger, A. and Gruber, N. (2010), 'Ocean deoxygenation in a warming world', *Marine Science* **2**, 199–229.

Kideys, A. E. (1994), 'Recent dramatic changes in the black sea ecosystem: the reason for the sharp decline in turkish anchovy fisheries', *Journal of Marine Systems* **5**(2), 171–181.

Knowler, D. (2005), 'Reassessing the costs of biological invasion: *Mnemiopsis leidyi* in the black sea', *Ecological Economics* **52**(2), 187–199.

Kremer, P. (1976), *Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore Mnemiopsis leidyi*, Vol. 1 of *Estuarine Processes*, Wiley ML edn, Academic Press, pp. 175–215.

Kremer, P. (1994), 'Patterns of abundance for *Mnemiopsis* in us coastal waters: a comparative overview', *ICES Journal of Marine Science: Journal du Conseil* **51**(4), 347–354.

Kremer, P. and Nixon, S. (1976), 'Distribution and abundance of the ctenophore,*Mnemiopsis leidyi* in narragansett bay', *Estuarine and Coastal Marine Science* **4**(6), 627–639.

Kremer, P. and Reeve, M. R. (1989), 'Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. ii. carbon budgets and growth model', *Journal of Plankton Research* **11**(3), 553–574.

Kreps, T. A., Purcell, J. E. and Heidelberg, K. B. (1997), 'Escape of the ctenophore *Mnemiopsis leidyi* from the scyphomedusa predator *Chrysaora quinquecirrha*', *Marine Biology* **128**(3), 441–446.

Kube, S., Postel, L., Honnef, C. et al. (2007), '*Mnemiopsis leidyi* in the baltic sea–distribution and overwintering between autumn 2006 and spring 2007', *Aquatic Invasions* **2**(2), 137–145.

Lehtiniemi, M., Lehmann, A., Javidpour, J. and Myrberg, K. (2012), 'Spreading and physico-biological reproduction limitations of the invasive american comb jelly *Mnemiopsis leidyi* in the baltic sea', *Biological invasions* **14**(2), 341–354.

Lenhart, H. J., Mills, D. K., Baretta-Bekker, H. et al. (2010), 'Predicting the consequences of nutrient reduction on the eutrophication status of the north sea', *Journal of Marine Systems* **81**(1), 148–170.

Lowe, S., Browne, M., Boudjelas, S. and De Poorter, M. (2000), *100 of the world's worst invasive alien species: a selection from the global invasive species database*, Invasive Species Specialist Group Species Survival Commission, World Conservation Union (IUCN), Auckland, New Zealand.

Mackinson, S. and Daskalov, G. (2007), 'An ecosystem model of the north sea to support an ecosystem approach to fisheries management: description and parameterisation', *Cefas Science Series Technical Report* **142**, 195.

Martindale, M. Q. (1987), 'Larval reproduction in the ctenophore *Mnemiopsis mccradyi* (order lobata)', *Marine biology* **94**(3), 409–414.

McNamara, M. E. and Lonsdale, D. J. (2014), 'Interannual differences in microplankton drive changes in the feeding and fecundity of *Mnemiopsis leidyi* in a long island estuary', *Estuarine, Coastal and Shelf Science* **144**, 1–7.

McNamara, M. E., Lonsdale, D. J. and Cerrato, R. M. (2013), 'Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance and composition enhancing prey conditions for larval ctenophores', *Estuarine, Coastal and Shelf Science* **133**, 2–10.

Mianzan, H. W., Mari, N., Prenski, B. and Sanchez, F. (1996), 'Fish predation on neritic ctenophores from the argentine continental shelf: a neglected food resource?', *Fisheries Research* **27**(1), 69–79.

Mianzan, H. W., Martos, P., Costello, J. H. and Guerrero, R. A. (2010), 'Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (ctenophora: Lobata) in open-sea populations from patagonia, argentina', *Hydrobiologia* **645**(1), 113–124.

Miller, R. J. (1974), 'Distribution and biomass of an estuarine ctenophore population, *Mnemiopis leidyi* (a. agassiz)', *Chesapeake Science* **15**(1), 1–8.

Mills, C. E. (2001), Jellyfish blooms: are populations increasing globally in response to changing ocean conditions?, *in* 'Jellyfish Blooms: Ecological and Societal Importance', Springer, pp. 55–68.

Munk, P. and Nielsen, J. (2005), *Eggs and larvae of North Sea fishes*, Biofolia, Frederiksberg, Denmark.

Mutlu, E. (1999), 'Distribution and abundance of ctenophores and their zooplankton food in the black sea. ii. *Mnemiopsis leidyi*', *Marine Biology* **135**(4), 603–613.

National Research Council (2011), *Climate stabilization targets: emissions, concentrations, and impacts over decades to millennia*, National Academic Press, Washington, chapter 5, pp. 159–215.

Oliveira, O. M. et al. (2007), 'The presence of the ctenophore mnemiopsis leidyi in the oslofjorden and considerations on the initial invasion pathways to the north and baltic seas', *Aquatic Invasions* **2**(3), 185–189.

Oviatt, C. A. and Kremer, P. M. (1977), 'Predation on the ctenophore, *Mnemiopsis leidyi*, by butterfish, *Peprilus triacanthus*, in narragansett bay, rhode island', *Chesapeake Science* **18**(2), 236–240.

Paramor, O. A. L., Allen, K. A., Aanesen, M. et al. (2009), *MEFEPO North Sea Atlas*, University of Liverpool. ISBN 0 906370 60 4.

Pereladov, M. V. (1988), Some observations for biota of sudak bay of the black sea, *in* 'The Third All-Russian Conference on Marine Biology', pp. 237–238. (in Russian).

Planka, H. D. (1974), *Ctenophora. Reproduction of marine invertebrates*, Vol. 1, Academic Press, New York, pp. 201–265. Eds. Giese, A. C. and Pearse, J. S.

Purcell, J. E. and Arai, M. N. (2001), 'Interactions of pelagic cnidarians and ctenophores with fish: a review', *Hydrobiologia* **451**(1-3), 27–44.

Purcell, J. E. and Cowan, J. H. (1996), 'Predation by the scyphomedusan *Chrysaora quinquecirrha* on *Mnemiopsis leidyi* ctenophores', *Oceanographic Literature Review* **43**(7).

Purcell, J. E. and Decker, M. B. (2005), 'Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in chesapeake bay during 1987-2000', *Limnology and Oceanography* **50**(1), 376–387.

Purcell, J. E., Decker, M. B., Breitburg, D. L. and Broughton, K. J. (2014), 'Fine-scale vertical distributions of *Mnemiopsis leidyi* ctenophores: predation on copepods relative to stratification and hypoxia', *Marine Ecology Progress Series* **500**, 103–120.

Purcell, J. E., Nemazie, D. A., Dorsey, S. E. et al. (1994), 'Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in chesapeake bay', *Marine Ecology Progress Series* **114**, 47–58.

Purcell, J. E., Shiganova, T. A., Decker, M. B. and Houde, E. D. (2001), The ctenophore *Mnemiopsis* in native and exotic habitats: Us estuaries versus the black sea basin, *in* 'Jellyfish Blooms: Ecological and Societal Importance', Springer, pp. 145–176.

Rapoza, R., Novak, D. and Costello, J. H. (2005), 'Life-stage dependent, in situ dietary patterns of the lobate ctenophore *Mnemiopsis leidyi* agassiz 1865', *Journal of Plankton Research* **27**(9), 951–956.

Reeve, M. R., Syms, M. A. and Kremer, P. (1989), 'Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. i. carbon biomass, feeding, egg production, growth and assimilation efficiency', *Journal of Plankton Research* **11**(3), 535–552.

Reeve, M. R., Walter, M. A. and Ikeda, T. (1978), 'Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores', *Limnology and Oceanography* **23**(4), 740–751.

Reusch, T. B., Bolte, S., Sparwel, M. et al. (2010), 'Microsatellites reveal origin and genetic diversity of eurasian invasions by one of the worlds most notorious marine invader, *Mnemiopsis leidyi* (ctenophora)', *Molecular Ecology* **19**(13), 2690–2699.

Richardson, A. J., Bakun, A., Hays, G. C. and Gibbons, M. J. (2009), 'The jellyfish joyride: causes, consequences and management responses to a more gelatinous future', *Trends in ecology & evolution* **24**(6), 312–322.

Riisgård, H. U., Bøttiger, L., Madsen, C. V. and Purcell, J. E. (2007), 'Invasive ctenophore *Mnemiopsis leidyi* in limfjorden (denmark) in late summer 2007assessment of abundance and predation effects', *Aquatic Invasions* **2**(4), 395–401.

Riisgård, H. U., Madsen, C. V., Barth-Jensen, C. et al. (2011), 'Population dynamics and zooplankton-predation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in limfjorden (denmark)', *Aquatic Invasions* **7**(2), 147–162.

Rodhe, J. (1987), 'The large-scale circulation in the skagerrak; interpretation of some observations', *Tellus A* **39**(3), 245–253.

Rosland, R. and Giske, J. (1997), 'A dynamic model for the life history of *Maurolicus muelleri*, a pelagic planktivorous fish', *Fisheries Oceanography* **6**(1), 19–34.

Rowshantabari, M., Finenko, G. A., Kideys, A. and Kiabi, B. (2012), 'Effect of temperature on clearance rate, daily ration and digestion time of *Mnemiopsis leidyi* from the southern caspian sea', *Caspian Journal of Environmental Sciences* **10**(2), 157–167.

Salihoglu, B., Fach, B. A. and Oguz, T. (2011), 'Control mechanisms on the ctenophore *Mnemiopsis* population dynamics: A modeling study', *Journal of Marine Systems* **87**, 55–65.

Shiganova, T. A. (1998), 'Invasion of the black sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure', *Fisheries Oceanography* **7**(3-4), 305–310.

Shiganova, T. A., Dumont, H. J., Sokolsky, A. F., Kamakin, A. M., Tinenkova, D. and Kurasheva, E. K. (2004), Population dynamics of *Mnemiopsis leidyi* in the caspian sea, and effects on the caspian ecosystem, *in* 'Aquatic Invasions in the Black, Caspian, and Mediterranean Seas', Vol. 35 of *Nato Science Series: IV: Earth and Environmental Sciences*, Springer, pp. 71–111.

Shiganova, T., Mirzoyan, Z., Studenikina, E. et al. (2001), 'Population development of the invader ctenophore *Mnemiopsis leidyi*, in the black sea and in other seas of the mediterranean basin', *Marine biology* **139**(3), 431–445.

Siapatis, A., Giannoulaki, M., Valavanis, V. D. et al. (2008), Modelling potential habitat of the invasive ctenophore *Mnemiopsis leidyi* in aegean sea, *in* 'Essential Fish Habitat Mapping in the Mediterranean', Springer, pp. 281–295.

Simberloff, D., Martin, J. L., Genovesi, P. et al. (2013), 'Impacts of biological invasions: what's what and the way forward', *Trends in Ecology & Evolution* **28**(1), 58–66.

Stanlaw, K. A., Reeve, M. R. and Walter, M. A. (1981), 'Growth, food, and vulnerability to damage of the ctenophore *Mnemiopsis mccradyi* in its early life history stages', *Limnology and Oceanography* **26**(2), 224–234.

Sullivan, L. J. and Gifford, D. J. (2004), 'Diet of the larval ctenophore *Mnemiopsis leidyi* a. agassiz (ctenophora, lobata)', *Journal of Plankton Research* **26**(4), 417–431.

Sündermann, J. and Pohlmann, T. (2011), 'A brief analysis of north sea physics', *Oceanologia* **53**(3), 663–689.

Tendal, O. S., Jensen, K. R. and Riisgård, H. U. (2007), 'Invasive ctenophore *Mnemiopsis leidyi* widely distributed in danish waters', *Aquatic Invasions* **2**(4), 455–460.

Tiessen, M., Fernard, L., Gerkema, T. et al. (2014), 'Numerical modelling of physical processes governing larval transport in the southern north sea', *Ocean Science* **10**(3), 357–376.

Tilves, U., Purcell, J. E., Marambio, M. et al. (2013), 'Predation by the scyphozoan *Pelagia noctiluca* on *Mnemiopsis leidyi* ctenophores in the nw mediterranean sea', *Journal of Plankton Research* **35**(1), 218–224.

Titelman, J., Hansson, L. J., Nilsen, T. et al. (2012), 'Predator-induced vertical behavior of a ctenophore', *Hydrobiologia* **690**(1), 181–187.

Turrell, W. R., Henderson, E. W., Slesser, G. et al. (1992), 'Seasonal changes in the circulation of the northern north sea', *Continental Shelf Research* **12**(2), 257–286.

Turrell, W. R., Slesser, G., Payne, R. et al. (1996), 'Hydrography of the east shetland basin in relation to decadal north sea variability', *ICES Journal of Marine Science* **53**(6), 899–916.

Valdés, L., Peterson, W., Church, J., Brander, K. and Marcos, M. (2009), 'Our changing oceans: conclusions of the first international symposium on the effects of climate change on the world's oceans', *ICES Journal of Marine Science: Journal du Conseil* **72**, 1435–1438.

van der Molen, J., Aldridge, J. N., Coughlan, C. et al. (2013), 'Modelling marine ecosystem response to climate change and trawling in the north sea', *Biogeochemistry* **113**(1-3), 213–236.

van der Molen, J., Rogers, S. I., Ellis, J. R. et al. (2007), 'Dispersal patterns of the eggs and larvae of spring-spawning fish in the irish sea, uk', *Journal of Sea Research* **58**(4), 313–330.

van der Molen, J., van Beek, J., Augustine, S. et al. (2015), 'Modelling survival and connectivity of *Mnemiopsis leidyi* in the southern north sea and scheldt estuaries', *Ocean Science Discussions* **11**(3), 1561–1611.

Van Ginderdeuren, K., Hostens, K., Hoffman, S. et al. (2012), 'Distribution of the invasive ctenophore *Mnemiopsis leidyi* in the belgian part of the north sea', *Aquatic Invasions* **7**(2), 163–169.

van Leeuwen, S. M., van der Molen, J., Ruardij, P. et al. (2013), 'Modelling the contribution of deep chlorophyll maxima to annual primary production in the north sea', *Biogeochemistry* **113**(1-3), 137–152.

van Walraven, L., Langenberg, V. T. and van der Veer, H. W. (2013), 'Seasonal occurrence of the invasive ctenophore *Mnemiopsis leidyi* in the western dutch wadden sea', *Journal of Sea Research* **82**, 86–92.

Vichi, M., Pinardi, N. and Masina, S. (2007), 'A generalized model of pelagic biogeochemistry for the global ocean ecosystem. part i: Theory', *Journal of Marine Systems* **64**(1), 89–109.

Viitasalo, S., Lehtiniemi, M. and Katajisto, T. (2008), 'The invasive ctenophore *Mnemiopsis leidyi* overwinters in high abundances in the subarctic baltic sea', *Journal of plankton research* **30**(12), 1431–1436.

Vinogradov, M., Shushkina, E., Musaeva, E. I. and Sorokin, P. Y. (1989), 'Ctenophore *Mnemiopsis leidyi* (a. agassiz) (ctenophora, lobata)-new settlers in the black sea', *Okeanologiya* **29**(2), 293–299. (in Russian).

Visser, A. (1997), 'Using random walk models to simulate the vertical distribution of particles in a turbulent water column', *Marine Ecology-Progress Series* **158**, 275–281.

Volovik, S. P., Mirzoyan, I. A. and Volovik, G. S. (1993), *Mnemiopsis leidyi*: biology, population dynamics, impact to the ecosystem and fisheries, *in* 'ICES (Biological Oceanography Committee)', Vol. 69, pp. 1–11.

Waggett, R. J. and Sullivan, L. J. (2006), 'Feeding efficiency of the larval ctenophore *Mnemiopsis leidyi* a. agassiz (ctenophora, lobata)', *Journal of Plankton Research* **28**(7), 719–723.

Wolk, F. (2003), Three-dimensional Lagrangian tracer modelling in Wadden Sea areas, Phd dissertation, Carl von Ossietzky University Oldenburg, Hamburg, Germany.

Yazdani Foshtomi, M., Abtahi, B., Esmaili Sari, A. and Taheri, M. (2007), 'Ion composition and osmolarity of caspian sea ctenophore, *Mnemiopsis leidyi*, in different salinities', *Journal of Experimental Marine Biology and Ecology* **352**(1), 28–34.

Zaika, V. E. and Revkov, N. K. (1994), 'Anatomy of gonads and regime of spawning of ctenophore *Mnemiopsis* sp. in the black sea', *Zoologichesky Zhurnal* **73**(3), 5–10. (in Russian).