Environmental drivers and advective transport of harmful phytoplankton in North West European shelf seas

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DOCTOR OF PHILOSOPHY (AWARDED BY OU/ABERDEEN)

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Environmental drivers and advective transport of harmful phytoplankton in North West European shelf seas

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A dissertation submitted for the degree of Doctor of Philosophy of the University of Aberdeen, the University of Highlands and Islands and the Scottish Association for Marine Science

Department of Microbial and Molecular Biology

2017
Declaration

This thesis has been composed by the candidate. No portion of the work contained in this document has been submitted in support of an application for a degree or qualification of this or any other university or other institution of learning. All verbatim extracts have been distinguished by quotation marks, and all sources of information have been specifically acknowledged.

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Salient Points

- Harmful phytoplankton can negatively affect aquaculture, causing large economic losses to the industry. To reduce damage to aquaculture caused by harmful algal blooms (HABs), it is necessary to improve knowledge of HAB development and transport in coastal shelf sea waters. An early detection system coupled with a predictive model is also needed.

- The phytoplankton community on the North West European Shelf and adjacent oceanic waters was assessed during two research cruises to provide information about the occurrence and distribution of harmful phytoplankton. Seasonal fronts, the shelf edge and the European Slope Current (ESC) were identified as main features dividing phytoplankton community. This information is relevant to the development of offshore HAB monitoring, that is currently not feasible.

- Phytoplankton communities, including several potentially harmful genera, were structured by water temperature, salinity, light availability, and nutrient concentrations.

- The potential of gliders to be used in offshore detection and surveillance of harmful high density blooms is demonstrated. The use of this technology for routine offshore monitoring programs is suggested to improve early detection and early warning of such blooms.

- The use of optical water property data, which can be routinely measured by gliders, to provide information on phytoplankton community is discussed. Further work is needed in this area to use such optical data to its full potential.

- The benefits and limitations of using an individual based, coupled bio-physical numerical model to study the growth and advection of HABs are described. The model described in this thesis could potentially provide an early warning of coastal HAB occurrence if more information about offshore HAB seed populations was available.

- The model’s hindcast capacity is demonstrated by comparing model output to coastal cell counts and satellite imagery.

- The model results linked coastal HAB occurrence to advective transport of cells within the ESC and showed the importance of inter-annual variations in current strength and direction in coastal HAB predictions.
Abstract

Harmful phytoplankton occur naturally in British waters. However, little is known about the environmental drivers that lead to the formation and advection of harmful algae blooms (HABs). To minimise adverse effects of HABs it is necessary to improve our understanding of links between advection, environmental changes and HAB development.

The aims of this PhD project were therefore to:
1) Provide a better understanding of the relationship between harmful phytoplankton, environmental drivers and key hydrodynamic features such as the shelf edge;
2) Determine the role of advection in bloom transport and development;
3) Utilise computational modelling to study environmental drivers and advection of HABs.

To achieve these aims, field data was collected from two cruises and a glider mission. During the cruises, data on phytoplankton community was collected alongside physical data with a focus on key features such as the shelf edge and seasonal coastal fronts. This data provided an updated, detailed assessment of phytoplankton across the Hebridean and Malin Shelves. Field data showed that the European Slope Current (ESC) and Islay front can separate phytoplankton communities on the shelf. Lack of community differences along the ESC suggested stronger transport and exchange of phytoplankton within the ESC than adjacent shelf waters. Nutrients, nutrient ratios and light conditions were also found to play major structuring roles in determining phytoplankton assemblage. Data collected during field work can also be useful for regulatory assessment of shelf seas by providing baseline information about phytoplankton communities in the area.

The glider mission provided an additional high resolution dataset of biological and physical water column properties across the Malin shelf. Vertical resolution showed that phytoplankton distribution was strongly linked to thermal stratification and temperature changes. Horizontal resolution was highly patchy, suggesting that scientific cruises could easily miss high density blooms with small spacial extent. The glider successfully monitored a high density HAB, suggesting that gliders could potentially be used for phytoplankton surveillance and detection of high biomass blooms.

In addition to field data, a bio-physical individual based model (IBM) was used to simulate HAB progression. The IBM was coupled with a hydrodynamic ocean model to show the role of advection and importance of offshore seed populations in coastal HAB development. Model output was compared to coastal count data and satellite images whenever possible. Running the model under different conditions for phytoplankton growth and behaviour, suggest that it was crucial to include
biological processes to simulate HABs. The IBM could be initialised with data from satellite images, field data or discrete seed populations. Model simulations with different initial cell concentrations and locations could help to explain observed bloom pathways and suggest possible offshore origins for observed exceptional HABs.

The results from field work and model simulations showed the role of the ESC in structuring phytoplankton community and transporting seed populations of HABs along the Scottish west coast. This suggests that future cruises and offshore monitoring should focus on the ESC and shelf break region. The bio-physical model could hindcast HAB pathways along the ESC, suggesting that modelling of HAB pathways of known seed populations could be integrated into an early warning system for aquaculture sites along the Scottish west coast in the future. Such an early warning system would allow the protection, relocation or early harvesting of affected aquaculture sites.
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Published manuscripts


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List of Abbreviations

AFBI Agri-Food and Bioscience Institute
ANOSIM ANalysis Of SIMilarity
BADC British Atmospheric Data Centre
bb Backscatter
CDOM Coloured Dissolved Organic Matter
CPR Continuous Plankton Recorder
CTD Conductivity, Temperature and Depth
DO Domoic Acid
ESC European Slope Current
FSA Food Standard Agency
FSS Food Standard Scotland
GES Good Ecological Status
HAB Harmful Algal Blooms
IBM Individual Based Model
IOP Inherent Optical Property
ISP Initial Seed Population
MODIS MODe rate resolution Imaging Spectroradiometer
NAO North Atlantic Oscillation
NEOMO Nucleus for European Modelling of the Ocean
NEODAAS NERC Earth Observation Data Acquisition and Analysis Service
NERC Natural Environmental Research Council
nMDS non-Metric Multidimensional Scaling
NWES North West European Shelf
OA Okadaic Acid
OSPAR OSlo and PARis convention
PC Principal Component
PCA Principal Component Analysis
PLM Population Model
POLCOMS Proudman Oceanographic Laboratory Coastal Ocean Modelling System
RUV Remotely controlled Underwater Vehicle
SCC Scottish Coastal Current
Sea-WiFS Sea-viewing Wide Field-of-view Sensor
UPSS UPwards Swimming Speed
VIIRS Visible Infrared Imagine Radiometer Suite
1 Introduction

1.1 The North West European shelf sea environment

This PhD project studied the phytoplankton of the shelf sea and adjacent oceanic waters of the Scottish west coast approximately between 54°N and 61°N and between 0° and 15°W. The area includes the Malin and the Hebridean Shelves and any adjacent shelf and oceanic waters (Figure 1.1). The coastline is characterised by deep, narrow and sheltered sea lochs, shallow bays and estuaries and stretches of long exposed coastline. Major West Scottish estuaries are the Solway Firth and the Clyde Sea. Despite those estuaries and high rainfall, the input of nutrients via river runoff accounts only for a small percentage of nutrient input in the shelf sea; most of the nutrients originate in the Atlantic and the Irish Sea (Proctor et al. 2003).

Figure 1.1: Map of Scotland and Scottish coastal areas.

The 200 m deep shelf and adjacent 2000 m deep oceanic waters are separated by a steep continental slope alongside which the European Slope Current (ESC also known as Continental Slope Current) is steered (Figure 1.2). Slope and slope
current act as a mixing barrier and limit exchange between shelf and oceanic waters. Mixing is mainly caused by wind driven small surface eddies (Ellett et al. 1986). The ESC originates in the Atlantic and flows northwards with an average speed of 0.2 m s$^{-1}$ displaying a strong seasonality with weaker flows in summer and a faster flow in winter (Inall et al. 2009). It has a characteristic high salinity core with salinities over 35.36 (Hill & Mitchelson-Jacob 1993). The Scottish Coastal Current (SCC) (Figure 1.2) transports water masses originating in Iberia and flow through the Irish Sea, carrying mainly Irish Sea water, with minor dilution effects from land runoffs and river inputs, giving the SCC salinities generally below 35.0 (Hill et al. 1997). It flows parallel to the ESC along the west Scottish coast until it reaches the Outer Hebrides, where the current splits with currents running north at both sides of the Hebrides (Figure 1.2). The SCC moves with an average speed of 0.024 - 0.06 m s$^{-1}$ with seasonal winds in winter strongly influencing current speed and direction (Inall et al. 2009).

Figure 1.2: Map showing the ESC (red) and SCC (green).

The circulation in the North Atlantic Ocean is driven by the southern subtropical
The subtropical gyre drives the North Atlantic Current (aka North Atlantic Drift), carrying warm, saline North Atlantic Water polewards past Ireland and the UK at the surface. The deep water current is driven by the Thermohaline or Meridional Overturning Circulation carrying polar water back southwards thought the Faroe-Shetland channel and forced westwards by the Wyville-Thomson Ridge, until it overspills in the deep Rockall Trough. This creates two distinct water layers with deep bottom water consisting of Labrador Sea Water, entering from the north and travelling southwards, while the top 1500 m mainly contain East North Atlantic Water. The constant characteristics of deeper water masses suggest a regular renewal (Ellett et al. 1986).

The Malin and Hebridean Shelves are strongly influenced by seasonality. The water column is well mixed during winter and thermally stratified over summer. Strong seasonal winds also influence the speed and direction of surface currents which can lead to short term reversal of the direction of smaller currents in winter (Ellett et al. 1986). A strong salinity front, known as the Islay front, is permanently present in the Malin shelf where high salinity Atlantic water meets water entering the Malin shelf from the Irish sea with a distinctly lower salinity, generally below 35.0 (Hill & Simpson 1989). The front changes its structure and position seasonally, when a stratification front develops on top of the salinity front in summer, separating tidally mixed Irish sea water from thermally stratified water with Atlantic origin.

The shelf seas are a highly dynamic environment that do not only change seasonally, but also show great inter-annual variations in their physical properties; variation in the North Atlantic Oscillation (NAO), caused by changes in the pressure differences between the north and south of the North Atlantic, can lead to inter-annual changes in wind and current regimes. Changes in the signature of water masses entering the Rockall Channel was recently linked to a weakening trend in the strength of the subpolar gyre (Johnson et al. 2013). The strength of the subpolar gyre determines how much nutrient rich water enters the channel from the north. Years with stronger gyres temporarily increases nutrient influx, leading to strong variations in measured nutrient concentrations (Johnson et al. 2013). The effect of these and other oceanographic changes on phytoplankton species composition, succession and bloom development is largely unknown (Johnson et al. 2013).

1.2 Phytoplankton and harmful blooms in UK waters

Marine phytoplankton are microscopic algae that drift in the sunlit surface layer of the ocean. As autotrophs, they produce complex organic molecules from inorganic nutrients and solar radiation and form the basis of pelagic food webs. Cell size can vary between 2 µm to 2 mm for different species. Phytoplankton are often divided
into three groups: Diatoms (Bacillariophyceae), dinoflagellates (Dinophyceae) and micro flagellates. Diatoms are generally immobile single celled or colony-forming organisms that require silica for the growth of their exoskeleton or frustule. Dinoflagellates and micro flagellates are motile due to the possession of one or more flagellae.

Of the estimated 5000 or more phytoplankton species, only $\sim 300$ are considered harmful (Landsberg 2002). Some harmful species can grow rapidly under favourable environmental conditions and form harmful algal blooms (HABs). HABs can be caused by toxin producing species or by high biomass producing species. Toxin producing species can also be harmful at low densities. In British waters the main toxin producing species are *Pseudo-nitzschia*, *Dinophysis*, and *Alexandrium*, that produce domoic acid (DA), okadaic acid (OA) and saxitoxins respectively (Davidson et al. 2011). These toxins are biological active secondary metabolites that can have detrimental effects on human health or ecosystem functioning. Humans can be exposed to toxins directly while swimming or accidentally ingesting seawater containing algae, via aerosols (e.g. *Karenia brevis*), or via the accumulation in marine filter feeders feeding on toxic phytoplankton (Davidson et al. 2011).

Contamination of shellfish by toxins poses the greatest threat from HABs to human health in the UK. Therefore, a regulatory monitoring program is in place to stop the harvest and sale of contaminated shellfish. As a result of this monitoring, human intoxication with phytotoxins is rare in the UK. The first record of domoic acid, caused by *Pseudo-nitzschia*, in British waters was in 1999 when a wide shellfish harvesting area (49 000 km$^2$) was closed in west Scotland for nearly a year due to the presence of DA in scallops (Fehling et al. 2004b).

Reports in Scotland of blooms of the toxin producing dinoflagellate *Dinophysis* date back to 1900 (Davidson et al. 2011). In summer 2006 and 2013, several people fell ill after eating mussels contaminated with OA from a Scottish harvesting site (Davidson et al. 2011, Whyte et al. 2014). Symptoms were gastrointestinal and include diarrhoea, nausea, vomiting and abdominal cramps. Symptoms occur in the first 30 minutes after consumption but resolve completely after three days (Davidson et al. 2011). Even though thousands of incidents are reported worldwide, it is likely that these numbers are underestimated as OA poisoning can often be wrongly diagnosed as bacterial food poisoning and mild intoxications might not be reported at all.

Saxitoxins, which can be produced by *Alexandrium* in UK waters, are highly toxic, which means that even small numbers of *Alexandrium* can cause a toxic event. *Alexandrium* is often part of the natural phytoplankton community in low numbers, with the only recorded outbreak of saxitoxin poisoning in the UK in 1968 (Joint et al. 1997). During this toxic event at least 78 people were hospitalised. Afterwards a
regular monitoring program was put in place, avoiding any further recorded event causing human illness (Joint et al. 1997). Harmful *Alexandrium* have a very complex life cycle including benthic cysts (Anderson 1998). This makes it extremely difficult to determine whether low density toxic events are linked to advection, *in situ* growth or cyst germination as a response to changing environmental conditions.

The second type of HABs are high biomass events. These are typically not linked to shellfish poisoning in humans and are therefore less well monitored. Even though some species were found to produce compounds toxic to marine life, the damage caused by such blooms is normally a direct consequence of their high biomass. High density blooms can damage marine organisms by shading or causing low oxygen events upon bloom decay (Robin et al. 2013). Examples for high biomass HABs in British waters are *Karenia mikimotoi* (Davidson et al. 2009), *Chaetoceros* (Treasure et al. 2003) and *Phaeocystis* (Lancelot et al. 1987). Damage caused by these species is normally reflected in the economic impact of losses of farmed finfish (Jones et al. 1982, Treasure et al. 2003, Rogers & Lockwood 1990), but shellfish can also be affected in some cases (Peperzak & Poelman 2008).

*K. mikimotoi* blooms are considered harmful as high biomass can cause low oxygen conditions following bloom decay, as seen in India during an exceptional bloom in 2004. During this bloom toxicity assays indicated the absence of toxins and fish mortality was explained by the effects of high biomass (Robin et al. 2013). However, other studies clearly show that *K. mikimotoi* can produce several bioactive compounds which can be hemolytic and ichtyotoxic (Brand et al. 2012). An exceptional bloom in 1980 caused the loss of over 3000 farmed salmon in the Firth of Clyde. No toxins were reported, but the fish gills were severely damaged and dead fish showed a complete necrosis of lamellar tissues (Jones et al. 1982). During a bloom in 2006 that affected large areas around the Scottish coast, no mortalities of farmed fish occurred, however several mortalities of benthic species were reported (Davidson et al. 2009).

*Phaeocystis* blooms can be made from single cells or colonies containing thousands of cells (Schoemann et al. 2005). Colonies can produce large amounts of extracellular polysaccharide mucus that can accumulate on beaches as a nuisance foam (Lancelot et al. 1987). Even though *Phaeocystis* were found to produce some toxins (Hansen et al. 2004), oxygen depletion upon bloom decay is often found to be the reason for mortalities of marine life (Peperzak & Poelman 2008, Rogers & Lockwood 1990). In North Wales, high densities of *Phaeocystis* led to localised patches of anoxia after bloom decay that were associated with fish mortalities of juvenile fish (Rogers & Lockwood 1990). The density of fish was generally reduced near the bloom area, suggesting that fish were, at least to some degree, able to detect and avoid unfavourable conditions (Rogers & Lockwood 1990). Therefore,
damage can be more severe for caged fish or sessile organisms. For example, a high density bloom at the coast of the Netherlands caused the mortality of 10 million kg of farmed mussels, most likely due to the development of anoxic conditions during bloom decay.

*Chaetoceros* does not produce any known ichthyotoxins and fish kills caused by this genus are generally caused by physical damage to fish gills and guts (Treasurer et al. 2003). Moralities of farmed salmon were reported in the UK in 1988 (Bruno et al. 1989) and 1998 (Treasurer et al. 2003). High densities of *Chaetoceros* were also found to have sub lethal effect on farmed salmon such as reduced feeding, leading to reduced growth, and thereby further economic losses (Treasurer et al. 2003). As neither *Chaetoceros* nor *Phaeocystis* are included in regulatory monitoring, blooms often remain unrecorded except in coastal observatories such as L4 or the Scottish coastal observatory.

Several studies have attempted to link both toxic and non-toxic harmful events to changes in environmental conditions (see chapter 1.3) and physical advection towards coastal sites (see chapter 1.4). However, advection can be difficult to study for genera that cause harm in low numbers or have prolonged benthic stages in their life cycle such as *Alexandrium*. Studies on advection are therefore focused on high biomass blooms which makes it easier to tell whether a sharp increase in cell numbers could be caused by *in situ* growth alone or if physical accumulation is necessary to explain observed cell densities.

### 1.3 Environmental drivers of harmful phytoplankton

HABs are often sporadic and difficult, if not impossible, to predict. However, in some cases, HAB occurrence can be linked to physical conditions favouring bloom formation. Estuaries and coastal bays can provide a good growth environment for harmful phytoplankton if their growth rate is higher than the tidal flushing rate (Raine 2014). Tidal fronts, which form at the boundary between stratified and well mixed water, also provide good growth conditions for HABs. *Dinophysis* and *K. mikimotoi* blooms are often linked to strong thermal stratification (Raine 2014). Immotile diatoms like *Pseudo-nitzschia* rely on turbulence to stay in the surface layer and are generally not associated with thermal stratification. In non-stratified regions, turbulence can impair growth and initiate morphological changes in some dinoflagellates. For *K. mikimotoi*, Gentien et al. (2007) proposed that turbulence increases collision of cells and thereby increases the effect of autotoxicity, leading to cell mortality.

During stratification, *K. mikimotoi* (Raine 2014), *Dinophysis* (Raine et al. 2010a, Farrell et al. 2012), and *Pseudo-nitzschia* (Raine 2014) can accumulate near the py-
cnocline, where growth conditions are optimal due to sufficient sunlight and nutrient influx due to mixing with deeper layers. Accumulation at certain depth might be associated with the biological behaviour of cells or might be caused by gyrotactic trapping, i.e. retention near pycnocline due to physical forcing (Raine 2014). Such layers were often found with up to 5 times higher chlorophyll levels than surrounding water (Farrell et al. 2012). For example, *D. acuminata* blooms were found in 20 cm thin subsurface blooms containing a 5 cm thin layer of *D. acuta* in Bantry Bay, Ireland (Raine 2014). Thin layers can make it more difficult to sample, model and predict blooms (Raine 2014). Even though *Karenia* blooms normally correlate with thermally stratified water columns, there was no correlation between the 2006 *K. mikimotoi* bloom and wind speed and direction or temperature, which are main factors affecting water column stability (Davidson et al. 2009).

HABs are frequently associated with upwelling areas that provide nutrient rich water from deeper layers. For example, blooms of *Dinophysis* (Reguera et al. 2012) and *Pseudo-nitzschia* (Palma et al. 2010) were found to grow to harmful densities under strong stratification and upwelling conditions on the Iberian shelf. However, stronger upwelling does not necessarily result in more intense blooms, possibly due to turbulence and dispersion (Palma et al. 2010). Indeed, decreasing intensity of upwelling, causing an increase in flushing time, was linked to an increase in HABs on the Iberian shelf (Pitcher et al. 2010). An exceptional *D. acuminata* bloom in 2012 in the Bay of Biscay might be linked to an unusual wind and temperature regime (Diaz et al. 2013); a warm winter causing stratification followed by upwelling could have facilitated an unusually early bloom formation. Interestingly, the early initialisation of the bloom was followed by an early bloom decline under good growth conditions, potentially indicating a biological clock (Diaz et al. 2013). In the region of the Galician Rias Baixas, blooms were favoured by periods of upwelling, followed by a downwelling period (Velo-Surez et al. 2014).

Another environmental driver often associated with HAB development is nutrient availability and, for mixotrophs and heterotrophs, prey availability. The *K. mikimotoi* bloom in 1980 in the Firth of Clyde followed a period of heavy rainfall which might have increased nutrient input via land runoff and riverine input (Jones et al. 1982). The *K. mikimotoi* bloom in 2006, however, was negatively correlated to rainfall, possibly due to increase disturbance without increase in nutrients (Davidson et al. 2009). For the heterotrophic harmful genus *Dinophysis*, the presence and the size of prey may be an important factor for bloom development. However, lack of knowledge and difficulties identifying prey species makes predictions based on prey difficult (Velo-Surez et al. 2014).

HABs often display rapid growth, followed by rapid termination of the bloom. The reasons for the termination of HABs and other phytoplankton blooms are often
unknown. For example, during a *Dinophysis* bloom parasitic dinoflagellates were
found prior to bloom decline, indicating a biological bloom control. However, 70% of
cells at end of bloom were viable which suggests that parasites cannot fully explain
the rapid bloom decline (Velo-Surez et al. 2014). During other *Dinophysis* blooms
the cell maximum sunk to a greater depth by the end of a bloom which might be part
of their natural life cycle and might indicate overwintering cells or physical forcing
(Escalera et al. 2012). On the other hand, the density maxima of *D. acuta* shallowed
over winter which could be explained by higher light availability in shallower water
(Escalera et al. 2006) or prey availability.

In summary, there are several published case studies linking HAB events to the
environmental conditions surrounding them in European waters. However, base-
line knowledge about phytoplankton community on the west Scottish shelf sea and
adjacent areas is poor. This is necessary to study presence and distribution of po-
tentially harmful phytoplankton in the area. Such baseline knowledge would allow
a better understanding of the link between environmental changes and HAB oc-
currence in the North West European Shelf seas. This fundamental knowledge is
provided as part of this thesis from fieldwork undertaken in the area (chapter 2 to
4). Phytoplankton data was collected together with environmental data to explore
links between harmful phytoplankton occurrence and possible environmental drivers
with a high resolution data collection near potentially important physical features
such as the shelf break, the ESC and seasonal fronts on the Malin shelf.

1.4 Advection of harmful phytoplankton

Once established, a bloom can be advected to different locations by tides or currents.
The *K. mikimotoi* bloom in 2006, for example, was first found at the West Scottish
cost, moving clockwise around the coast up to Orkney and Shetland (Figure 1.3).
Rapid increase of cells at sampling sites suggested that blooms reached high densities
by advection of cells rather than *in situ* growth alone. However, the time needed
for passive particles to travel along the SCC did not match with the time the bloom
needed to travel between stations (Davidson et al. 2009). Even though there might
be some influence from the ESC evidence suggests that biological growth or physical
accumulation at bloom sites play a major role in explaining the observed pattern
(Davidson et al. 2009).

In Irish waters *K. mikimotoi* blooms frequently develop offshore before being
transported to coastal areas (Raine et al. 1993). In summer 1991 high temperatures
led to stratification and a *K. mikimotoi* bloom developed at an offshore tidal front.
Subsequent onshore advection was either caused by upwelling relaxation and onshore
flow or by direct wind forcing by onshore winds (Raine et al. 1993). Similarly, *K.*
Figure 1.3: Peak and timing of cell concentrations at sampling sites around the Scottish coast during an extensive *K. mikimotoi* bloom in 2006 (Davidson et al. 2009).
mikimotoi developed at an offshore front in 2004 in West Indian waters (Robin et al. 2013) before it was transported to coastal waters. Bloom formation was linked to a period of strong thermal stratification followed by persistent on shore directed winds, transporting cells onshore. Noticeably, wind speed was found to be very low, allowing blooms to be transported without causing a high turbulent regime (Robin et al. 2013).

In the Iberian shelf region *Dinophysis* blooms established in the southern Region of Aveiro under good stratification and upwelling conditions in late summer 2005 (Escalera et al. 2010). A sharp decline in cells in Aveiro was followed by an increase in the Ria Vigo, north of Aveiro, during transition from upwelling to downwelling conditions (Figure 1.4). During the bloom in the Ria Vigo cell division rates were low and cell densities could not be explained by in situ growth and advection from adjacent shelf seas only accounted for a small percentage of the observed cell numbers, strongly suggesting influx of cells from the Aveiro region. Moreover, the two week delay between peaks in Aveiro and Ria Vigo agreed with the calculated time needed for particles to travel between the two locations. Similarly, Batifoulier et al. (2013) found that high densities of *Dinophysis* in Arachon Bay, Bay of Biscay, are advected from sites further south where the bloom developed under good growth conditions.

Advection of potentially toxic *Pseudo-nitzschia* blooms is well studied around the coast of Washington State (Adams et al. 2006, Trainer et al. 2002, Horner et al. 2000). Blooms occur frequently in the Juan de Fuco eddy and other smaller eddies offshore Washington State (Trainer et al. 2002). There is an apparent relationship between offshore development, current direction and bloom progression in the area (Horner et al. 2000). Under upwelling conditions cold, saline and nutrient rich water fuels offshore blooms. Downwelling provides suboptimal growth conditions, however, currents flow onshore and can potentially advect bloom onshore (Horner et al. 2000). Unfortunately, the underlying processes are not completely clear; for example, in 1998 upwelling caused an offshore bloom which was advected towards the shore following a period of downwelling. In the previous year an offshore bloom was initiated by upwelling, but downwelling did not lead to onshore advection. Slight differences in environmental conditions might be responsible for inter-annual variation (Trainer et al. 2002).

A further study showed a link between the Columbia River plume and wind driven onshore advection of *Pseudo-nitzschia* (Adams et al. 2006). A storm with downwelling favouring winds in early September in 2002 caused an advection of offshore *Pseudo-nitzschia* into the Columbia River plume. The plume itself, containing the diatom bloom, was advected towards the Washington coast and reached it in 3-4 days in agreement with the time needed for the plume to travel 160 km. After
a second storm in the subsequence week a *Pseudo-nitzschia* bloom was advected onshore without the expected time delay. This was explained by the plume being retained in the area and reintroduced with the second storm. A third storm, not causing an increase in *Pseudo-nitzschia*, was suspected to not be strong enough to advect the plume to the study location (Adams et al. 2006).

Despite our increasing awareness of the role of advection in HAB transport, bloom prediction based on our knowledge of environmental drivers (chapter 1.3) and advective transport remains challenging. In the North West European Shelf sea, the ESC plays an important role in transport and separation of water masses (Ellett et al. 1986), which is likely to affect phytoplankton distribution (Holt & Proctor 2008, Davidson et al. 2009). However, the role of the ESC in HAB transport is currently poorly studied and therefore addressed as part of this thesis (chapter 2, 5 and 6). There is a high inter-annual variation of speed and strength of the ESC, but the effects of that on bloom dynamics are largely unknown. This is specifically
addressed in chapter 6. Our understanding of the interaction between biological
growth and advective transport is also limited and further addressed in chapters 5
and 7.

1.5 Study methods

1.5.1 Phytoplankton counts and HAB monitoring

Information about species occurrence and community composition is commonly ob-
tained by collecting and preserving water samples and subsequently counting phyto-
plankton cells in the sample. Samples can be taken from coastal stations or on-board
research vessels. Water can be collected at different depths of the water column or
with a depth integrated net haul. Phytoplankton are subsequently fixed with 1% to
5% Lugols solution and analysed using Utermöhl sedimentation Chambers (Fehling
et al. 2012).

Phytoplankton identification is a skilled activity and doing a full species count
can be time consuming. However it is currently the only method to accurately de-
terminate phytoplankton species occurrence and abundance. A continuous plankton
recorder (CPR) can also be used to determine the presence and absence of phyto-
plankton as well as relative changes in abundance (Edwards et al. 2006). However,
this method is limited to the location of fixed CPR tracks and does not provide total
species counts.

Toxin producing phytoplankton species are frequently monitored to avoid hu-
man exposure to toxins. In Scotland, there are about 260 shellfish harvesting sites
and 176 classified production areas. Only about 40 sites are monitored for HABs,
chosen in consideration of geographical location, accessibility and history of harm-
ful phytoplankton occurrence (Swan & Davidson 2011). Sampling frequency varies
from weekly to monthly depending on the species and time of the year. All sampling
sites are currently at coastal locations with no offshore monitoring done in Scotland.
Species that do not pose a direct threat to human health, such as *Phaeocystis* or
*Chaetoceros* are not included in regulatory monitoring.

1.5.2 Chlorophyll a as phytoplankton index and satellite imagery

Measurement of chlorophyll fluorescence is commonly used to study phytoplankton.
Chlorophyll is considered the best optical index for phytoplankton (Huot et al. 2007)
and can be easily measured *in situ* or remotely by satellite sensors.

Chlorophyll fluorescence and real colour images are easily and freely available
from the satellite sensors such as the Sea-viewing Wide Field-of-view Sensor (Sea-
WiFS) or the MOderate resolution Imaging Spectroradiometer (MODIS) that can
provide ocean colour in six and nine spectral bands respectively (Miller et al. 2006).
Due to its availability, large coverage and ease of use, satellite derived chlorophyll is often used to study phytoplankton (see e.g. Joint & Groom 2000, Behrenfeld et al. 2009).

Some obvious limitations of satellite imagery are that the approach is limited by cloud cover and that chlorophyll measurements are limited to the sea surface without the ability to detect sub-surface chlorophyll maxima (e.g. Farrell et al. 2012) or the structure of three-dimensional phytoplankton distribution (Babin et al. 2005, Hemsley et al. 2015, Gregg & Casey 2007). Sediment and non-phytoplankton coloured material can also influence the quality of satellite data, however estimates of absorption and backscatter of light from ocean colour data allows differentiation of signals from phytoplankton from other coloured material to some degree (Smyth et al. 2006).

Individual absorption and backscatter profiles of phytoplankton can allow species differentiation which has been demonstrated in the laboratory for mono cultures of 29 species (Vaillancourt et al. 2004) and is currently being developed for satellite data for harmful species such as *K. mikimotoi* and *Phaeocystis* (Miller et al. 2006, Kurekin et al. 2014).

### 1.5.3 Underwater gliders

An alternative way of collecting chlorophyll data is through the use of remotely controlled underwater vehicles (RUVP) such as underwater gliders. Gliders are capable of diving up to 1000 m and travelling at a speed of approximately 0.1 m s\(^{-1}\). They are driven by small changes in their internal buoyancy, which requires little battery power and allows gliders to be deployed for several month at a time, covering thousands of kilometres. Satellite links allow glider pilots to communicate with the vehicle every time it surfaces. That means data is available in near real time, while changes to diving depth, travel path and frequency of measurements can be altered easily. Gliders are routinely equipped with sensors to measure water temperature, salinity and depth and can be equipped with additional sensors, e.g. to measure current speed and direction or dissolved oxygen concentrations. Such data can give information about water mass origin and transport and has been used in oceanography for decades to study the three-dimensional structure of the water column physical properties (see Eriksen et al. 2001, Davis et al. 2002, Graver 2005 for reviews).

Recently optical sensors have been mounted on gliders with the capacity to provide a high resolution vertical profile of chlorophyll distribution (e.g Davis et al. 2008, Zhao et al. 2013, Seegers et al. 2015). Gliders are suitable to study blooms in detail as they can provide information about the three-dimensional structure of a bloom by sampling multiple sites and depth within an area (Zhao et al. 2013). Such
data, together with routinely collected physical data, can reveal links between short term small scale changes in abiotic factors and phytoplankton response (Frajka-Williams et al. 2009). For example, some harmful species are strongly associated with thermal stratification (Raine 2014). Gliders can be used to study small scale changes in stratification by measuring changes in salinity and temperature; by additionally recording chlorophyll, the response of phytoplankton to such changes can be evaluated.

There are limitations to the use of gliders such as bio-fouling, i.e. the growth of micro or macro organisms on or near the sensors. This can change readings in temperature and salinity, by trapping water in micro environments close to the sensor, but is especially inhibitory to optical sensors that rely on the cleanliness of their surface (English et al. 2009).

Recently gliders have been used successfully in HAB studies (Seegers et al. 2015, Zhao et al. 2013). Glider data was used to reveal the underlying physical mechanism of *Pseudo-nitzschia* bloom formation in southern California (Seegers et al. 2015). The bloom developed in a subsurface layer before accumulating near the surface due to the development of an upwelling system (Seegers et al. 2015). A *Karenia brevis* bloom off the shore of California was also found to develop as a sub surface bloom that would not have been visible from satellite images alone (Zhao et al. 2013).

### 1.6 Modelling

#### 1.6.1 Model frameworks

For HAB management it would be desirable to develop an operational forecast or early warning system for coastal HAB occurrence. For advective species this is likely to require the use of computational models to predict bloom development and transport. For this task coupled bio-physical models are deemed the most realistic; biological behaviour can be modelled by simple growth equations or complex trophic interactions and coupled with a hydrodynamic model providing information about environmental conditions at the study site. The resolution of physical models can be important for the model functioning (Fulton et al. 2003) and lack of knowledge about small scale influences might decrease the model reliability (Hellweger & Bucci 2009).

Phytoplankton dynamics are commonly modelled using either population models (PLM) or individual based models (IBM) as a model framework (Davidson 2014). Choosing the right level of complexity can be difficult; if the model complexity is too low it might be incapable of representing all processes from a natural system. If the model is too complex it might compromise the model efficiency (Fulton et al.


PLMs treat the population of a species or functional group as a whole, continuous field. An eulerian approach is commonly used whereby each grid point of the model domain is assigned a value for the biomass of the population at this point (Hense 2010). The whole population is subjected to the same rate constants for e.g. growth and mortality. This makes it difficult to account for different life stages or adaptation and acclimatisation of different sub-populations with different life histories (Hense 2010, Woods et al. 2005b). Advection can be included in the model equations.

Some of the limitations of PLMs can be overcome by using IBMs. IBMs provide a framework where individuals of a population are treated as discrete units coupled with a Lagrangian framework following individual cells through the fluid motion. Individuals can be modelled with their own set of equations making it easier to include age, size, life-stages, acclimatisation and biofeedback (Hellweger & Bucci 2009). This can be of importance for phytoplankton, e.g. when looking at photoacclimatisation of individual cells leading to different photosynthetic efficiency of the same population due to individual life history (Hellweger & Bucci 2009). Including the age or life cycle of harmful algae might help to explain the rapid growth and decline of HABs; unfortunately, this approach is currently limited by the lack of information about the life cycle of harmful algae (Hense 2010).

Furthermore, in an IBM it is easier to account for internal processes within a cell, e.g. using cell quota kinetics, which is considered more realistic for modelling phytoplankton growth than assuming nutrient uptake and utilisation depends solely on external nutrient availability (Hellweger & Bucci 2009). Equations for biological processes can be defined directly from experimental results and applied to individuals (Woods 2005a). However, IBMs generally need more computational power than PLMs. When simulating phytoplankton which can reach densities of over 1 million cells per litre it can be unfeasible to consider each individual cell. Instead, a fixed number of cells can be modelled as super-individuals or parcels (Hellweger & Bucci 2009). Another limitation is that only including a single species does not allow to explore interspecies interactions and top-down or bottom-up controls of food webs (Fulton et al. 2003).

### 1.6.2 HAB models

There have been multiple attempts to explain and predict HABs. Below a few examples are described, showing recent development in HAB modelling. The examples range from relatively simple predictions of HABs from a few environmental variables (Xie et al. 2007, Raine et al. 2010b) to complex bio-physical PML models (Vanhoutte-Brunier et al. 2008).

*Dinophysis* blooms in the Bay of Biscay (Xie et al. 2007) and the Irish coast
(Raine et al. 2010b) can be, at least to some degree, predicted by using relatively simple models that link environmental factors to HAB likelihood; small scale anticyclonic mid-depth eddies were predicted to retain *Dinophysis* with an accuracy of 41.2% for eddies lasting 1 week and 64.7% for eddies lasting 3 weeks (Xie et al. 2007). Around the Irish coast weather forecasts of wind strength and direction can be used as an index for bloom likelihood (Raine et al. 2010b). Seaward blowing wind carries surface water outwards and cold nutrient rich water inwards. This is followed by a change in wind direction. This leads to influx of warm surface water in bays which can onset a bloom (Raine et al. 2010b). Even though this approach has a good accuracy in summer, predictions are limited to the time span of a reliable weather forecast. The model is relatively simple and consequently cannot give any insight about bloom development and decline or actual cell densities.

Bloom formation of *Pseudo-nitzschia* was also linked to upwelling eddies in the Santa Barbara Channel (Anderson et al. 2006). Cells can grow rapidly in the nutrient rich upwelling water and accumulate in the eddy centre by advection. Growth conditions in the eddy centre are often suboptimal with higher toxin levels per cell as a response to nutrient stress (Anderson et al. 2006). Further advection of the high density of accumulated cells is then directly linked to eddy advection which might lead to further onshore transport of the bloom (Anderson et al. 2006). Absence or presence of *Pseudo-nitzschia* cells in the Santa Barbara Channel was modelled using temperature, nutrients and satellite ocean colour data (Anderson et al. 2006, 2011). The model could identify 98% of *Pseudo-nitzschia* blooms, however, 29% of non *Pseudo-nitzschia* blooms were wrongly identified (Anderson et al. 2011).

Yanagi et al. (1995) used an IBM coupled with a local hydrodynamic model to study the development of a *K. mikimotoi* bloom in the West Seto Sea in Japan. Locations and concentrations for initial populations were estimated from field observations. Initial population are seeded within the hydrodynamic model and are transported across a three dimensional grid as a function of advection, diffusion/dispersal and phototaxis (Yanagi et al. 1995). A set number of cells were treated as parcels or super-individuals. Parcels were associated with a specific growth and mortality formulation. Growth was nutrient dependent with Michaelis-Menten kinetics for nutrient uptake and cell quota equations to model cell growth. Growth was considered independent of temperature and light for the model domain. Mortality was described as a loss term of cell concentration multiplied by a mortality constant obtained from laboratory cultures. The model allowed a quantitative description of the bloom however there was some disagreement with the distribution of high biomass. The initial location of the seed population and an accurate representation of bloom advection was crucial to recreate the bloom pattern (Yanagi et al. 1995)

Biophysical PLMs coupled with local hydrodynamic models were previously
used to recreate harmful bloom events on the French Atlantic coast (Sophie et al. 2001) and the English Channel (Vanhoutte-Brunier et al. 2008). The biological model consists of three functional phytoplankton groups (diatoms, dinoflagellates and nanophytoplankton) and an additional sub compartment for *K. mikimotoi*. Compartments for zooplankton and nutrients were included in the biological model together with benthic-pelagic coupling, allowing the majority of the detritus pool to sink to the benthos where it is re-mineralised and re-suspended to the available nutrient pool (Sophie et al. 2001, Vanhoutte-Brunier et al. 2008).

In the sub-model for *K. mikimotoi* nutrient uptake is modelled using Michaelis-Menten kinetics with no nutrient limitation below 15 m (Sophie et al. 2001, Vanhoutte-Brunier et al. 2008). Field data was used to fit temperature dependent growth to a 3rd order polynomial function whereby growth at temperatures below 13°C is close to zero and optimal between 15 °C and 18 °C. Light dependent growth follows a Michaelis-Menten like curve with no light limitation in the top 20 m. The model assumes no grazing control; mortality is determined by shear stress as increased turbidity (shear) increases the likelihood of cells colliding. After collision cells can stick together due to the production of extracellular polysaccharides which increases both sinking and the risk of autotoxicity. The likelihood of cells aggregating is determined by $\alpha$, the stickiness coefficient, which is temperature dependent. The vertical migration of cells is not included in the model as cells accumulate at the pycnocline with a migratory minimum during stratification.

Both studies attempted to recreate a specific bloom event. The density of modelled blooms was lower than field measurements. This could be due to the lack of representation of fine scale physical processes or an underestimation of the role of nutrient re-mineralisation (Sophie et al. 2001). Bloom initiation was later than the model predicted (Vanhoutte-Brunier et al. 2008) This might be explained the presence of benthic filter feeders in the study area that might delay the bloom due to grazing and increased velocity shear. Observed bloom termination is very abrupt, possibly due to nutrient limitation and self-shading. As density is underestimated in the model, these effects are weakened and the modelled bloom termination is less abrupt than the observation (Vanhoutte-Brunier et al. 2008).

These examples show that phytoplankton models have clearly increased in complexity since the relatively simple Nutrient-Phytoplankton-Zooplankton-Detritus model introduced by (Fasham et al. 1990). Unfortunately, increased complexity also increases the potential of error and issues arise when several unknown factors or poorly understood interactions have to be included (Fulton et al. 2003, Davidson 2014). In some cases it might be appropriate to develop models with a very low model complexity. Lagrangian transport models, for example, can be used to study bloom advection while strongly reducing the biological behaviour of phytoplankton cells.
Recent studies reported success in modelling advection of HABs by using Lagrangian particle transport models that include no biology of phytoplankton and treat HABs as parcels of passive cells (Hai et al. 2010, Dippner et al. 2011, Pinto et al. 2016, Silva et al. 2016, Ruiz-Villarreal et al. 2016).

Recent advancements in HAB forecasting in European coastal waters uses a combination of information of HAB presence at coastal monitoring sites (Silva et al. 2016) or satellite images for high density blooms (Blauw et al. 2010), and forecast of direction and strength of wind and currents. Such approaches can be combined with Lagrangian transport models to predicted likelihood of coastal advection of HABs (Pinto et al. 2016, Ruiz-Villarreal et al. 2016). This forecasting system is limited by the availability of reliable wind and currents forecast which is often limited to three days (Silva et al. 2016). Another potential issue is that excluding any biological behaviour could oversimplify modelling by not permitting crucial biological factors such as cell growth and mortality. In the study area of the North West European shelf sea, changes of wind and current directions were recently linked to HAB occurrence in coastal regions (Whyte et al. 2014). Therefore, it would be desirable to assess the usefulness of a Lagrangian transport model for HAB advection in the area. In chapters 5 to 7 such a model is introduced and discussed with a focus on the importance of biology, model initiation, advective transport and the role of the ESC, inter-annual variations and combining data from field work, remote sensing and modelling.

1.7 Outline of Thesis

Despite the wealth of studies that have addressed HAB development there are still wide gaps in our understanding of biological and physical factors that lead to the development of HABs. For Scotland there is no functional forecast model to explain and predict HABs. The role of major hydrodynamic features such as the shelf break and ESC play in HAB development are still not fully understood. Lack of offshore data also makes early warning difficult.

To address the gaps in our current understanding, the following research questions will be considered within this thesis:
1. What is the role of environmental drivers in structuring phytoplankton communities on the North West European shelf with a focus on potentially important hydrodynamic features such as the shelf edge?
2. What is the role of advection in HAB occurrence and development on the shelf?
3. Can computational models provide information about origin and progression of observed blooms?

The steps that were taken to answer these questions are outlined below.
In chapters 2 and 3 a detailed assessment of phytoplankton community in shelf seas is presented with a high resolution at the shelf break and other hydrodynamic features such as the ESC, Islay front and Irish coastal front. This will provide a much needed update, as the last assessment of the area was done over ten years ago with little focus on hydrodynamic features and no samples taken from the shelf break (Fehling et al. 2012).

In chapter 2, data on water temperature, salinity and nutrients, together with phytoplankton community data was sampled across the Malin and Hebridean Shelves, the shelf break and adjacent oceanic waters during a RRS Discovery cruise in 2014. Multivariate statistical methods were used to study differences in phytoplankton communities between sampling stations. The role of the ESC and shelf break in phytoplankton community separation and transport are discussed.

In chapter 3, phytoplankton and environmental data was collected during a RS Corystes cruise to the Malin Shelf in summer 2015. Phytoplankton distribution was studied at the shelf break and at two salinity fronts that were identified in the study area. Potentially harmful concentrations of *Pseudo-nitzschia* and *Phaeocystis* were found offshore and areas of high biomass were identified. Results from this chapter were compared to the results from chapter 2 in terms of seasonality and inter-annual differences in oceanographic features.

Chapter 4 discusses the results of the first successful attempt in UK waters at using optical data collected during a glider deployment to survey phytoplankton on the Malin shelf. The glider was able to record a high resolution vertical and horizontal dataset, showing the distribution of phytoplankton in relation to small scale physical changes on the Malin shelf. The three dimensional structure and vertical extent of a potentially harmful *Phaeocystis* bloom was recorded, and the benefits and challenges of using gliders in offshore phytoplankton bloom surveillance is discussed.

The next three chapters focus on the development and implementation of a coupled bio-physical model to study advection of high biomass HABs around the Scottish west coast.

In chapter 5, a bio-physical individual based model for *K. mikimotoi* is introduced. The model is coupled with off-line velocity and temperature fields produced from a hydrodynamic open ocean model to study advective transport of cells across the North West European shelf sea. The model was originally run with the hydrodynamic model POLCOMS that was later replaced with NEMO. In this chapter the model is used to explain advective transport and explore the potential origins of high density *K. mikimotoi* blooms in Scottish waters in 2006, 2010 and 2011.

Building on the results of chapter 5, the IBM model is further used to study advection of potential seed populations with a focus on inter-annual variation of
wind and current regimes in chapter 6.

In chapter 7, the biological formulations in the IBM used in chapter 5 and 6 were then altered to model potential pathways of the *Phaeocystis* bloom reported in chapter 3.

The final chapter of this thesis summarises the main findings from previous chapters to address the overall aims of this thesis. Field data from chapters 2, 3 and 4 addressed the first and second aim of this thesis and provided information on links between environmental drivers and phytoplankton distribution on the shelf edge with respect to hydrodynamic features such as density fronts, the ESC and the shelf break. Community similarity was used to draw conclusions of exchange and advection of phytoplankton populations. Modelling data from chapters 5, 6 and 7 addressed the second and third aim of this thesis. Advection was described in the model and results can help explain HAB transport along the Scottish coast. Even though the model does not represent an operational forecast model, it improves our understanding of HAB development and paves the way for further work on model improvement.
2 Phytoplankton distribution in relation to environmental drivers on the west Scottish shelf in autumn

This chapter was published as


2.1 Introduction

Phytoplankton account for roughly half of global primary production (Field et al. 1998) with an estimated 25% of global production taking place in coastal shelf areas, which account for less than 10% area and 0.5% of the total volume of the ocean (Simpson & Sharples 2012). Shelf sea phytoplankton are therefore particularly important for global carbon cycling (Muller-Karger et al. 2005) and also form the base of coastal marine food webs underpinning coastal fisheries and aquaculture (Frederiksen et al. 2006). Coastal blooms of harmful phytoplankton species also pose a threat to fishing and aquaculture industries as well as to tourism and human health (Davidson et al. 2011, Berdalet et al. 2016). The EU Marine Strategy Framework Directive (MSFD) requires member states to assess if their plankton communities achieve Good Environmental Status by 2020. Thus there is an increasing requirement to understand the diversity dynamics of phytoplankton communities in all areas of the North West European Shelf (NWES) and how these relate to environmental conditions (Gowen et al. 2011).

Topographic features such as the shelf edge may play a key role in stimulating phytoplankton production through their generation of mixing (Sharples et al. 2009, Davidson et al. 2013). In N.W. European waters the 200 m deep continental shelf and adjacent oceanic waters are separated at the shelf break by a steep slope, alongside which the European Slope Current (ESC) is steered. While the ESC and shelf break inhibit direct oceanic-shelf water interactions (Ellett et al. 1986), chlorophyll fluorescence measurements suggest that this boundary condition can provide optimal growth conditions for phytoplankton (Holligan 1981).

Despite its importance, phytoplankton distribution across the NWES seas are relatively poorly studied in comparison to the hydrography of the area (Ellett et al. 1986, Proctor et al. 2003, Inall et al. 2009), particularly the region west of Scotland. The few existing studies conducted in this location have generally found different phytoplankton communities on the shelf compared to adjacent oceanic waters (Savidge & Lennon 1987, Gowen et al. 1998, Fehling et al. 2012); diatoms and
larger dinoflagellates (>20 \mu m), were dominant on the shelf, while dinoflagellates were dominant off shelf (Savidge & Lennon 1987, Fehling et al. 2012). An exception to that was the diatom Chaetoceros, which was found to be dominant off shelf in spring (Savidge & Lennon 1987) and summer (Gowen et al. 1998), implying there are also important seasonal factors to consider. For example, during spring and summer, phytoplankton communities were structured by different levels of stratification and mixing between the shelf break and thermal or salinity fronts (Savidge & Lennon 1987, Gowen et al. 1998). In contrast, during autumn weakened stratification, increased nutrient availability and stronger mixing caused by seasonal winds and stronger heat loss to the atmosphere were considered to be a major driving force underlying differences in phytoplankton communities (Fehling et al. 2012).

Even the most recent of the above studies was based on observations collected over a decade ago from a single transect comparing shelf and oceanic stations with no data collected near the shelf edge (Fehling et al. 2012). This study is the first to compare data from multiple cross shelf transects with data collected from the potentially important shelf edge. This study will give a novel insight about differences and similarities of phytoplankton communities on both latitudinal and longitudinal gradients in the NWES. The aim of the study is to draw conclusions of the structuring forces and environmental drivers of phytoplankton occurrence on the Malin and Hebridean shelves and to provide some much needed baseline data for the MSFD. This was achieved through a systematic set of transects that sampled phytoplankton and environmental data from the shelf, shelf break, and oceanic water across a range of different latitudes on the NWES. Understanding phytoplankton dynamics and their environmental controls is crucial to allow further work on the effect of environmental changes on the biological carbon pump provided by phytoplankton. Moreover, information on the connectivity and separation of phytoplankton on the shelf edge can be used to support modelling work on advection of harmful phytoplankton in the area.

### 2.2 Methods

Samples were collected on seven cross-shelf transects across the shelf edge during RRS Discovery cruise DY017 to the Hebridean (A1, B1, transect C-D) and the Malin (transect E-G) Shelves between the 23rd October 2014 and 3rd November 2014 (Figure 2.1). Weather conditions were stormy prior to and during the cruise inhibiting sampling at some of the planned stations. A total of 17 sites were sampled, including seven shelf, five shelf break and five off shelf stations (Table 2.1).

Densities of microphytoplankton in Niskin bottle samples were below the detection limit in 50 ml Utermöhl method microscopy analysis. Phytoplankton abundance
Figure 2.1: Cruise track and sampling sites of the RRS Discovery cruise DY017 to the N.W. European shelf break. Full details of stations where net samples were taken are given in Table 2.1.

Data presented is therefore based on cells collected via a 20 μm phytoplankton net haul to the bottom of the mixed layer depth which varied between 50 m and 100 m at each station (Figure 2.1, Gowen et al. 1998). The total volume of filtered seawater was calculated as the volume of a cylinder: Volume = \( \pi \times r^2 \times h \) with \( r \) being the radius of the net opening and \( h \) the depth of the net haul. Net collected samples were stored in 60 ml brown plastic bottles rinsed with seawater. Samples were immediately fixed with 1 ml acidic Lugol’s Iodine solution and subsequently
settled for at least 22 hours at room temperature in 10 ml or 25 ml settling chambers. Cells were identified under 200x magnification using a Zeiss Axiovert 100 inverted light microscope. Species counts from net hauls were divided by the filtered volume and calculated as cells per litre to account for different depth sampled by the haul. Species and genera present at greater than 1 cell l$^{-1}$ $\times 10^2$ were *Tripos furca*, *T. fusus*, other *Tripos* spp., *Prorocentrum* spp., *Dinophysis* spp. and *Pseudo-nitzschia* spp. (N.B. we used the current taxonomic convention for describing species formally recognised as belonging to the *Ceratium* genus; (Lee et al. 2014)). Cell counts were calculated as cells l$^{-1}$ to account for differences in the total sampled volume. Phytoplankton cell densities were found to be very low at the time of the study, with an average of 8 phytoplankton cells per litre. This was consistent with the low number of phytoplankton cells found in Niskin bottle samples. Cell counts were fourth root transformed prior to statistical analysis to down weight high species abundance (Fehling et al. 2012).

Table 2.1: Details of stations where net samples were taken and maximum depth for each net tow.

<table>
<thead>
<tr>
<th>Station</th>
<th>Position</th>
<th>Date</th>
<th>Time</th>
<th>Water depth (m)</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Depth of net tow (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1</td>
<td>Shelf</td>
<td>23.10.14</td>
<td>11:06</td>
<td>105</td>
<td>58.60</td>
<td>-5.80</td>
<td>50</td>
</tr>
<tr>
<td>B1</td>
<td>Shelf</td>
<td>27.10.14</td>
<td>03:52</td>
<td>75</td>
<td>58.44</td>
<td>-7.19</td>
<td>50</td>
</tr>
<tr>
<td>C1</td>
<td>Shelf</td>
<td>27.10.14</td>
<td>10:00</td>
<td>75</td>
<td>58.02</td>
<td>-7.71</td>
<td>70</td>
</tr>
<tr>
<td>C4</td>
<td>Shelf break</td>
<td>27.10.14</td>
<td>22:08</td>
<td>190</td>
<td>58.22</td>
<td>-8.83</td>
<td>100</td>
</tr>
<tr>
<td>C7</td>
<td>Oceanic</td>
<td>28.10.14</td>
<td>21:24</td>
<td>1860</td>
<td>58.43</td>
<td>-10.07</td>
<td>100</td>
</tr>
<tr>
<td>D5</td>
<td>Oceanic</td>
<td>29.10.14</td>
<td>05:13</td>
<td>955</td>
<td>57.62</td>
<td>-9.70</td>
<td>80</td>
</tr>
<tr>
<td>D4</td>
<td>Shelf break</td>
<td>29.10.14</td>
<td>10:13</td>
<td>190</td>
<td>57.61</td>
<td>-9.38</td>
<td>60</td>
</tr>
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<td>D1</td>
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<td>115</td>
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<td>-8.18</td>
<td>100</td>
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<td>30.10.14</td>
<td>08:51</td>
<td>130</td>
<td>56.87</td>
<td>-8.18</td>
<td>60</td>
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<tr>
<td>E3</td>
<td>Shelf break</td>
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<td>17:07</td>
<td>190</td>
<td>56.86</td>
<td>-9.05</td>
<td>50</td>
</tr>
<tr>
<td>E5</td>
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<td>31.10.14</td>
<td>13:45</td>
<td>1850</td>
<td>56.87</td>
<td>-9.70</td>
<td>70</td>
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<tr>
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<td>Oceanic</td>
<td>01.11.14</td>
<td>18:12</td>
<td>1980</td>
<td>56.12</td>
<td>-10.09</td>
<td>100</td>
</tr>
<tr>
<td>F4</td>
<td>Shelf break</td>
<td>02.11.14</td>
<td>06:26</td>
<td>185</td>
<td>56.11</td>
<td>-9.17</td>
<td>50</td>
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<tr>
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<td>17:46</td>
<td>100</td>
<td>56.11</td>
<td>-8.10</td>
<td>80</td>
</tr>
<tr>
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<td>23:52</td>
<td>60</td>
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<tr>
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<td>190</td>
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<td>70</td>
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<td>17:36</td>
<td>1125</td>
<td>55.36</td>
<td>-10.10</td>
<td>100</td>
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</tbody>
</table>

Data on chlorophyll fluorescence, turbidity, light attenuation, temperature, salinity and density were collected *in situ* during CTD casts. Chlorophyll was measured from three different depths at each station by filtering 500 ml through a 47 mm glass fibre filter (Whatman GF/F). Filters were stored in the dark at -20 °C prior to extraction. Filters were thawed overnight in the dark with 8 ml of 90% acetone at 4 °C and subsequently sonicated for 1 min and centrifuged for 5 min at 3000 rpm. Chlorophyll a was measured with a Turner trilogy fluorometer. The fluorometer was calibrated using a chlorophyll a standard (spinach extract) at concentrations
from 1 to 5 µg l⁻¹, verified using a scanning spectrophotometer (Nicolet evolution 300, Thermo Electron Corporation, Cambridge, UK). Chlorophyll measurements were used to calibrate CTD fluorescence for chlorophyll using the linear relationship Chlorophyll = 0.14225 + 0.710× Fluorescence (p < 0.001) that was evident between measured chlorophyll and CTD fluorescence.

Samples for nitrate, silicate and phosphate concentrations were collected from Niskin bottle deployments associated with the CTD casts and measured on board using a Skalar San+ segmented flow autoanalyser following methods described by Kirkwood (1996). Environmental data were standardised using Wisconsin double standardization as the data were recorded in different units and would not be comparable otherwise (Everitt & Hothorn 2011, Oksanen 2014). Moreover environmental data was averaged over the depth sampled by the parallel phytoplankton net deployment to provide average values for environmental parameters in the mixed surface layer.

Analysis of Similarity (ANOSIM) was calculated using the MATLAB toolbox fathom. All other analyses were undertaken in R using the packages vegan and MASS. Non-metric multidimensional scaling (nMDS) and principal component analysis (PCA) were used for biological and environmental data respectively. Environmental data was then fitted to the biological ordination using the R vegan function envfit(), calculating r² to assess the goodness of fit for a linear model (Oksanen et al. 2013).

2.3 Results
2.3.1 Overview
Due to a large number of data points during depth profiling the average value for the top 20 meters for CTD data and top 50 meters for nutrient data is presented to allow a comparison of the surface waters between sites (Figure 2.2). The surface salinity at shelf stations varied from 34.73 (A1) to 35.25 (D1) but had a narrower range of 35.32 to 35.35 at all shelf break and oceanic stations (Figure 2.2 a). The highest recorded surface temperature was 12.8 °C at the southernmost shelf station G1 and temperature decreased both northwards on shelf and westwards towards oceanic stations with the minimum recorded surface temperature of 11.6 °C measured at the north-westerly oceanic station C7 (Figure 2.2 b). Average density of the top 20 m was highest (1026.98 kg m⁻³) in the cool, saline water at the shelf break and oceanic waters. Water densities were lower in the less saline shelf waters and the warmer waters in the south of the study area (Figure 2.2 c). Nitrate and phosphate distribution displayed the reversed pattern to temperature, being highest in the north and along the shelf break (Figure 2.2 d, f). Silicate concentrations were also
Figure 2.2: Average surface concentration of the top 20 m for (a) salinity, (b) water temperature, (c) density, and for the top 50 m for (d) nitrate, (e) silicate, (f) phosphate, and (g) chlorophyll from fluorescence.
highest in the northernmost stations but concentrations were generally patchy over much of the shelf (Figure 2.2 e). The pattern of surface chlorophyll fluorescence did not coincide with any of the nutrient distributions with highest fluorescence at stations E3 and E5 and lowest values for station C4 (Figure 2.2 g).

The different water masses present in the study area can be best identified from their salinity and temperature properties (Figure 2.3). Shelf stations had characteristic water properties with lower salinities and higher temperature (Figure 2.3 a, box 1). The highest salinities were found at shelf break stations and the top 200 m of oceanic stations. Stations C7, D4, D5, E3, E5, F4, G5 and G6 had an increased salinity over 35.4 psu, which is characteristic for the ESC (Figure 2.3 a, box 2, Figure 2.3 b Souza et al. 2001). Shelf break station C4 and oceanic station F6 are located east and west of the slope current respectively. Waters below 200 m at oceanic stations revealed evidence of several different water masses. Water below the high salinity waters of the ESC showed characteristics of the East North Atlantic Water with water temperature ranging from 8 °C to 10 °C and salinity from 35.22 to 35.53. At an intermediate depth between 600 and 1200 m Wyville Thomson Overflow water flowing into the region from the north and gradually mixed with the deep Labrador Sea water entering from the south, with characteristically low water temperatures below 4 °C and salinities around 34.9 (Johnson et al. 2013, Figure 2.3 a, box 3).

Species counts at station C4 were at least an order of magnitude lower than for other stations, with less than 1 cell l$^{-1}$, while station G1 had the highest cell count with 18 cells l$^{-1}$ (Table 2.2). *Tripos fusus*, followed by *Tripos furca*, were the most abundant species and both were present in all samples together with other *Tripos* spp. (Table 2.2). *Dinophysis*, *Pseudo-nitzschia* and *Prorocentrum* were less numerous and present in all shelf stations but were absent or rare (less than 1 cell l$^{-1}$) in shelf break and oceanic stations (Table 2.2).
Figure 2.3: Water temperature and salinity diagram with isopycnals as dotted lines of (a) all stations. Box 1 shelf water, box 2 surface water for shelf break and oceanic stations, box 3 water below 200 m at oceanic stations. (b) Shelf break stations and top 200 m of oceanic stations.
Table 2.2: Cells l⁻¹ x 10² and percentage of the genera/species present at each station (St).

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2.3.2 Shelf environment and associated phytoplankton

Based on the hydrography and topography at sampling locations, stations were divided into shelf (between 80 m and 120 m depth), shelf break (around 200 m depth) and oceanic stations (1000 m to 2000 m depth). Density indicated that shelf stations were well mixed with the exception of E1, where density increased with depth (Figure 2.4 c). Salinity was lowest throughout the water column at station A1 (34.9) and highest at stations D1, E1 and F1 (Figure 2.4 a). Water temperature increased from around 12.1 °C at the northern stations to 12.9 °C at the southern station G1. Temperature for the stratified station E1 decreases from 12.7 °C at the surface to 11.5 °C below 120 m (Figure 2.4 b, c). Nutrient concentrations and chlorophyll fluorescence showed opposing trends (Figure 2.4 d-g); throughout the water column for all stations, except station E1, chlorophyll fluorescence was constant around 0.2 to 0.3 µg l⁻¹ and nutrients were lowest with 2 to 4 mmol N m⁻³, 1.4 to 2.3 mmol Si m⁻³ and 0.3 to 0.4 mmol P m⁻³. As chlorophyll fluorescence decreased to near zero below 80 m at station E1, nutrient concentrations increased to 8.8 mmol N m⁻³, 3.5 mmol Si m⁻³ and 0.6 mmol P m⁻³ (Figure 2.4 d-g).

All identified phytoplankton species were found at all shelf station, however, the dominant species/genus changed along the north-south gradient (Table 2.2).
Figure 2.4: Contour plots for on shelf stations (whole water depth) for (a) salinity, (b) water temperature, (c) density, and (d) nitrate, (e) silicate, (f) phosphate and (g) chlorophyll from fluorescence.
Prorocentrum was dominant in the northern shelf stations, making up to 50% and 34% of the population at station A1 and B1 respectively, but decreased rapidly to less than 1% at G1 in the south. T. fusus showed the opposite trend, accounting for 5% at A1 but being the most dominant species at the southern stations F1 and G1. At stations C1, D1 and E1 other Tripos species were most dominant. T. furca decreased from around 10% at northern stations to nearly zero (0.1%) at station G1. The pattern for Pseudo-nitzschia was less clear and varied between 3% at station D1 and 37% at station G1. Dinophysis had the overall lowest presence representing 11% of the community at station A1 and 3% at station D1 (Table 2.2).

2.3.3 Shelf break environment and associated phytoplankton

At shelf break stations salinity, water temperature and density profiles suggested a surface mixed layer to a depth of 60 to 100 m (Figure 2.5 a–d). The high salinity core with salinities over 35.4 which is characteristically from the slope current was found below 50 m at stations D4 to G5. Station C4 was the only shelf break station to not reach salinities over 35.4, indicating that the station was located east of the slope current. Station C4 also displayed the lowest water temperatures and deepest mixing depth compared to other stations, which might be linked to its position outside the ESC and the lack of stratification caused by salinity. Both surface and deep water temperatures increased with decreasing latitude. Nutrient concentrations (Figure 2.5 d-f) were low throughout the surface mixed layer with concentrations of 3.8 mmol N m\(^{-3}\), 0.8 mmol Si m\(^{-3}\) and 0.3 mmol P m\(^{-3}\), but concentrations rapidly increased below the mixed layer depth to 12.8 mmol N m\(^{-3}\), 4.6 mmol Si m\(^{-3}\) and 0.8 mmol P m\(^{-3}\). Chlorophyll fluorescence was between 0.13 and 0.32 \(\mu g\) l\(^{-1}\) in the surface layer, without any visible maxima, and declined rapidly to near zero concentrations at depth (Figure 2.5 g). The phytoplankton assemblage was dominated by Tripos with an average of 0.4% of phytoplankton accounted for by non Tripos cells (Table 2.2). T. fusus was the dominant species at all shelf break stations and accounted for an average of 56% of cells in the sample, followed by T. furca (29%, Table 2.2).
Figure 2.5: Contour plots for shelf break stations (whole water depth) for (a) salinity, (b) water temperature, (c) density, (d) nitrate, (e) silicate, (f) phosphate, and (g) chlorophyll from fluorescence.
2.3.4 Oceanic environment and associated phytoplankton

The water depth at oceanic stations varied between 1000 and 2000 m (Figure 2.6 h). Similar to shelf break stations, a surface mixed layer depth of 60 to 100 m was evident from salinity, water temperature and density profiles at oceanic stations (Figure 2.6 a-d). Increased salinities below 100 m indicated that the path of the slope current included all oceanic stations except F6 that lay west of the slope current (Figure 2.6 a, Figure 2.1). Nutrient concentrations were similar to shelf break stations with low concentrations throughout the surface mixed layer of 2.8 mmol N m\(^{-3}\), 0.4 mmol Si m\(^{-3}\) and 0.3 mmol P m\(^{-3}\), and increased concentrations of up to 12.2 mmol N m\(^{-3}\), 4.3 mmol Si m\(^{-3}\) and 0.8 mmol P m\(^{-3}\) below the mixed layer depth (Figure 2.6 d-f). The phytoplankton community was similar to shelf break stations with \textit{T. fusus} being the most common species accounting for an average of 51\% of cells in each station, followed by \textit{T. furca} which accounted for 36\% of cells (Table 2.2). The remaining percentage consisted of mainly other \textit{Tripos} with less than 0.1\% accounted for by non \textit{Tripos} cells (Table 2.2).
Figure 2.6: Contour plots for oceanic stations (top 250 m) for (a) salinity, (b) water temperature, (c) density, (d) nitrate, (e) silicate, (f) phosphate, (g) chlorophyll from fluorescence and (h) water depth.
2.3.5 Intra-regional variability

Phytoplankton community at the shelf, shelf break and oceanic sites were significantly different (ANOSIM, p = 0.001, r =0.5481). Shelf stations were significantly different to shelf break stations (ANOSIM, p = 0.001, r =0.6793) and oceanic stations (ANOSIM, p = 0.001, r =0.9779) while shelf break and oceanic stations were not significantly different to one another (ANOSIM, p = 0.25, r =0.0720). Different grouping was visualised by a dendrogram of the Bray-Curtis distance (Figure 2.7) and non-metric multidimensional scaling (nMDS) of phytoplankton counts (Figure 2.8). In the nMDS diagram increasing distance between sites represents higher dissimilarities between the species composition at each site (Figure 2.8).

All stations displayed an average of around 50% dissimilarity (Figure 2.7) but shelf break and oceanic stations were no more than 35% dissimilar to each other with the exception of station C4, which was the most dissimilar of any sampled station (Figure 2.7, Figure 2.8). Ordination of shelf stations showed a stronger response to the north-south gradient than to the cross-shelf gradient between shelf and shelf break/oceanic stations. Around 20% dissimilarity were observed between northern stations A1-D1 and southern stations E1-G1 with the northernmost station A1 being the least similar to the southernmost station G1 within the on shelf group (Figure 8).

![Figure 2.7: Dendrogram of the average Bray-Curtis distance between sites and site groupings based on phytoplankton count data (S = shelf, SB = shelf break, OC = oceanic station).](image)

Based on their physical (salinity, water temperature, density) and chemical (nitrate, phosphate, silicate) properties there was no statistically significant difference
Figure 2.8: Non-metric multidimensional scaling (nMDS) ordination of fourth root transformed species data at each site sampled during cruise DY017 to the N.W. European shelf. The stress is 0.036 indicating that ordination is representative of real patterns rather than randomness in the data. (Triangle = oceanic stations, circle = shelf break stations, diamond = shelf stations).
between groups (ANOSIM, \( p = 0.29, r = -0.06 \)) with all sites being no more than 20% dissimilar (Figure 2.9, Figure 2.10). However, the similarity analysis indicated a grouping of shelf stations and a separate grouping of the remaining stations with the exception of G5 (grouped with shelf stations) and D1 (grouped with oceanic/shelf break stations) (Figure 2.9). Increasing distance between sites in the PCA plot represents higher dissimilarity in the chemical and physical properties of the site. A total of 86.88% of variance in the data could be explained by the two dimensional representation. 59.47% of it was explained by the principal component 1 (PC1). Shelf stations were separated from other stations along the PC1 axis with all shelf stations (including G5) having a negative PC1 value while all other sites had a positive PC1 value (Figure 2.10). An additional 27.42% of the variance in the data was explained by the principal component 2 (PC2). Along the PC2 axis the north-south gradient was visualised with northern transects A-D having a negative PC2 value and southern transects E-G having positive or close to zero PC2 values Figure 2.10).

![Figure 2.9: Dendrogram of the average Bray-Curtis distance between sites and site groupings based on environmental data (S = shelf, SB = shelf break, OC = oceanic station).](image)

Vectors of environmental variable were fitted to the nMDS ordination of phytoplankton data to visualise the relationship between environmental data and phytoplankton composition and distribution (Figure 2.11). The length of the environmental vector is proportional to the correlation between the environmental factor and the phytoplankton ordination. The arrow indicates the direction towards which the environmental variable increases (Figure 2.11). The significance of the relation between an environmental driver and the phytoplankton ordination is determined by
Figure 2.10: Principal component analysis (PCA) ordination of Wisconsin standardised environmental data at each site sampled. (Triangle = oceanic stations, circle = shelf break stations, diamond = shelf stations).

calculating their goodness of fit ($r^2$) and their p-value (Table 2.3). Turbidity, nitrate and phosphate concentrations, the nitrate to phosphate ratio and light attenuation had a statistically significant relation to phytoplankton community structure (Figure 2.11, Table 2.3). Turbidity and light attenuation were highest on the shelf while nitrate, phosphate and the nitrate to phosphate ratio were highest at oceanic and shelf break stations. Turbidity was also higher in northern shelf stations than southern shelf stations, opposite to light attenuation. However, the difference between shelf and oceanic stations was higher for turbidity than for light attenuation.
Figure 2.11: Vectors of environmental factors plotted on the nMDS ordination of species composition indicating the relation between environmental factors and species composition. The value of an environmental factor increases towards the direction of the arrow while significance is indicated by arrow length (Tur = Turbidity, Att = light attenuation, Temp = temperature, S = salinity, D = density, NO3 = nitrate, PO4 = phosphate, Si = silicate, N.Ph = nitrate to phosphate ratio, N.Si = Nitrate to silicate ratio).
Table 2.3: Environmental factors ordered the by significance of their relationship to dataphytoplankton ordination, with $r^2$ value for goodness of fit and their significance, with $p$ being significant for $p < 0.05$.

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2.4 Discussion

2.4.1 Hydrodynamics

The ESC flows along the steep continental slope between 200 m and 2000 m depth and is characterised by a high salinity core with salinities over 35.36 (Hill & Mitchelson-Jacob 1993). In this study salinities higher than 35.4 were detected at stations C7, D4, D5, E3, E5, F4, G5 and G6 (Figure 2.3). Stations C4 and F6, with salinities generally below 35.4, were located to the east and west of the slope current respectively. Station F6 was 2000 m deep with the 2000 m isobaths indicating the end of the continental slope. Station C4 was located at 200 m, the same approximate depth as the shelf break stations, however, drifters released along the continental slope showed dispersion of the ESC towards deeper waters around this location due to its irregular bathymetry (Burrows & Thorpe 1999). Shelf stations were located east of the slope current with salinities below 35.32, caused in part by terrestrial fresh water input. Lower temperatures at shelf break and oceanic stations are most likely caused by heat loss to deeper waters as stratification weakens over autumn.

The ESC is considered to act as a boundary between the shelf and oceanic water with limited water exchange from wind driven surface eddies (Ellett et al. 1986). However, increased cross shelf water exchange can often be found when the bottom slope increases, causing leakage of high salinity slope water onto the shelf (Hill 1995). Such leakage can potentially transport oceanic phytoplankton into shelf waters (Gowen et al. 1982). Recent model studies also suggested that intrusion from slope current water might provide a seed population for harmful phytoplankton to the shelf (Gillibrand et al. 2016). In this study shelf stations had distinctly low salinities, giving no indication of cross shelf edge exchange despite
strong seasonal winds. Phytoplankton communities were also significantly different at shelf stations compared to shelf break and oceanic stations, suggesting that there was little exchange of phytoplankton during the study period (Figure 2.7, Figure 2.8). The potentially toxin producing genera Dinophysis and Pseudo-nitzschia were found in much higher numbers at shelf sites than sites within the ESC suggesting that the ESC did not provide a seed population of harmful phytoplankton to the shelf during the study period. Phytoplankton at station F6 were very similar to other oceanic and shelf break stations despite being west of the slope current. The phytoplankton community at C4 was most dissimilar to other shelf break and oceanic stations, but also exhibited little similarity the shelf stations indicating a different, but unknown, structuring factor at this site.

The ESC and parallel running coastal currents are known to play an important role in the transport of phytoplankton; e.g. a potentially harmful patch of Dinophysis was observed to travel with the same speed and direction as the jet like coastal current along southwest Ireland (Farrell et al. 2012), while a major bloom of the fish killing Karenia mikimotoi is thought to have been advected northwards along the west Scottish coast (Gillibrand et al. 2016, Davidson et al. 2009). In this study nMDS of phytoplankton showed that northern and southern shelf stations were about 20% dissimilar, suggesting that limited connectivity between stations allowed for the formation of different communities along the latitudinal gradient. However northern and southern shelf stations were still more similar to each other than to shelf break/oceanic stations. This suggests there was a higher degree of connectivity and exchange of phytoplankton on the south to north gradient on the shelf than along the longitudinal gradient. In contrast, there was no latitudinal gradient in the community similarity index for shelf break or oceanic stations, which suggests a stronger exchange of phytoplankton along the shelf edge by the slope current.

2.4.2 Phytoplankton counts and chlorophyll fluorescence

Phytoplankton communities were significantly different in terms of species composition, richness and abundance between shelf stations and shelf break/oceanic stations (Figure 2.7, Figure 2.8). Diatoms exhibited their maximum abundance on the shelf as previously found on the Malin shelf in spring and summer (Savidge & Lennon 1987) and autumn (Fehling et al. 2012). However, in contrast to previous studies, dinoflagellates were more numerous than diatoms on the shelf (Table 2.2). Phytoplankton blooms are often characterised by an early diatom dominance which is replaced by dinoflagellate dominance in later bloom stages. In this study, samples were taken in late autumn and dinoflagellate dominance together with generally low cell numbers suggested that samples were taken at the end stages of the autumn bloom or after bloom termination. At shelf break and oceanic stations diatoms were
absent or accounted for less than 3% of the total species count. Dinoflagellates were previously found to dominate oceanic waters adjacent to the shelf, however, some diatoms were also found more numerous at oceanic stations (Savidge & Lennon 1987, Fehling et al. 2012). Here, the dinoflagellate *Tripos* dominated all oceanic and shelf break stations while shelf stations supported a greater diversity with *Prorocentrum* spp. dominant at one station and *Dinophysis* spp. present at all shelf stations. The potentially toxin producing genera *Dinophysis* and *Pseudo-nitzschia* were found in low cell concentrations and might not pose an immediate threat to human health. Even low cell numbers can provide a seed population for subsequent development of harmful blooms once growth conditions improve as suggested by Raine (2004) and Davidson et al. (2009), although this is less likely in the late autumn conditions of this study.

All species identified in this study are common members of the phytoplankton community at the Malin and Hebridean Shelves (Savidge & Lennon 1987, Fehling et al. 2012, Johns 2015). Continuous Plankton Recorder (CPR) data from tracks at the northern edge of the study area suggest that *Tripos* often reach their maximum numbers in autumn (Johns 2015). While Hinder et al. (2012) found that dinoflagellates generally declined in abundance in the North East Atlantic with *Tripos* and *Prorocentrum* having declined noticeably in the early 2000s compared to previous decades, our results are in accordance with Johns (2015) who found *Tripos* to be the dominant genus in late October 2014.

Under good growth conditions phytoplankton can form early autumn blooms. Chlorophyll concentrations of 2.3 µg l\(^{-1}\) were reported on the Malin Shelf by Fehling et al. (2012), which is about 10 times higher than chlorophyll concentrations recorded in this study. Our values are however consistent with other studies, for example, a late autumn bloom in November 1985 on the Armorican and Celtic shelves caused by sunny and calm conditions reached chlorophyll concentrations of up to 0.7 µg l\(^{-1}\) in the shelf break region and slightly lower concentrations in adjacent oceanic waters (Garcia-Soto & Pingree 1998). In this study chlorophyll increased slightly over the shelf break and oceanic waters within the path of the slope current with chlorophyll concentrations being about half of those observed by Garcia-Soto & Pingree (1998). Differences in chlorophyll concentrations might be partly linked to differences in picophytoplankton; however picophytoplankton was not accounted for here or in previous studies of the area (Garcia-Soto & Pingree 1998, Savidge & Lennon 1987, Gowen et al. 1998, Fehling et al. 2012). CPR measurements in the area showed that there is high inter-annual variability in microphytoplankton cell numbers in autumn with cell abundance occasionally being close to zero (Johns 2015), which could explain discrepancies in chlorophyll measurements between studies.

One explanation for this inter-annual variability might be differences in timing
and intensity of seasonal storms. Generally storms increase mixing, which can in turn increase nutrient availability in the surface layer and enhance phytoplankton growth (Davis & Yan 2004, Wetz & Paerl 2008) although they can also delay bloom formation on some occasions due to the increase of suspended particulate matter in surface waters (Gohin et al. 2015). Few studies have measured immediate phytoplankton response in situ in shelf or oceanic waters to heavy storms. Malone et al. (1993) found that phytoplankton would decrease by 70% as an immediate storm response, followed by a sharp increase in productivity as new available nutrients were utilised. Similarly, primary production showed a sharp decline following a storm event in the Celtic Sea (Davidson et al. 2013). There was no noticeable decrease in phytoplankton cell numbers during the sampling period, despite the presence of heavy winds. Strong winds were already affecting the study area prior to the cruise and the low cell numbers found here might be the result of a decline in phytoplankton due to heavy winds prior to the study.

2.4.3 Nutrients

Nutrient concentrations were lowest in surface waters, where chlorophyll fluorescence was above 0.2 µg l\(^{-1}\). Below the mixed surface layer fluorescence rapidly decreased to close to zero values, while nutrient concentrations displayed their maximum values (Figure 2.4, Figure 2.5, Figure 2.6). This pattern suggested that uptake by phytoplankton was a strong structuring force over nutrient distribution. The same pattern was observed by Fehling et al. (2012) in the region in autumn, however, nitrate concentrations were up to 4 mmol m\(^{-3}\) lower. Higher nitrate concentrations in this study could be caused by wind driven deep turbulent mixing or low uptake of nutrients by phytoplankton. Both studies found a mixed layer depth of 50 to 100 m, suggesting there was little difference in deep mixing between studies. However, there was a clear difference between studies in the amount of phytoplankton that was present. Chlorophyll concentrations found by Fehling et al. (2012) were ten time higher than chlorophyll in this study. Lower phytoplankton numbers would lead to less nitrate uptake and therefore result in higher concentrations of nitrate in this study.

We found differences in nitrate and phosphate concentrations were significantly related to phytoplankton community structure (Figure 2.11, Table 2.3). Both nutrients were present at higher concentrations in the surface of oceanic and shelf break stations compared to shelf stations. Phytoplankton counts and chlorophyll fluorescence were also noticeably higher at oceanic and shelf break stations compared to shelf stations, which is consistent with phytoplankton growth being higher due to increased nutrient availability. Silicate responded stronger to the latitudinal gradient than the longitudinal gradient with highest concentrations in the north of the
study area. It has been suggested that changes in nutrient ratios can play a crucial role in structuring species composition (Davidson et al. 2012). In this study the nitrate to phosphate ratio was one of the most significant environmental parameters separating phytoplankton communities. The nitrate to phosphate ratio was between 8:1 (station G1) and 15:1 (stations C7 and E5, Appendix A, Table A.1). Based on the Redfield ratio of 16:1 this would suggest that all sites were limited by nitrate (Redfield 1934). However, more recent work suggests that the nitrate: phosphate requirements have large variations and can fall between 10:1 to 40:1 and are often below 16:1 without phytoplankton being nitrate limited (Geider & La Roche 2002).

Changes in nitrate to silicate ratio can affect the balance between dinoflagellates and diatoms (Officer & Ryther 1980). Several studies suggest that increases in N:Si can shift diatom to dinoflagellate dominance (Davidson et al. 2012). We found the nitrate to silicate ratio was higher at shelf break and oceanic stations (Appendix A, Table A.1) in agreement with results from 2001 that suggested the relative higher availability of silicate per unit nitrate on the shelf was an important driver of phytoplankton community differences (Fehling et al. 2012). In this study and as reported for observations made in 2001 (Fehling et al. 2012) diatoms had their maximum abundance at shelf stations where more silica per unit nitrate was available. In fact diatom presence was highest (37%) at shelf station G1 where the nitrate to silicate ratio was lowest. While different diatoms have different silicate requirements, studies suggest that at a nitrate to silicate ratio around 2:1 to 3:1, silicate becomes limiting for diatom growth (Davidson et al. 2012). Here most stations had ratios around 2:1 or higher which could explain the overall dominance of dinoflagellates throughout the study area. The surface silicate concentrations were also generally below the suggested 2 µM threshold for diatom dominance (Egge & Aksnes 1992) with the exception of stations A1 and C1 where silicate concentrations were higher.

2.4.4 Light availability

A significant relationship between phytoplankton community and light availability was also evident. Both light attenuation and turbidity were highest on the shelf, indicating reduced light availability for phytoplankton. Such conditions were most likely caused by strong winds leading to mixing and resuspension of sediment at some shallow shelf stations. Chlorophyll fluorescence and cell counts were also generally lower at shelf sites, making it unlikely that cell numbers added significantly to measured turbidity. Turbidity and poor light conditions are often considered to limit phytoplankton growth, however most studies on turbidity focus on estuary environments (McMahon et al. 1992, Gameiro et al. 2011). Jones & Gowen (1990) related light, linked to stratification conditions, to changes in the phytoplankton community at the Malin Shelf. Samples collected in well-lit waters were dinoflagellate
dominated while shifts towards a diatom dominated community at sites following a small decrease in light availability. This is consistent with the hypothesis that diatoms are better adapted to higher turbulence, often associated with lower light availability in summer if sufficient nutrients are available Jones & Gowen (1990), Margalef (1978). Here we find that diatoms were indeed more numerous at shelf sites with lower light availability, however, as noted above low silicate availability most likely inhibited the development of diatom dominated community.

2.5 Conclusion

We have presented new observations of the phytoplankton community of the Malin and Hebridean continental shelves. We find that stations could be separated by their hydrography into shelf stations and slope current stations with the exception of station C4 at the shelf break which was east of the slope current and oceanic station F6 which was west of the slope current. Consistent with this, phytoplankton communities were broadly divided into two groups; Shelf stations and shelf break/oceanic stations with the exception of C4, which was the most dissimilar to any other station as a result of the different water mass that was evident at this location. In contrast, the phytoplankton community at station F6 was similar to other oceanic and shelf break stations despite being outside the ESC. Dissimilarities between shelf and shelf break phytoplankton communities supported the hypothesis that the ESC acted as a mixing barrier with low salinities on the shelf confirming limited cross shelf water exchange during the study period. While a latitudinal gradient existed for stations on the shelf, this was not evident for stations within the ESC, indicating a northerly transport of water and phytoplankton within the ESC.

At all stations the phytoplankton community was dominated by dinoflagellates. At shelf break/oceanic stations over 97% of all identified cells belonged to the genus *Tripos*. At shelf break stations phytoplankton diversity was highest and diatoms displayed their maximum abundance representing 37% of the community at station G1. Phytoplankton richness and abundance were generally lower than previously recorded for the Malin shelf in autumn (Fehling et al. 2012) however, it has to be noted that samples in this study were collected later in the autumn season and during a period of heavy winds, which might have had negative impacts on phytoplankton numbers. In this study nutrient concentrations and light conditions had the strongest relation to phytoplankton community differences. The *Tripos* dominated shelf break/oceanic stations had a higher species abundance also had better light conditions and higher nitrate and phosphate concentrations. Light availability was generally lower at shelf stations. Nitrate and phosphate concentrations were also lower, but more silicate was available for phytoplankton which might explain
why diatoms displayed their maximum abundance at shelf stations. The high seasonal and inter-annual variability in both cell numbers and species presence makes it difficult to define a community that would indicate a Good Environmental Status (GES) for MSFD monitoring and assessment.

This study presents valuable baseline information to further our understanding of how to determine GES for the MSFD. The practical and financial difficulties in sampling along and off the shelf edge means that cruise data will have an important role to play in this assessment. Currently a plankton life form approach as described by Tett et al. (2008) is being used. The dataset generated here will potentially be useful to begin to populate the state space model used in this assessment for the shelf edge and off shelf regions. Data from future cruises will be required to further our understanding of the difference in the phytoplankton community on and off the shelf, if it is changing over time and if changes observed in more coastal stations can also be observed in the offshore. These questions are all key to our understanding of what GES is, and how the criteria that describe it may change over time. While data from the CPR will play a key role in this, net haul data as generated in this study will make an important contribution owing to the variety of physical and chemical parameters collected that will further our understanding of the environment the phytoplankton community inhabits.
3 Phytoplankton distribution in relation to environmental drivers on the Malin Shelf in summer

3.1 Introduction

The Malin Shelf is comprised of the, up to 200 m deep, shelf sea to the north of Ireland and west of Scotland (Figure 1.1 and 3.1). West of the shelf is the steep continental slope that separates the shelf from deep oceanic water. As discussed previously, the ESC is steered northwards along the continental slope (chapter 1.1) where it can act as a boundary between shelf and oceanic water (chapter 2; Ellett et al. 1986). Physical forcing steers the ESC parallel to isobaths on the slope (Huthnance 1995, Brink 1998, Simpson & Sharples 2012), which are especially narrow and irregular at the south west corner of the Malin shelf. This irregularity can lead to an overspill of Atlantic water from the ESC onto the Malin shelf (Burrows & Thorpe 1999, Jones 2016). Strength of the ESC and potential for overspill can vary with season. Overspill was suggested to be linked to changes in wind speed and direction and changes in ESC flow, which is stronger in winter (Jones 2016).

The Malin shelf is characterised by the development of strong Type I and Type II fronts. Salinity fronts are classed as Type I fronts that are present all year, while Type II fronts only occur in summer and separate seasonally stratified water from tidally mixed water (Hill & Simpson 1989). North of the Irish coast, a Type I salinity front develops between the more saline water on the shelf with Atlantic origin and the fresher coastal water (Gowen et al. 1998). West of the Scottish Islands a Type I salinity front is present between Malin Shelf water with Atlantic origin and fresher water entering the shelf from the Irish Sea (Hill & Simpson 1989). This front is referred to as the Islay front as it is found west of the Scottish island Islay. Over summer, a Type II front develops alongside the Islay front as shelf water becomes thermally stratified while water with Irish Sea origin remains tidally mixed (Hill & Simpson 1989, Hill et al. 2008). The seasonal change from a Type I to a combined Type I and Type II front can change the vertical structure of the Islay front, which is generally a straight vertical line between waters of different salinities, but develops an S-shaped profile in summer as the density difference between the high salinity cool water below the thermocline on the shelf and the mixed water from the Irish Sea is stronger than the density difference between high saline, warm shelf water above the thermocline and mixed water with Irish Sea origin (Hill & Simpson 1989).

Gowen et al. (1998) concluded that the Irish coastal and Islay front connect into a continuous density front from the north of Ireland to the west of Scotland. Alongside the density front a narrow jet like coastal current is steered (Hill et al.
The Irish jet current is a seasonal current that is only present during summer. The current is known to flow from the south of Ireland along the Irish west coast and up north towards the Scottish west coast (Hill et al. 2008, Brown et al. 2003).

Oceanographic boundary conditions such as the ESC and frontal systems have previously been found to be strongly linked to phytoplankton occurrence in spring and summer (Savidge & Lennon 1987, Gowen et al. 1998). Type II fronts especially, such as the Islay front in summer, can support high phytoplankton growth by providing an optimal environment between mixing and stratification (Simpson et al. 1979, Hill & Simpson 1989). Earlier studies focused on chlorophyll a distribution on the shelf, with limited information about phytoplankton community structure and changes in phytoplankton occurrence associated with frontal systems (Simpson et al. 1979, Savidge & Lennon 1987). Available data on phytoplankton community suggested the formation of distinct phytoplankton communities separated by the
Islay front (Gowen et al. 1998). Well mixed waters east of the front generally supported a greater diversity of diatoms, while dinoflagellates developed dominance in the thermally stratified waters west of the front (Gowen et al. 1998).

The previous chapter described phytoplankton distribution and their environmental drivers on the Hebridean and Malin shelves in autumn 2014. Phytoplankton numbers were low, possibly due to strong seasonal winds prior to and during the sampling period. The phytoplankton community was dominated by four taxa, *Tripos*, *Prorocentrum*, *Dinophysis* and *Pseudo-nitzschia* (chapter 2.3.1). Phytoplankton communities were separated into shelf stations and shelf break/oceanic stations in agreement with previous studies (Savidge & Lennon 1987, Gowen et al. 1998, Fehling et al. 2012). Nutrients and light conditions showed the strongest relationship to phytoplankton grouping (chapter 2.3.5). The hydrography/topography (chapter 1.1) was found to play a major role in structuring phytoplankton community. Results suggested that the ESC separated shelf phytoplankton from shelf break/oceanic phytoplankton while providing connectivity for oceanic stations (chapter 2.4.1).

For this chapter phytoplankton and environmental data were collected from the Malin shelf during a AFBI research vessel Corystes cruise in summer 2015. The aims of this chapter were to first identify the oceanographic features of the area such as the position of fronts and if there was an overspill of Atlantic water onto the shelf. After identifying prominent physical features the next aim was to determine if and how these oceanographic features structured the phytoplankton community on the Malin Shelf. Another major driver behind community differences might be differences in the mixing/stratification environment at different sides of frontal boundaries that are often associated with different nutrient availability. Both total nutrient availability and nutrient ratios can structure phytoplankton communities. As discussed in chapter 2, baseline information of phytoplankton occurrence in the region is needed for assessing GES for MSFD as suggested by Tett et al. (2008).

Results from this chapter are compared to data collected during the autumn Discovery cruise (chapter 2), to improve our understanding of seasonal changes of both phytoplankton and their environment in the region. Data collected for this chapter also provides a baseline for data collected from a SAMS sea glider that was deployed parallel to the cruise (chapter 4). Data on phytoplankton presence provides baseline information for bio-physical modelling in chapter 5.

### 3.2 Methods

Data on phytoplankton taxonomy, water temperature, salinity and nutrient concentrations was collected from 44 stations on board the AFBI research vessel *Corystes* across the Malin shelf and adjacent oceanic waters between the 15th and 21st of July.
2015 (Figure 3.2). The cruise track was chosen to sample important oceanographic features on the Malin Shelf such as the shelf break, the Islay front and the Irish coastal jet current. To plot changes in vertical water column structure, stations were divided into five transects (Figure 3.2). Transects were designed to cross over the Islay front (transects 1 and 2), the Irish coastal front (transects 3, 4 and 5), the shelf break (transects 2 and 3) and the Irish coastal jet (all transects).

In situ CTD casts at every station recorded data on water temperature and salinity in 0.5 m intervals. Samples for the determination of chlorophyll a fluorescence and nutrient concentrations (nitrate, nitrite, ammonium, phosphate, silicate) were collected from the niskin bottle samples close to the surface at each station (around 2 to 5 meters depth). Chlorophyll a was measured on board by filtering 500 ml through a 47 mm glass fibre filter (Whatman GF/F). Filters were stored in the dark at -20 °C prior to extraction. Filters were thawed overnight in the dark with
8 ml of 90% acetone at 4 °C. Chlorophyll a was measured with a Turner trilogy fluorometer (Gowen et al. 1982). For nutrient analysis, 500 ml seawater were filtered through a 10 mm glass fibre filter (Whatman GF/F) and filtrates were frozen at 20 °C until analysed using a Seal Analytical QuAAtro AutoAnalyser (Seal Analytical 2011a,b,c,d,e).

Phytoplankton was sampled via a 20 µm phytoplankton net haul to a depth of 30 m at 35 stations as weather permitted. Phytoplankton from discrete niskin bottle samples taken near the surface were also counted at 11 stations (Table 3.1). Phytoplankton samples were immediately fixed with 1 ml acidic Lugol’s Iodine solution (1% final concentration) and stored in brown glass bottles pre-rinsed with seawater. Phytoplankton was identified and counted using the Utermöhl method, where samples were settled for at least 22 hours at room temperature in 10 ml settling chambers for net samples and 50 ml settling chambers for discrete depth samples. Cells were identified under 200x magnification using a Zeiss Axiovert 100 inverted light microscope. Data from net hauls is presented as presence/absence data while counts from discrete depth were calculated as cells per litre.

Statistical analyses were undertaken in R using the packages vegan and MASS. Environmental data was standardised using Wisconsin double standardization as data was recorded in different units and would not be comparable otherwise (Everitt & Hothorn 2011, Oksanen 2014). Non-metric multidimensional scaling (nMDS) and principal component analysis (PCA) were used for biological and environmental data respectively. Environmental data was then fitted to the biological ordination using the R vegan function envfit(), calculating $r^2$ to assess the goodness of fit for a linear model (Oksanen et al. 2013).
Table 3.1: Details of the sampling station locations (Figure 3.2) where net tows and discrete water samples for phytoplankton counts were sampled.

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3.3 Results

3.3.1 Malin Shelf surface water

In this section the average value for water temperature, salinity and density for the top 30 m are presented to allow comparison with data from phytoplankton net hauls that were taken over the top 30 m of the water column. Salinity and water temperature profiles suggested that there was a strong influx of cool, less saline water from the Irish Sea in the south-east of the study area with surface salinities between 34.2 and 34.7 and surface water temperatures between 11.5 °C and 12.5 °C (Figure 3.3). Coastal waters north of Ireland had salinities around 35.0 and water temperatures up to 14 °C. Oceanic surface waters were characterised by high salinities around 35.3 to 35.4 and temperatures around 12.7 °C to 13.2 °C (Figure 3.3). Oceanic waters intruded on to the shelf over the shelf break and formed strong density fronts where the high density oceanic water met the lower density waters near the coast and the Irish Sea. West of the Scottish coast strong changes in salinity formed a front known as the Islay front, separating the cool, less saline, low density Irish Sea water from the warm, saline waters on the shelf. South of the shelf, the shelf water was separated from warm, low density coastal waters by the Irish coast front. Both fronts combine into a continuous density front (Figure 3.3 c) alongside which the Irish coastal jet current was steered.

Chlorophyll a concentrations were generally patchy with the highest chlorophyll a concentrations (around 1.7 µg l\(^{-1}\)) recorded at stations 11 and 12A, which were west of the Islay front (Figure 3.4a). Phosphate and silicate concentrations were close to zero near the north Irish coast but highest in the Irish Sea. Both nutrients also increased towards the north of the Malin shelf (Figure 3.4b and c). Both nutrients were generally low in concentration where chlorophyll a was high. Elevated nitrate concentrations generally corresponded to the salinity front and concentrations west of the front were generally higher than east of the front. Concentrations near the coast were lowest and close to zero (Figure 3.4d). Nitrite concentrations were highest in the Irish Sea and at stations 33 and 12 which are close to the salinity front and high in chlorophyll a (Figure 3.4e). Ammonium had its highest concentrations in the Irish Sea but decreased to near zero on the Malin shelf and adjacent oceanic waters (Figure 3.4f).
Figure 3.3: Average surface values of the top 30 m for (a) salinity, (b) temperature, (c) density.
Phytoplankton on the Malin Shelf in summer

(a) Chlorophyll a (µg l⁻¹)

(b) Phosphate (mmol m⁻³)

(c) Silica (mmol m⁻³)
Figure 3.4: Surface concentration from one measure taken in the top 10m for (a) chlorophyll a, (b) phosphate, (c) silicate, (d) nitrate, (e) nitrite, (f) ammonium.
3.3.2 Grouping of surface stations

Station groups were determined by their similarity based on the Bray-Curtis distance between each station. Based on the average water temperature, salinity and nutrient concentrations of the top 30 meters, sites were divided into three different groups (Figure 3.5). The first group was comprised of stations close to the north Irish coast (Figure 3.5, yellow). These stations had the highest recorded temperatures during the study but were low in salinity and nutrient concentrations were close to zero. The second group included all stations that showed a strong inflow of water from the Irish sea (Figure 3.5, red). The water temperatures and salinities had the lowest recorded surface values but nutrient concentrations were generally high compared to the rest of the study area. The third group was made up from stations west of the Islay front with a strong influx from oceanic water over the shelf edge (Figure 3.5, blue). Stations had high salinity, density and nitrate concentrations with variable concentrations of other nutrients.

Figure 3.5: Dendrogram of the average Bray-Curtis distance between sites and site groupings based on salinity, water temperature and nutrient concentrations. Blue = Malin shelf group, yellow = coastal group, red = Irish Sea group.

Increasing distance between sites in the PCA plot represents higher dissimilarity in the chemical and physical properties of the sites (Figure 3.6a). A total of 89.0% of variance in the data could be explained by the two dimensional representation.
Figure 3.6: (a) Principal component analysis (PCA) ordination of Wisconsin standardised environmental data at each site sampled. (b) Stations marked accordingly on the map. Blue = Malin shelf group, yellow = coastal group, red = Irish Sea group.
61.6% of it was explained by the principal component 1 (PC1). The three groups are separated along PC1 with the coastal group having negative PC1 values, the Irish Sea group having positive PC1 values and the Malin group having PC1 values of zero +/- 0.1. An additional 27.4% of the variance in the data was explained by the principal component 2 (PC2). PC2 mainly separated the Malin shelf group with mostly positive PC2 Values to Coastal and Irish Sea sites with negative PC2 values. Malin shelf stations with negative PC2 values are also the closest to Coastal and Irish sea stations on the map (Figure 3.6). Noticeably, the separation of stations on the PC axes reflected the location of sampling stations on the map; Separation of groups along PC1 reflected the separation of groups by longitude and the separation of groups along PC2 reflected differences in latitude (Figure 3.6).

Absence and presence data of phytoplankton was used to study community differences between sites. All stations displayed an average of around 50% dissimilarity (Figure 3.7) with sites 21, 36 and 12 being the most dissimilar to other sites. The remaining sites are clustered in two different groups (Figure 3.7) that were roughly divided by the Islay front. The first group, together with stations 12, 21, and 36 included all but one station that were grouped together as Malin shelf stations based on the physical and chemical properties of the water (Figure 3.8, blue). The second group included all stations that were grouped as coastal stations and Irish sea

Figure 3.7: Dendrogram of the average Bray-Curtis distance between sites and site groupings based on phytoplankton presence and absence data. Colour coding was chosen to represent grouping based on PCA of environmental data: Blue = Malin shelf group, yellow = coastal group, red = Irish Sea group.
stations based on their environmental properties. Based on their phytoplankton composition, there was no difference between the coastal group and Irish Sea group. Station 6, which was grouped with Malin stations based on its environment was part of the coastal/Irish Sea group based on its phytoplankton presence (Figure 3.7).

Figure 3.8: Non-metric multidimensional scaling (nMDS) ordination of phytoplankton presence and absence data. The stress is 0.1024 indicating that ordination is representable for real patterns rather than randomness in the data. Colour coding was chosen to represent grouping based on PCA of environmental data: Blue = Malin shelf group, yellow = coastal group, red = Irish Sea group.

A full list of genera presence and absence and counts is given in Appendix B. Stations in the Malin shelf group, as defined by their environmental parameters and phytoplankton community, had a generally lower abundance and the main genera present were the diatoms *Pseudo-nitzschia*, *Cylindrotheca*, *Rhizosolenia*, and *Thalassiosira* and the dinoflagellate *Dinophysis*. These genera were also present in coastal and Irish Sea stations, but diversity at those stations was a lot higher and commonly present genera included the diatoms *Chaetoceros*, *Coscinodiscus*, *Cerataulina*, *Leptocylindrus*, *Podosira*, *Guinardia*, *Paralia*, *Dactyliosolen* and *Lauderia* and the dinoflagellates *Prorocentrum* and *Scripsiella*. Presence and absence data
from nets suggested that there was a higher diversity of diatoms in both coastal and Irish Sea groups compared to the Malin Shelf group.

Full phytoplankton cell counts were undertaken for nine stations on the Malin shelf (Appendix B). The diatoms *Pseudo-nitzschia* (maximum cell density of 24460 cells l\(^{-1}\) at station 24), *Rhizosolenia* (maximum cell density of 42358 cells l\(^{-1}\) at station 14), *Thalassiosira* (maximum cell density of 9960 cells l\(^{-1}\) at station 21) and *Cylindrocetha* (maximum cell density of 14200 cells l\(^{-1}\) at station 24) were present in all nine surface water samples from the Malin shelf. The dinoflagellates *Dinophysis*, *Prorocentrum*, *Protoperidinium* and *Gyrodinium* were present in most net samples with a maximum of 780 cells l\(^{-1}\). *Tripos* was present at some stations and reached concentrations of over 2600 cells l\(^{-1}\) at station 26. The haptophytes *Phaeocystis* and the dinoflagellate *Karlodinium* were the most numerous genera and present in all nine samples. *Phaeocystis* was present with over 1 million cells l\(^{-1}\) at station 37 and *Karlodinium* with nearly 200 000 cells l\(^{-1}\) at station 28.

Vectors of environmental variables were fitted to the nMDS ordination of phytoplankton data to visualise the relationship between environmental data and phytoplankton composition and distribution (Figure 3.9). Environmental data plotted were water temperature and salinity, along with nutrient concentrations and nutrient ratios (nitrate to silicate and nitrate to phosphate), as nutrient ratios are known to be important factors structuring phytoplankton communities (Redfield 1934, Officer & Ryther 1980).

The length of the environmental vector is proportional to the correlation between the environmental factor and the phytoplankton ordination. The arrow indicates the direction towards which the environmental variable increases (Figure 3.9). The significance of the relation between an environmental driver and the phytoplankton ordination was determined by calculating their goodness of fit (r\(^2\)) and their p-value (Table 3.2). Nitrate, salinity and water temperature had a statistically significant relation to phytoplankton community structure (Figure 3.9, Table 3.2).
Figure 3.9: Redundancy analysis using envfit. S = Salinity, T = Temperature, NO3 = Nitrate, PO4 = Phosphate, Si = Silicate, NO2 = Nitrite, NH4 = Ammonium, N.PO4 = Nitrate to phosphate ratio, N.Si = Nitrate to silicate ratio. Significant factors marked with *.

Table 3.2: Environmental factors ordered by significance of its relation to biological data.

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</tr>
<tr>
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3.3.3 Transects

Stations were divided into 5 transects (Figure 3.2). Transect 1, 2 and 3 followed the longitudinal gradient from the west (Figure 3.10 station 36, Figure 3.11 station 27 and Figure 3.12 station 26) to the east (Figure 3.10 station 50, Figure 3.11 station 3 and Figure 3.12 station 6). To the west, water on the Malin shelf had high salinities over 35.2. The water column was thermally stratified with a strong thermocline between 30 m and 50 m separating surface waters with 13 °C to 14 °C from waters
below 50 m with 11 °C to 9.5 °C (Figure 3.10 station 36 to 38, Figure 3.11 station 27 to 12A and Figure 3.12 station 26 to 20). On transect 1 and 2 cool, well mixed water with salinities below 34.6 entered the domain from the east (Figure 3.10 station 39 to 50 and Figure 3.11 stations 40 to 3). The Islay front between the high salinity, thermally stratified shelf water and the less saline, well mixed water from the Irish Sea was visible between station 38 and 39 at transect 1 and station 12A and 40 at transect 2 (Figure 3.10, Figure 3.11). Coastal waters in the east of transect 3 waters had a lower salinity, but high surface temperatures and stratification caused by both salinity and temperature (Figure 3.12 station 19 to 6). Coastal waters and Malin shelf waters were separated by the Irish coastal front that was visible around station 19 (Figure 3.12). Transect 4 and 5 followed a latitudinal gradient starting in coastal waters in the south (Figure 3.13 station 18 and Figure 3.14 station 7) and across the Irish coastal front (Figure 3.13 between station 18 and 14 and Figure 3.14 between station 8 and 12).
Figure 3.10: Contour plots for transect 1 stations for (a) salinity, (b) temperature, (c) density.
Figure 3.11: Contour plots for transect 2 stations for (a) salinity, (b) temperature, (c) density.
Figure 3.12: Contour plots for transect 3 stations for (a) salinity, (b) temperature, (c) density.
Figure 3.13: Contour plots for transect 4 stations for (a) salinity, (b) temperature, (c) density.
Figure 3.14: Contour plots for transect 5 stations for (a) salinity, (b) temperature, (c) density.
3.3.4 Seasonal changes on the Malin Shelf

Transects from stations 18 to 26 and stations 27 to 34 covered a similar area to transects G and F of the Discovery cruise in autumn 2014 (Chapter 2, Figure 3.15). The Discovery stations were sampled in early November 2014, while the Corystes stations were sampled in mid July 2015. Depth profiles showed that there were strong seasonal differences in stratification. In July the water column was stratified at 30 m to 50 m with both water temperature and salinity causing stratification (Figure 3.16 and Figure 3.17). Stratification weakened over autumn with salinity being well mixed and thermal stratification at 70 m to 100 m. During autumn the high salinity core of the slope current with salinities over 35.4 was clearly visible at stations F4, G5 and G6. During summer salinities reached up to 35.4 at stations 27 to 34, but for stations 18 to 26 salinities generally stayed below 35.4 (Figure 3.16 and Figure 3.17).

Figure 3.15: Section of sampling sites from the Corystes cruise (red) and Discovery cruise (blue).
Figure 3.16: Contour plots for stations 27 to 34 (Corystes cruise) for (a) salinity, (c) temperature, (e) density and for transect F (Discovery cruise) for (b) salinity, (d) temperature, (f) density.
3.4 Discussion

3.4.1 Oceanographic features on the Malin Shelf

During this study the Islay front, Irish coastal front, Irish coastal Jet current and ESC were identified. Changes in salinity and stratification showed the location of the Islay front and Irish coast front (Figure 3.3 and 3.10 to 3.14). The two fronts
merge into one continuous density front as previously found by Gowen et al. (1998) alongside which the Irish jet current is steered (Hill et al. 2008).

Stations were divided into three groups based on their environmental properties (Figure 3.5 and Figure 3.6). The division showed a strong link to the frontal boundaries. The coastal group was separated from the Malin Shelf by the Irish coastal front and the Irish Sea group was separated from the Malin Shelf by the Islay front. Even though the frontal system appeared to be a continuous feature, station 6 which is located between the coastal group and Irish Sea group, was clustered with the Malin shelf group despite being positioned south east of the density front. Temperature and salinity profiles of station 6 (Appendix C) showed the station had a different physical signature to stations on the Malin shelf and was not of Atlantic origin, but rather presented a temperature and salinity signature that showing the transition from low salinity Irish Sea water to higher salinity coastal water.

The ESC signature of salinities over 35.36 (Hill & Mitchelson-Jacob 1993) was found in the top 250 m of the continental slope and adjacent oceanic waters. The ESC did not act as a divider between oceanic water and water on the Malin shelf during this cruise. Spillover of Atlantic water onto the shelf was evident and Atlantic water with salinities between 35.4 and 35.2 intruded well onto the Malin shelf until salinity rapidly decreased at the frontal boundaries. Spill over of Atlantic water at this location of the continental slope is linked to both narrowing of the slope, combined with an irregular bathymetry. Generally, the slope current flows parallel to depth contours based on the physical principle known as Taylor-Proudman theorem (Huthnance 1995, Brink 1998, Simpson & Sharples 2012). Sharp changes in direction of depth contours as present on the Malin Shelf slope can break the constrains of the Taylor-Proudman theorem. This can lead to a current flow across the continental slope and thereby transport of Atlantic water onto the shelf (Burrows & Thorpe 1999, Jones 2016).

### 3.4.2 Phytoplankton distribution in relation to oceanographic boundary conditions

Frontal systems on the Malin Shelf are known to influence phytoplankton productivity and occurrence (Simpson et al. 1979, Gowen et al. 1998). In agreement with previous studies, phytoplankton community differences strongly correlated to the positions of the continuous density front that combines the Islay front and the Irish coast front. NMDS suggested that there were two different phytoplankton community groups that were separated by the frontal boundary system (Figure 3.8). Redundancy analysis showed that there was a statistical significant correlation between phytoplankton community structure and water temperature and salinity (Figure 3.9).
Three stations, 12, 21 and 36, were clustered with the Malin Shelf group based on their environmental data, but did not fall in either phytoplankton group. One noticeable difference to the other Malin shelf stations was the absence of *Pseudo-nitzschia*, which was present in every other Malin shelf station. The stations were also on the inner Malin shelf close to the Islay front. Station 6 was grouped with Malin shelf stations based on its physical properties, but grouped with coastal/Irish Sea stations based on its phytoplankton composition. This is consistent with the temperature and salinity signature, which suggested that water at station 6 was more similar to coastal and Irish sea stations (Appendix C). Surprisingly, phytoplankton composition from the Irish sea group and coastal group was not distinctly different to each other, despite the differences in environment. The temperature difference between the warm coast and the cold Irish sea was nearly 2.4 °C and salinity difference was 0.5 to 0.8. Nutrient concentrations were generally highest in the Irish Sea group and lowest in the coastal group.

Grouping revealed in this study was similar to the grouping of phytoplankton in the same area in August 1996 (Gowen et al. 1998). In 2015 and 1996 different phytoplankton communities were found either side of the Islay front. In 1996 each group could be further divided into two groups suggesting a possible role of the ESC to structure phytoplankton on the shelf and a different phytoplankton community associated with the frontal region itself (Gowen et al. 1998). In 1996 communities divided by the Islay front contained distinctly different species, suggesting that the front could inhibit cross shelf transport. In this study it was not possible to conclude that the Islay front acted as a physical barrier for phytoplankton transport as most genera that were found on west of the Islay front were also found east of it. Genera found to the east of the front might be able to physically cross over the front but growth might be inhibited due to the pronounced change in environment from tidally well mixed waters to thermally stratified waters.

Previous studies have suggested the potential role of the Irish jet current in harmful phytoplankton transport (Farrell et al. 2012, Raine et al. 2010a). During this study only a small section of the current was sampled and there was no clear pattern between stations associated with the Irish current and phytoplankton community, making it difficult to determine the role of the jet current in northwards phytoplankton transport in this chapter.

3.4.3 The role of different mixing and nutrient regimes on phytoplankton structure

Peaks in chlorophyll are often associated with frontal boundaries that separate stratified and mixed water (Simpson & Sharples 2012). This might be explained by generally higher nutrients in well mixed side due to turbulent deep mixing, while
calmer, stratified waters provide a better growth environment, but are often lower in nutrients as mixing with deeper layers is strongly limited. Frontal boundaries can therefore provide an optimal growth environment that combines stratification with nutrient availability.

In agreement with previous studies (Simpson et al. 1979, Gowen et al. 1998), chlorophyll a was generally higher at the stratified side of the Islay front than the well mixed side in this study. This increase in chlorophyll was found to support concentrations of over 1 million cells l\(^{-1}\) of the harmful genus *Phaeocystis*. This was not found by Gowen et al. (1998). It is possible that small single cells of *Phaeocystis* could be missed by net sampling. This would not be the case for larger colonies of *Phaeocystis* and this genus might simply not have been present during sampling in that study (Gowen et al. 1998).

The relationship between stratification and nutrient concentrations was not consistent. Surface concentrations of nitrate, which were significantly related to phytoplankton community ordination (Figure 3.9), were generally higher in stratified waters of the Malin shelf than in well mixed waters entering from the Irish Sea. However, silicate and phosphate were higher at well mixed stations with Irish Sea influx, compared to stratified coastal or Malin Shelf stations.

Diatom diversity was higher in shallow, well mixed waters in agreement with Margalef (1978), who suggested that diatoms were better adapted to grow in well mixed nutrient rich waters than dinoflagellates. Smayda & Reynolds (2001) suggested that shallow, coastal, nutrient rich waters can also favour the growth of certain harmful dinoflagellate species. They suggest nine different regimes from onshore (Type I) to offshore (Type IX), that favour different HAB species. Type II describes shallow coastal environments with generally good nutrient availability that would favour growth of the dinoflagellates *Scrippsiella* and *Prorocentrum*. Here, *Scrippsiella* and *Prorocentrum* were found in all but one coastal/Irish Sea stations, but only at one Malin shelf station. Interestingly, the phytoplankton community was not markedly different between the Irish sea group with well mixed water and generally high nutrient concentrations and the coastal group with weak stratification and the lowest nutrient concentrations measured during the study.

### 3.4.4 Nutrient ratios as structuring factors of phytoplankton community

Despite the apparent difference in nutrient concentrations between the coastal group and Irish sea group, nutrient ratios were relatively similar (Appendix A, Table A.2), which might help to explain why a similar phytoplankton community was present. Surface waters of stations in the coastal group and the Irish Sea group had a nitrate to phosphate ratio of 1 to 3.5 and 4 to 5 respectively and a nitrate to silicate ratio of 1 to 3 and 1 to 1.5 respectively. This suggests that all sites were nitrate
limited (Geider & La Roche 2002). Silica concentrations were generally below the suggested 2 µM threshold for diatom dominance (Egge & Aksnes 1992), however relative availability of silicate per unit nitrate was enough to support diatom growth (Redfield 1963, Officer & Ryther 1980). This is in agreement with the lower levels of chlorophyll, but higher diversity of diatoms that were found in coastal and Irish Sea stations compared to stations in the Malin shelf group.

Stations in the Malin shelf group had surface nutrient ratios of around 10 nitrate to phosphate and up to 13 nitrate to silicate, suggesting that the surface waters were not necessarily limited in nitrate (Geider & La Roche 2002) but in silicate (Redfield 1963). This is in agreement with the high numbers of the flagellates Karlodinium and Phaeocystis found on Malin shelf stations together with the generally higher levels of chlorophyll. Station 6 that was grouped with Malin shelf stations based on temperature, salinity and nutrient concentrations had nitrate to phosphate and nitrate to silicate ratios that were more similar to stations in the Irish Sea group and coastal group. This might explain why phytoplankton at station 6 was more similar to coastal/Irish sea phytoplankton than phytoplankton in the Malin Shelf group.

Officer & Ryther (1980) suggested that shifts in the nitrate to silicate ratio can change from diatom to dinoflagellate dominated communities which would increase the risk of HAB occurrence as most HAB species are dinoflagellates. Here, diatom diversity decreased with increasing nitrate to silicate ratios in the Malin shelf group, compared to the Irish sea and coastal group. A Phaeocystis bloom was also present at some stations of the Malin shelf group with concentrations reaching over 1 million cells l⁻¹. Phaeocystis can form high density, polysaccharide producing HABs that can form large amounts of decaying polysaccharide foam after a bloom.

Despite the low concentrations of silicate and high nitrate to silicate ratio on the shelf, elevated densities of the potentially toxic diatom Pseudo-nitzschia were present at some stations. The highest recorded density was 24 460 cells per litre, which was below the 50 000 cells l⁻¹ threshold above which Pseudo-nitzschia concentrations are considered potentially harmful in the UK. Toxin (Domoic acid) production requires nitrate (Bates et al. 1998), which suggests that toxin production in the nitrate limited coastal and Irish sea stations might be low. Pseudo-nitzschia blooms in the silicate limited waters of the Malin shelf would be short lived but could be toxic (Fehling et al. 2004a).

3.4.5 Seasonal differences on the Malin Shelf

During summer most of the Malin shelf was well stratified with a strong thermocline at about 30 m to 50 m. In stratified waters phytoplankton was limited to the surface layer as indicated by chlorophyll measurements taken below the mixed surface
layer (Appendix D). Nutrient concentrations were highest below the thermocline where they were unavailable for phytoplankton uptake (Appendix D). Nitrate concentrations in the top 30 m in stratified water were between 1.5 mmol N m\(^{-3}\) and 3 mmol N m\(^{-3}\) but up to 11.5 mmol N m\(^{-3}\) in waters below 200 m. Concentrations in shallow, tidally mixed waters were generally below 1.5 mmol N m\(^{-3}\).

Over autumn, stratification deepened to about 50 m to 100 m depth. Concentrations of nitrate in early autumn were around 1 mmol N m\(^{-3}\) to 2 mmol N m\(^{-3}\) in the surface and up to 11 mmol N m\(^{-3}\) in deeper waters (Fehling et al. 2012). Nitrate concentrations during the discovery cruise in autumn (chapter 2) were twice as high in surface waters but only slightly higher in water below the thermocline. Higher surface concentrations during autumn can be caused by lower uptake of phytoplankton and/or reintroduction of nutrients by deep mixing. Phytoplankton concentrations in late autumn were lower by several orders of magnitude and the mixed surface layer depth was generally below 50 m in autumn (chapter 2, Fehling et al. 2012), but around or above 50 m in summer (this chapter, Gowen et al. 1998), suggesting a relevance of both deep mixing and phytoplankton uptake.

Changes in stratification affect the position and vertical profile of the Islay front; The front is present in absence of thermal stratification as a type I salinity front with a straight vertical profile. When stratification intensifies over summer a type II front develops that changes the vertical profile into an S-shape (Hill & Simpson 1989). The Islay front was found between 8°W and 7°W and would not have been sampled during the autumn Discovery cruise as stations in autumn were west of 8°W. The profile found of the Islay front during the summer cruise showed clear evidence of both a type I salinity and type II stratification front, with the density differences representing the S-shaped profile described by Hill & Simpson (1989). The coastal front is also present all year and was sampled during the summer cruise (this chapter) and autumn cruise (chapter 2). Here, the front was visible between stations 20 and 18 where salinities decreased rapidly below 35.0. During the Discovery cruise salinities decreased noticeable at station G1, but salinities stayed above 35.0 (Figure 3.17).

The ESC flow is stronger in winter (Ellett et al. 1986) and during the autumn discovery cruise the high salinity core of the ESC was clearly visible in most oceanic and shelf break stations with salinities above 35.4. During this study the high salinity core of the ESC was less visible with salinities reaching 35.4 but no higher (Figure 3.16 and 3.17). In both autumn 2014 and summer 2015 the shelf break/continental slope did not stop water with oceanic properties intruding onto the shelf.

The stations sampled during this cruise roughly covered the same area as transects F and G during the Discovery cruise in 2014 (Figure 3.15). This study had, however, a much better resolution of the Malin shelf and stations that were grouped
as the coastal and Irish sea group were outside the area that was sampled by the Discovery cruise. The Malin shelf group covered a similar area to the shelf, shelf break and oceanic stations from transect F and G that were sampled during the discovery cruise 2014. During the Discovery cruise stations were separated into a shelf group and shelf break/oceanic group with roughly 15% dissimilarity based on their environment. Here, there was a similar division within the Malin group; At 15% dissimilarity the group divided into two parts; The first part included stations that were near the shelf break or in waters deeper than 200m. The second part included stations on the inner Malin shelf that were closer to the Islay front. The grouping of stations was surprisingly similar, considering that they were sampled in different seasons and different environmental parameters were used for PCA between chapters.

Comparing phytoplankton clustering between summer (this chapter, Figure 3.8) and autumn (chapter 2, Figure 2.8) shows that seasonal changes in physical oceanography on the Malin shelf are reflected in the grouping of phytoplankton communities. In autumn, two distinct communities formed, that were separated by the slope current (chapter 2, Figure 2.8). During summer there was no structuring effect of the ESC on phytoplankton community. Different groups of phytoplankton were separated by the Islay front instead.

3.5 Summary

The aims of this chapter were to identify oceanographic features and determine the link between such features and phytoplankton distribution. Here, the Islay front was the main driver for community separation. Stations were clustered into three groups based on their physical attributes and nutrient concentrations (Malin, coastal, Irish Sea). Based on their phytoplankton composition, sites were only clustered into two groups (Malin, coastal/Irish Sea). The two groups of phytoplankton were separated by a continuous density front that connected the Irish coast front and the Islay front. The front can provide a physical barrier for phytoplankton exchange, however environmental parameters were also different each site. That makes it difficult to determine whether phytoplankton was unable to cross the density front or if cross over was possible, but local conditions on the other side of the front might not support growth. There is no density barrier between coastal water north of Ireland and Irish Sea water but station were grouped separately based on environmental parameters. Phytoplankton community between coastal and Irish sea stations was not distinctly different.

The main differences between environments separated by the frontal system were differences in stratification and nutrient availability. The Malin shelf north west
of the front was thermally stratified with high concentrations of nutrients below the thermocline where it is unavailable for phytoplankton. Highest cell numbers were found on the stratified Malin shelf, close to the Islay front, where a bloom of *Phaeocystis* was found with over 1 million cells l$^{-1}$. Species found on the Malin shelf were generally also found at the coastal/Irish sea stations, while a higher diversity of diatoms were found in the tidally mixed waters south east of the Islay front. Nutrient concentrations between coastal sites and Irish sea sites were different, however nutrient ratios were similar which might help to explain why phytoplankton community was similar as well.

The Islay front and ESC are persistent all year round, but change in intensity, position and structure between seasons. The flow of the ESC is known to be stronger in winter (Ellett et al. 1986), while frontal systems become stronger over summer as type II fronts develop (Hill & Simpson 1989). In agreement with the changes in strength we find that the ESC is the main structuring factor of phytoplankton community in late autumn and the Islay front in summer. That suggests that it is easier for oceanic phytoplankton to intrude onto the Malin Shelf in summer than in winter. Such seasonal changes in phytoplankton distribution are important factors to consider when trying to determine a GES for the area as phytoplankton distribution is likely to change in response to changes in oceanographic features.
4 The use of gliders for phytoplankton bloom detection and possible HAB surveillance

4.1 Introduction

Harmful phytoplankton, that are known to cause shellfish poisoning, are frequently monitored for in UK coastal waters. Regulatory monitoring is done by Food Standard Scotland (FSS) to ensure human health and avoid consumption of contaminated shellfish and human intoxication (see Chapter 1.2). If HABs do not directly affect human health little to no monitoring is done by the FSS. High biomass HABs that are responsible for mass mortalities of farmed fish or other aquatic animals do occur in Scottish waters. These species do not cause shellfish poisoning, and are therefore poorly monitored.

An example is, the harmful diatom genus *Chaetoceros*, which has previously been found to cause mass mortalities and reduced growth of farmed Atlantic salmon, leading to an economic loss of over £400,000 (Treasurer et al. 2003). Cells of *Chaetoceros* can cause physical damage to fish gills with no evidence of toxin production (Treasurer et al. 2003). Another example is the harmful dinoflagellate *Karenia mikimotoi*, which caused mortality of over 3000 farmed salmon in the Firth of Clyde during a high density bloom event (Jones et al. 1982). *Phaeocystis* is another phytoplankton genus that is harmful if present in high numbers. It has the potential to cause anoxic events that are linked to fish (Rogers & Lockwood 1990) and shellfish mortality (Peperzak & Poelman 2008). *Phaeocystis* are also known to produce certain toxins (Hansen et al. 2004) and extracellular polysaccharide mucus that can accumulate on beaches as a nuisance foam (Lancelot et al. 1987). While *K. mikimotoi* is enumerated from samples collected by FSS, no regulatory monitoring is done for *Chaetoceros* or *Phaeocystis*.

To reduce economic loss by high density, fish killing phytoplankton, a new method for HAB surveillance and detection needs to be developed. Early detection and prediction of bloom advection would allow the reduction of economic losses in the aquaculture industry as shellfish could be harvested prior to the harmful event and finfish pens could be relocated or protected by tarpaulins. The advective nature of many of these blooms means that early detection of blooms requires surveillance of off shore waters. As noted above, not all harmful species are monitored for and regulatory monitoring is limited to coastal sites with no offshore water sampling included.

Satellites offer an opportunity to observe potentially harmful blooms offshore, using chlorophyll a concentrations as an indicator for high biomass blooms. This study, therefore, focuses on such blooms, as the remote detection of toxic, low biomass HAB
would require an algorithm for species specific discrimination, which is currently in development (Kurekin et al. 2014, Miller et al. 2006).

There are some major limitations to using satellite derived data; Chlorophyll data from satellite imagery is strongly weather dependent with no data availability if cloud cover is high. As cloud coverage is frequently high over Scotland, weekly or monthly averages of chlorophyll concentrations are likely to be overestimated as most data will be recorded during calm and sunny weather that might naturally enhance phytoplankton growth (Gregg & Casey 2007).

Another shortcoming of satellite derived chlorophyll data is that only chlorophyll near the sea surface is captured. Sub-surface chlorophyll maxima are a common feature for phytoplankton blooms (e.g. Weston et al. 2005) and data from the surface waters alone are likely to underestimate the amount of phytoplankton present in the whole water column (Jacox et al. 2015, Hemsley et al. 2015). This is especially important for HAB surveillance as HABs can have subsurface maxima (Seegers et al. 2015) or occur in thin layers (Farrell et al. 2012) that would not be captured by satellites.

An effective method for high biomass HAB surveillance should therefore operate independent of cloud cover and be able to record the vertical structure of phytoplankton blooms. Such information can be collected during cruises (see Chapter 2 and 3); but these are too infrequent and expensive to be used for routine monitoring. Using gliders has been suggested as a cost effective and weather independent alternative (Zhao et al. 2013, Babin et al. 2005) for HAB surveillance. Gliders are buoyancy driven autonomous underwater vehicles that can dive up to 1000 m while making continuous measurements of a range of seawater properties such as salinity and temperature and chlorophyll fluorescence (Eriksen et al. 2001, see Chapter 1.5). Glider data can provide a depth integrated high resolution chlorophyll independent of cloud cover. Data from the whole water column can be collected making chlorophyll data more reliable than measurements only taken from the surface (Hemsley et al. 2015).

Giders are an excellent tool to study physical features such as fronts, eddies and changes in stratification that can be linked to changes in the structure of chlorophyll and therefore vertical phytoplankton distribution (Frajka-Williams et al. 2009, Davis et al. 2008). In spring 2005, glider data showed that the phytoplankton spring bloom in the northern, ice covered part of the Labrador sea extended to nearly 100 m depth; the spring bloom in the ice free, thermally stratified southern region extended down to about 50 m depth while the Labrador shelf was associated with a 5 m thin subsurface chlorophyll layer at 25 m (Frajka-Williams et al. 2009). Seegers et al. (2015) found that *Pseudo-nitzschia* blooms could develop in subsurface layers prior to being moved to the surface by upwelling. Zhao et al. (2013) used gliders...
to observe the development of the three dimensional structure of a *Karenia brevis* bloom, revealing high sub-surface concentrations that would not have been captured by satellite imagery.

With the appropriate sensors, gliders can also collect additional information on inherent optical properties (IOPs) of water such as backscatter (bb), coloured dissolved organic matter (CDOM) and chlorophyll fluorescence. The two main sources for CDOM are terrestrial run off near estuaries and phytoplankton production in the open ocean (Castillo et al. 2010). Increased bb readings can be caused by different particles, however in the surface ocean phytoplankton are considered to be the main source of bb (Behrenfeld et al. 2005).

It has been suggested that the bb to chlorophyll ratio can provide some information about size, shape, morphology and internal cellular structure of phytoplankton cells (Whitmire et al. 2010, Vaillancourt et al. 2004, Cunningham et al. 2003). Some species such as coccolithophores have a high bb to chlorophyll ratio relative to other phytoplankton due to the high bb of their coccoliths (Cunningham et al. 2003, Mckee, personal communication, Sep. 1st, 2016) Colony-forming species such as *Phaeocystis* can cause a high level of noise in *in situ* bb measures due to changes between high bb within high density colonies and lower bb outside colonies (Cunningham et al. 2003, Mckee, personal communication, Sep. 1st, 2016).

Vaillancourt et al. (2004) found differences in the bb signature of 29 different phytoplankton species. There was a general relation between bb and cell size, suggesting that with the same amount of chlorophyll present, blooms consisting of smaller cells would have higher bb than blooms of bigger cells. This relationship was explained with the different proportion of carbon per cell, associated with cell size. For example, some cyanobacteria, that were smaller than other phytoplankton, had the lowest bb recorded in the study (Vaillancourt et al. 2004). Dinoflagellates had generally higher bb than diatoms, probably due to a higher internal carbon concentrations and relatively high cell thickness (Vaillancourt et al. 2004). However there was a up to 10 fold difference in bb between different diatom species. For example, the fish killing diatom *Chaetoceros* had the lowest bb compared to any other tested phytoplankton. Furthermore, blooms of the toxin producing dinoflagellate *K. brevis*, that is responsible for neurotoxic shellfish poisoning, were found to have a bb to chlorophyll ratio that can be up to 20 times lower than observed for non *K. brevis* blooms with similar chlorophyll concentrations (Cannizzaro et al. 2009). Such results suggest that the bb to chlorophyll ratio can potentially be used to distinguish between harmful and non-harmful blooms.

This chapter reports the first mission of a sea glider to study vertical and horizontal distribution of phytoplankton in Scotland and, to our knowledge, in Europe. Previous studies have focused on the east and west coast of the United States (Davis
et al. 2008, Zhao et al. 2013, Seegers et al. 2015) or polar regions (Frajka-Williams et al. 2009, Schofield et al. 2015, Swart et al. 2015). This mission presents a unique case study for high biomass phytoplankton bloom detection and surveillance in European waters using a sea glider coinciding with a cruise mission. The sea glider 'Talisker' was deployed coincidently to the the Corystes cruise discussed in Chapter 3). The glider track replicated two of the transects that were covered during the cruise while other glider transects were designed to sample features that have previously been linked to chlorophyll changes such as the shelf edge and seasonal salinity fronts (chapter 2 and 3, Savidge & Lennon 1987, Gowen et al. 1998, Simpson et al. 1979, Hill & Simpson 1989). Such features create a boundary between calm, stratified and turbulent, tidally mixed water which can provide optimal growth condition for phytoplankton. Good growth conditions and increased phytoplankton density can be recorded by the glider as an increase in chlorophyll and would suggest areas where high biomass blooms could exist.

This study had five aims:
1) to test the potential for gliders to sample physical features such as fronts and the associated response of phytoplankton.
2) To use the information on changes in chlorophyll and the associated physical environment to identify associations between areas of high phytoplankton growth and their environment. Such areas could be important for the development of potentially harmful high biomass blooms.
3) To use the glider to investigate the three dimensional structure of shelf sea fluorescence and compare the information to data available from satellite surface only measurements. Here, information from multiple platforms (cruise, satellite, glider) was used and compared and the potential for multi-platform studies on high density blooms was evaluated.
4) to use data on IOPs, that can be routinely collected by gliders, to collect additional information on the composition of observed blooms.
5) to provide information about the advantages and disadvantages of using gliders in phytoplankton bloom monitoring in comparison to other methods such as remote sensing via satellite.

4.2 Methods
4.2.1 Gliders
The University of Washington sea glider (serial number sg156) 'Talisker' was deployed from the 24.06.2015 to the 18.08.2015. The glider was fitted with a Seabird CTD package to collect data on salinity, water temperature and depth. The glider was additionally equipped with and Eco-Triplet sensor (WET Labs Inc.), measuring
chlorophyll fluorescence at 470/695 nm, red backscatter at 700nm (bb) and coloured dissolved organic matter (CDOM) fluorescence. Talisker was deployed and recovered north of the island of Coll (56.8 N, -6.84 W) and piloted from the marine robotics facility based at SAMS to capture features such as the shelf edge and salinity fronts (Figure 4.1a). The glider moved with a speed up to 0.25 m s$^{-1}$ and the angle of dive profiles was 30°. Optical data was only collected in the top 150 m to increase battery life. Water temperature, salinity and density were recorded for the whole water column, but only results for the top 150 m are shown to match available optical data.

Talisker completed a total of 1238 dives, with each dive providing two data profiles (dive and climb). As gliders dived at an angle, a distance of roughly 200 m was covered between dives. After glider recovery the data was processed using Basestation 2.08 (Seaglider Quality Control Manual, University of Washington) and bin averaged to 5 m depth bins.

Optical sensor data were calibrated following the manufacturers instruction. Salinity data was calibrated using data collected during the Corystes cruise (Calibration for salinity data from the research cruise was checked against salinity analysis done at the CEFAS Laboratory). Glider and research cruise salinity data was compared for dives and depth at close proximity on 16th July. Glider salinity was found to have an offset of 0.1450, and data presented here was corrected for that offset.

The glider track was divided into 6 transects (Figure 4.1 b) to allow better identification of small scale changes. For the same reason parameters were scaled with different maximum and minimum values in the result section to allow visualisation of small scale physical changes and phytoplankton response that would be lost otherwise. For each transect the original glider track has been transposed on a straight transect line (Figure 4.1b). Tracks were transposed using the Barnes interpolation routine (Barnes 1994) in MATLAB. Such interpolations are commonly done (e.g. Porter et al. 2016, Mensah et al. 2016) to reduce bias caused by gliders sampling the same area multiple times when caught in tidal currents.

Note that the rapid changes in salinity to fresher than background or more saline than background values around the thermocline at approximately 50 m for transects 4 to 6, are likely to be caused by a thermal lag on the temperature-conductivity cell used by the glider to measure salinity. This is caused as temperature is measured outside the conductivity cell and conductivity is measured inside the cell. This can lead to a lag of the conductivity measurement compared to temperature measurement which is especially pronounced when the glider crosses the thermocline. This is a well known issue concerning glider salinity data (Lueck & Picklo 1990, Garau et al. 2011) and most data can be corrected during processing with Basestation 2.08, however, here, some artefact remained for transects 4 to 6 near the thermocline.
Figure 4.1: Map of the study area a) Sampling stations from the Corystes cruise (black) and sea glider track (red) b) Corystes stations and original Talisker track (grey) and straight line of transposed glider transect (black).

### 4.2.2 Satellite data

During the whole study period, the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS) provided close to real time satellite data for
chlorophyll (Figure 4.2). The data was used to identify a phytoplankton bloom on the Malin shelf in early July (Figure 4.2 c) and navigate the glider towards it.
4.2.3 Statistical analysis

The MATLAB statistical toolbox was used for correlation and regression analysis of IOPs. Optical data (chlorophyll, CDOM, bb) was not normally distributed (Kolmogorov-Smirnov normality test, $p < 0.01$). Therefore, to determine the correlation between factors non-parametric Spearman Rank correlation coefficients were calculated. Correlation coefficients were classed as weak ($< 0.3$), medium (0.3 - 0.5) or strong ($> 0.5$) relationship as suggested by Cohen (1977) (reviewed by Cohen et al. 2013 and Sedgwick 2014). The $p$ value for statistical significance for Spearman Rank correlations is depended on sample size (Sedgwick 2014). This dataset uses a high number of samples and using Cohen’s classification is therefore more appropriate than using $p$ values for statistical significance, as $p$ values might indicate a statistically significant relationship as a artefact of high numbers of samples.

4.2.4 Research cruise CTD data

Methods for data collection during the RS Corystes research cruise are described in chapter 3.2.

4.3 Results

4.3.1 Talisker transect

Over the whole length of transect 1 the water column was thermally stratified (Figure 4.3). Surface water had temperatures between 11 and 12.5°C. The thermocline deepened from around 20 m at the beginning of the transect to 50 m at the end of
the transect. Salinity added to stratification with low surface salinities under 35 in the first 25 km of the transect.

(a)

(b)

(c)
Chlorophyll was limited to the mixed surface layer with chlorophyll concentrations below the thermocline being close to zero. Chlorophyll was generally patchy; while satellite data was limited by clouds, a good relationship was noted between
the chlorophyll between 75 km and 100 km and the satellite image from the 3rd July (Figure 4.2 a), a few days after the glider passed that area. The highest chlorophyll recorded during the transect with concentrations around 5 µg l\(^{-1}\) was near the shelf break past 125 km. The increase in chlorophyll at the shelf break could also be seen in a later satellite image (Figure 4.2 d) as a yellow band along the shelf edge with around 3 µg chl l\(^{-1}\). Differences in estimated chlorophyll from satellite and glider could be due to timing differences between the two measurements. Also, the chlorophyll maximum recorded by the glider was sub surface and might therefore not be captured by satellite surface measurements.

CDOM was higher at the beginning of the transect near the surface where salinity was lowest, suggesting that CDOM might be linked to fresh water runoff from the coast. CDOM was lowest in the surface waters near the shelf break where chlorophyll concentrations were highest. Bb was highest near the surface between 75 km and 100 km. Both CDOM and bb increased near the bottom, suggesting they were caused by re-suspension of sediments.

The top 150 m of the water column of transect 2 were stratified by both temperature and salinity (Figure 4.4). Mixed surface waters extended down to 50 m depth with temperatures between 12 and 13°C and salinities around 34.3. Waters below the mixed surface layer had temperatures below 11°C and salinities around 34.38.

As in transect 1, chlorophyll and hence phytoplankton was limited to the surface layer. Chlorophyll was patchy along the transect and showed a subsurface maximum of around 4.7 µg l\(^{-1}\) between 20 m and 30 m at dives around 20 to 25 km. Note that lower measured chlorophyll concentrations near the surface can also be caused by chlorophyll quenching during the daytime (Hemsley et al. 2015). Chlorophyll was elevated near the shelf break at the beginning and the end of the transect. CDOM was between 1 and 2 ppb in the top 150 m with no clear peaks. Elevated bb was, like chlorophyll, limited to the mixed surface layer. Peaks in chlorophyll did not co-occur with peaks in bb.
Gliders for bloom detection

(a)

(b)

(c)
Figure 4.4: Contour plot for transect 2 for (a) salinity, (b) temperature, (c) density, (d) chlorophyll, (e) CDOM and (f) bb.

The third transect started in over 1000 m deep offshore water, crossed the shelf break around 15 to 20 km and reached shallow coastal waters at the end of the transect near Corystes station 20 (Figure 4.5). The transect ran close to Corystes
stations 26 to 20. The glider path was therefore transposed onto the straight line connecting station 26 to 20 to allow the comparison between cruise and glider data (Figure 4.5). Both datasets were collected within the same week (16.7.15 to 23.7.15).

Both glider and Corystes CTD deployment located the Irish coastal front (see chapter 3) with rapid changes in salinity and stratification. Talisker recorded the change of salinity characteristic for the front between around 75 km to the end of the transect, while the breakdown of stratification followed shortly after at the beginning of transect 4 (Figure 4.6). Salinity in the first 75 km of the transect was stratified with salinity around 35.25 in the surface layer and 35.35 below the surface layer. Increased salinity up to 35.4 below 50 m indicated the path of the slope current (Hill & Mitchelson-Jacob 1993). After 75 km salinity stratification disappeared and salinities decreased rapidly to approximately 35.0.

Ship measurements generally agreed with glider observations with similar physical values and stratification patterns being observed. The rapid decrease of salinity was also visible after 75 km with salinities as low as 35.00 during the transect. Salinity continued to decrease to 34.7 further coastal as recorded by Corystes (Chapter 3, Figure 3.12).

Water temperatures recorded by Talisker and on Corystes were similar with surface values above 12°C and a thermocline at around 40 m. The higher resolution of the Talisker transect showed the small scale variability of the depth of the thermocline, changing rapidly between 20 m and 60 m depth between 20 km and 25 km. Talisker recorded the deepening of the thermocline to 60 m near the coastal front. The same pattern was observed during the Corystes cruise, but a few km closer to the coast than recorded by Talisker, between station 20 and 19 (Chapter 3, Figure 3.12).

Glider measured chlorophyll was highest in stratified surface waters around the shelf break with concentrations up to 4.35 µg l\(^{-1}\). Chlorophyll decreased to near zero below the thermocline, following the small scale changes in thermocline depth found between 20 and 25 km. CDOM was lowest in surface waters and highest where salinity was lowest around the coastal front. Bb was mostly limited to the mixed surface layer with some small peaks near the seabed that were most likely caused by sediment. Changes in bb near the surface were not proportional to changes in chlorophyll. High peaks in bb were present in the surface where chlorophyll was present, but not in high concentrations.
4 Gliders for bloom detection

(a)

(b)

(c)

(d)
Figure 4.5: Contour plot for transect 3 for (a) salinity, (b) temperature, (c) density, (d) chlorophyll, (e) CDOM and (f) bb from the Talisker mission and (g) salinity, (h) temperature and (i) density from corresponding Corystes stations.

For the fourth transect Talisker was piloted north towards an area of high chlorophyll that had been identified from satellite (Figure 4.2c). The Corystes stations
most comparable to the Talisker transect are stations 20, 14, and 34 to 36. Note that in Figure 3.13 the distance covered by Corystes is larger than distance covered by Talisker as there is a small difference between glider transect and Talisker stations (see Figure 4.1).

The coastal front was seen at the end of transect 3 as the ship and glider crossed from high salinity Atlantic waters into fresher coastal waters. In this transect Talisker remained in the well mixed low salinity coastal waters for the first 10 km before crossing the coastal front again back into higher salinity water. The Corystes transect showed an overall good agreement despite the temporal and spacial differences of the data collection. After crossing the coastal front thermal stratification develops again, alongside a weak salinity stratification. Salinities recorded by Talisker are generally lower than values recorded during the research cruise. This is most likely explained by the glider track being pushed eastward towards coastal, fresher water by tides and currents.

At the beginning of the transect in the well mixed water chlorophyll concentrations extended throughout the whole water column. As the water column became thermally stratified, chlorophyll was limited to the surface layer again. Surface chlorophyll was around 1 µg l$^{-1}$ to 2 µg l$^{-1}$ near the front, but peaked at over 5 µg l$^{-1}$ at around 50 km. As for transect 1, CDOM was highest where salinity was lowest at the beginning of the transect. Bb was highest in the surface waters close to the chlorophyll peak. Bb was also high in the bottom waters below the chlorophyll peak and could be caused by sinking material or re-suspension of sediment near the sea bed.
Gliders for bloom detection

(a) 

(b) 

(c) 

(d)
Figure 4.6: Contour plot for transect 4 for (a) salinity, (b) temperature, (c) density, (d) chlorophyll, (e) CDOM and (f) bb from the Talisker mission and (g) salinity, (h) temperature and (i) density from corresponding Corystes stations.

Talisker reached the end of the fourth transect a week after the elevated satellite chlorophyll signature had been observed in the area (Figure 4.2 c). There had been
no usable satellite images of the area since. Talisker was piloted to run a straight transect between the Corystes stations 36 to 38 in an attempt to sample the bloom if it was still present (Figure 4.7). During transect 5, Talisker was slowed by strong tidal currents; after one week it only travelled 38 km compared to the nearly 90 km transect completed the week before. The error of sampling the same area due to circular movement caused by changing tides was removed from the data as data was plotted onto a straight transect. During transect 5, salinity remained stratified with a surface salinity of 35.0 and a bottom salinity of 35.2 at the beginning of the transect that decreased to a surface salinity of 34.7 and a bottom salinity to 34.8 by the end. Temperature remained stratified similar to the end of the previous transect.

At the beginning of the transect chlorophyll and bb were limited to the surface layer. After 10 km along the transect, chlorophyll, CDOM and bb started to increase throughout the whole water column. At this point the glider was close to the high chlorophyll signature previously found by satellite. The peak of chlorophyll (7.5 µg l$^{-1}$) was found in the mixed surface layer, with high concentrations of chlorophyll, CDOM and bb below the surface also evident. Close to the glider track Corystes net tow and surface water samples found a high abundance of *Phaeocystis* in the water with over 1 million cells l$^{-1}$ at Corystes station 37. *Phaeocystis* colonies have been recorded with sinking rates to up to 200 m d$^{-1}$ (Kiørboe 1993) which explains the observed vertical distribution of chlorophyll that extended throughout the water column. High cell densities of *Phaeocystis* have previously reported with high chlorophyll readings up to 40 µg l$^{-1}$ (Althuis et al. 1994) and can therefore explain the high chlorophyll readings of over 8 µg l$^{-1}$ found in this study (Figure 4.8).

While the glider successfully detected chlorophyll from the *Phaeocystis* bloom and demonstrated the depth to which it extended the extracellular mucus produced by *Phaeocystis* may have impacted its quantification as mucus produced by *Phaeocystis* likely attached to the optical sensors, potentially causing an increase in readings. Optical readings might therefore be overestimating the quantity of the cells present. Results suggested that the bb sensor was the most sensitive to bio-fouling, as this sensor saturated after 20 km, maintaining this value for the remainder of the deployment. This suggests that the bb sensor might have been completely covered by bio-fouling. While other sensors were affected, they were still able to record changes in CDOM and chlorophyll, making the *Phaeocystis* detection a qualitative rather than quantitative bloom detection. After the bloom chlorophyll decreased down to 2 µg l$^{-1}$, suggesting that readings might have been overestimated by approximately this value.
4 Gliders for bloom detection

(a)

(b)

(c)

(d)

(e)
Figure 4.7: Contour plot for transect 5 for (a) salinity, (b) temperature, (c) density, (d) chlorophyll, (e) CDOM and (f) bb.
At the beginning of August, Talisker was sent from her location at the end of transect 5, back to the recovery point north of the island Coll (Figure 4.8). During this last transect salinity, remained stratified but stratification deepened. Temperature remained stratified at around 50 m for the first 60 km of the transect. Between 60 km and 75 km stratification deepened to 120 m. After 75 km thermal stratification was weaker than before, but still present between 40 and 100 m. Chlorophyll was highest at the beginning of the transect but decreased back down to a minimum of 2.3 µg l\(^{-1}\). CDOM continued to increase with decreasing salinity. Bb was not analysed as the sensor remained saturated, presumably from bio-fouling, during the whole transect.
(a)

(b)

(c)

(d)
4.3.2 Analysis of optical properties

Chlorophyll recorded by Talisker was used as an index for phytoplankton. Phytoplankton cells in the surface ocean can be a major source of bb (Behrenfeld et al. 2005). A strong positive relationship was evident between chlorophyll and bb for transects 1 to 4 (Table 4.1). Linear regression analysis showed that bb generally increased with increasing chlorophyll (Figure 4.9). The regression equation and the percentage of change explained by regression are presented in Table 4.2.

Within transect 1, two locations with different bb to chlorophyll ratios were evident. Between 75 km and 100 km bb to chlorophyll ratio was noticeably higher than before 75 km or after 100 km (4.9 a). During transect 3, dives in the first 20 km of the transect were generally above the regression line and dives between 30 km
and 40 km below the regression line. During transect 4 both bb and chlorophyll in the first 50 km were lower than later in the transect.

Table 4.1: Spearman rank correlation between chlorophyll and bb, chlorophyll and CDOM and salinity and CDOM. The Spearman coefficient, the p value and the strength of the correlation as suggested by Cohen (1977) is given.

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<th>Spearman’s coefficient</th>
<th>p</th>
<th>Strength of correlation</th>
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</tr>
<tr>
<td>sal,CDOM</td>
<td>0.3039</td>
<td>&lt;0.001</td>
<td>weak to medium positive</td>
</tr>
<tr>
<td>Transect 3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl,bb</td>
<td>0.7534</td>
<td>0</td>
<td>strong positive</td>
</tr>
<tr>
<td>chl,CDOM</td>
<td>-0.4749</td>
<td>0</td>
<td>medium negative</td>
</tr>
<tr>
<td>sal,CDOM</td>
<td>0.2331</td>
<td>&lt;0.001</td>
<td>weak positive</td>
</tr>
<tr>
<td>Transect 4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl,bb</td>
<td>0.8737</td>
<td>0</td>
<td>strong positive</td>
</tr>
<tr>
<td>chl,CDOM</td>
<td>-0.3020</td>
<td>0</td>
<td>weak to medium negative</td>
</tr>
<tr>
<td>sal,CDOM</td>
<td>-0.5941</td>
<td>0</td>
<td>strong negative</td>
</tr>
<tr>
<td>Transect 5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sal,CDOM</td>
<td>-0.8771</td>
<td>0</td>
<td>strong negative</td>
</tr>
<tr>
<td>Transect 6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sal,CDOM</td>
<td>-0.6454</td>
<td>0</td>
<td>strong negative</td>
</tr>
</tbody>
</table>

Phytoplankton can also be a major source for CDOM (Castillo et al. 2010). For transects 1 to 4 the relationship between chlorophyll as an index of phytoplankton and CDOM was medium to weakly negative, and linear regression explained little of the variation in the data (Table 4.2). This suggests that the statistical significance for correlation found for transect 1, 3 and four might be an artefact of the high sample number used for the analysis rather than a true correlation (Cohen 1977, Sedgwick 2014). The relationship between chlorophyll and bb or CDOM was not explored for transects 5 and 6 as bio-fouling was likely to affect optical reading.
Figure 4.9: bb plotted against chlorophyll for transects a) 1, c) 2, e) 3 and g) 4. CDOM plotted against chlorophyll for transect b) 1, d) 2, f) 3, h) 4.
Table 4.2: Equation for regression lines in Figures 4.9 and 4.10 and $r^2$ given as percentage of data that is explained by the regression equation.

<table>
<thead>
<tr>
<th>Transect</th>
<th>x,y</th>
<th>Regression Equation</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (excl. 75 to 100 km)</td>
<td>chl, bb</td>
<td>$bb = 0.1703 + chl x (0.0687)$</td>
<td>59.03%</td>
</tr>
<tr>
<td>1 (75 to 100 km)</td>
<td>chl, bb</td>
<td>$bb = 0.0687 + chl x (0.8834)$</td>
<td>64.08%</td>
</tr>
<tr>
<td>1</td>
<td>chl, CDOM</td>
<td>$CDOM = 2.0838 + chl x (-0.1167)$</td>
<td>21.81%</td>
</tr>
<tr>
<td>1</td>
<td>sal, CDOM</td>
<td>$CDOM = 61.0556 + sal x (-1.6721)$</td>
<td>63.80%</td>
</tr>
<tr>
<td>2</td>
<td>chl, bb</td>
<td>$bb = 0.4256 + chl x (0.0720)$</td>
<td>40.51%</td>
</tr>
<tr>
<td>2</td>
<td>chl, CDOM</td>
<td>$CDOM = 1.5458 + chl x (0.0004135)$</td>
<td>0.0002%</td>
</tr>
<tr>
<td>2</td>
<td>sal, CDOM</td>
<td>$CDOM = -28.3797 + sal x (0.8443)$</td>
<td>8.50%</td>
</tr>
<tr>
<td>3</td>
<td>chl, bb</td>
<td>$bb = 0.1725 + chl x (0.1161)$</td>
<td>57.23%</td>
</tr>
<tr>
<td>3</td>
<td>chl, CDOM</td>
<td>$CDOM = 1.6775 + chl x (-0.0331)$</td>
<td>16.20%</td>
</tr>
<tr>
<td>3</td>
<td>sal, CDOM</td>
<td>$CDOM = 3.0413 + sal x (-0.0404)$</td>
<td>0.02%</td>
</tr>
<tr>
<td>4</td>
<td>chl, bb</td>
<td>$bb = 0.1639 + chl x (0.1916)$</td>
<td>81.55%</td>
</tr>
<tr>
<td>4</td>
<td>chl, CDOM</td>
<td>$CDOM = 1.9424 + chl x (0.0622)$</td>
<td>10.92%</td>
</tr>
<tr>
<td>4</td>
<td>sal, CDOM</td>
<td>$CDOM = 52.8398 + sal x (-1.4477)$</td>
<td>25.13%</td>
</tr>
<tr>
<td>5</td>
<td>sal, CDOM</td>
<td>$CDOM = 92.8909 + sal x (-2.5782)$</td>
<td>61.25%</td>
</tr>
<tr>
<td>6</td>
<td>sal, CDOM</td>
<td>$CDOM = 17.0230 + sal x (-0.3819)$</td>
<td>28.87%</td>
</tr>
</tbody>
</table>

Next to phytoplankton, a major source of CDOM is terrestrial input (Bowers & Brett 2008). Here salinity is used as an index for terrestrial input via freshwater run-off. The relationship between salinity and CDOM is strongly negative for transects 1, 4, 5 and 6, suggesting that salinity can be used as an index for terrestrial freshwater input. CDOM decreased with increasing salinity and decreasing freshwater input. For transect 1 and 5 the regression line could explain over 60% of variation in the data (Figure 4.10, Table 4.2). Transects 4 and 6 also showed a negative relationship but linear regression explained less than 30% of the variation in the data (Table 4.2).

For transect 2 and 3 the correlation coefficient indicated a weak correlation and the high statistical significance might again be caused by the high number of samples (Cohen 1977, Sedgwick 2014). During these transects salinity changes were low and were indicating little impact of changes in freshwater input. Linear regression for those transects explained less than 10% of the variation in data.
Figure 4.10: CDOM plotted against salinity for a) transect 1, b) transect 2, c) transect 3, d) transect 4, e) transect 5 and f) transect 6.

The Corystes stations 28, 26, 24, 23, 21, 20, 14 and 35 are all stations that were located close to the glider track and had a full phytoplankton count from surface waters. To find links between the bb to chlorophyll ratio and full species counts, bb was plotted against chlorophyll for the top 40 m from the 10 glider dives that were closest to these Corystes stations. *Phaeocystis* was the most numerous phytoplankter for all stations, except for station 21 and 28, where *Karlodinium* was most abundant. *Karlodinium* was present in high numbers for all stations except for station 35, where it was absent. If IOPs change with species composition, stations 21 and 28 would be expected to be similar to each other but different to other stations, especially
station 35. Surface glider data close to station 21 (dominated by Karlodinium) had low intercept and low slope, similar to data close to station 23 (Table 4.3), which had a different species composition (Appendix B). Data close to station 35 (Karlodinium absent) had a high slope and low intercept, similar to stations 14 and 28 (Table 4.3), where Karlodinium was present or dominant respectively.

![Figure 4.11: bb plotted against chlorophyll for the top 40 m for dives close to Corystes stations 28, 26, 24, 23 21, 20, 14 and 35.](image)

Table 4.3: Equation for regression lines in Figures 4.11 and r² given as percentage of data that is explained by the regression equation

<table>
<thead>
<tr>
<th>Station</th>
<th>Regression Equation</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>28</td>
<td>bb = 0.3102 + chl x (0.1113)</td>
<td>69.10%</td>
</tr>
<tr>
<td>26</td>
<td>bb = 0.3842 + chl x (0.0728)</td>
<td>43.47%</td>
</tr>
<tr>
<td>24</td>
<td>bb = 0.3321 + chl x (0.0973)</td>
<td>45.08%</td>
</tr>
<tr>
<td>23</td>
<td>bb = 0.2457 + chl x (0.0522)</td>
<td>51.74%</td>
</tr>
<tr>
<td>21</td>
<td>bb = 0.2227 + chl x (0.0644)</td>
<td>22.32%</td>
</tr>
<tr>
<td>20</td>
<td>bb = 0.0551 + chl x (0.2118)</td>
<td>36.29%</td>
</tr>
<tr>
<td>14</td>
<td>bb = 0.3035 + chl x (0.1489)</td>
<td>58.53%</td>
</tr>
<tr>
<td>35</td>
<td>bb = 0.2203 + chl x (0.1704)</td>
<td>65.39%</td>
</tr>
</tbody>
</table>
4.4 Discussion

4.4.1 Phytoplankton surveillance and small scale physical changes

Talisker successfully recorded a high resolution set of physical and optical water column properties on the Malin Shelf during this study. Such datasets provide a much more detailed picture of the vertical water column than would be possible with satellite, and a much higher horizontal resolution than would be possible from cruise on board measurements. The combination of high resolution physical and biological data allows us to investigate the horizontal and vertical phytoplankton response to small scale physical changes (Babin et al. 2005). This will provide information about how sensitive phytoplankton is to small changes in temperature and salinity, which is important for biological modelling (Gillibrand et al. 2016) and assessment of phytoplankton sensitivity to temperature and salinity changes caused by global warming (Edwards et al. 2006). However, for such analysis a larger dataset is needed.

During this study, the link between thermocline depth and phytoplankton distribution was clearly visible. During most dives the depth of the thermocline reflected the exact depth of chlorophyll distribution with chlorophyll below the thermocline generally being close to zero. Vertically, chlorophyll was clearly structured by temperature; Phytoplankton was generally limited to the surface layer above the thermocline on the Malin shelf in summer (Savidge & Lennon 1987, Gowen et al. 1998), however this is the first study to record the temperature response of phytoplankton in very high vertical resolution over an extended period of time.

Horizontal distribution of chlorophyll was very patchy with no simple correlation explaining the observed patchiness. This is important for phytoplankton surveillance as stations collected from scientific cruises are often far enough apart (10 km or more) to easily miss high density patches as observed here. Glider deployments offer a unique opportunity to capture such patterns and improve our understanding of phytoplankton distribution on the Malin shelf.

The glider successfully identified the Irish coast front and the high vertical sampling resolution allowed us to pinpoint the exact location of the front and the direct response of phytoplankton. Here we found that chlorophyll was elevated at the stratified side of the coastal front, but decreased directly at the front. Fronts between well mixed and stratified waters are considered optimal for phytoplankton growth if nutrients are introduced in the surface layer from vertical mixing at the well mixed site. Data from chapter 3 showed that nutrient concentrations were low in the well mixed waters near the coast which might explain why chlorophyll concentrations were not elevated near the front.

Chapter 2 described the importance of the shelf edge in structuring the phyto-
plankton community in autumn. During summer, the separation effect of the shelf break was reduced by the spillover of Atlantic water onto the shelf as far as the Islay front (chapter 3). In this chapter, the glider confirmed the spillover of Atlantic water as observed in chapter 3, with enhanced phytoplankton growth near the shelf break.

Here, we show the potential of a glider to be used in high density HAB surveillance in offshore waters. The glider successfully recorded a high density bloom of the nuisance genus *Phaeocystis*. The bloom was found centrally in the Malin Shelf (transect 5), around 50 km away from the shelf break, Irish coastal front or Islay front (see Chapter 3). The bloom was associated with strong thermal stratification and a thermocline around 40 m.

Other harmful high biomass blooms common in the area are *K. mikimotoi* and *Chaetoceros*, both of which can cause extensive fish kills and mortality of other benthic fauna (e.g. Davidson et al. 2009, Treasurer et al. 2003). Early detection in offshore waters and surveillance of such blooms would therefore be desirable with glider deployment offering the potential to do so (Babin et al. 2005). Gliders deployments offer a cheaper alternative to monitoring cruises, while providing a higher horizontal resolution and longer deployment time of several month. Unlike satellite data, glider measurement are not limited by weather and can record the depth structure of blooms with the potential to detect sub-surface thin-layer blooms (Raine et al. 2010a, Farrell et al. 2012).

Unfortunately it is currently not possible to discriminate between HAB and harmless blooms from chlorophyll data alone. There are currently no sensors available to detect HAB toxins *in situ* with the exception for *Karenia brevis*, which was successfully identified *in situ* by specific glider sensors (Zhao et al. 2013). However new sensors for phytoplankton discrimination are being rapidly developed and can be easily mounted to gliders (Babin et al. 2005). Newly developed sensors include the Jupiter Autonomous Microscope (Ziccarelli et al. 2016) that would allow identification of certain phytoplankton species or mobile flow cytometers that are currently being developed to be used during glider deployment (McLane Research Laboratories 2016 and personal communication, Oct. 15th, 2016).

### 4.4.2 Combining glider, cruise and satellite observations

The data collected from the glider showed an overall good agreement with data collected during the Corystes cruise (chapter 3). When comparing ship and glider data it is important to consider the differences between sampling methods. Glider data was collected at a much higher horizontal resolution with dives every 200 m compared to 10 to 20 km between cruise stations. Such data sets are therefore able to measure physical changes on a much smaller scale; for example small scale changes in
thermocline depth could be recorded accurately together with the direct response of chlorophyll distribution. The high resolution of glider data also allowed to pinpoint the location and extent of fronts with a higher precision. Another advantage is that glider deployment was possible over a longer time and larger area due to lower cost and less weather restrictions compared to scientific cruises.

Different timing of data collection has to be considered when comparing different data sets. All data was collected during summer 2015. The glider was deployed from the 24th June to the 18th August. Corystes data was collected between 15th and 21st of July 2015 with the ship moving considerably faster than the glider. Both ship and glider started transect 3 on the same date (16th July), with Corystes sampling all stations on the transect on the same day, while it took Talisker approximately one week to complete the transect. Data from transect 4 was collected two weeks apart. Phytoplankton blooms can be prolonged events, however a week or longer can result in significant changes in phytoplankton numbers and distribution. Despite the differences in resolution and timing, transects 3 and 4 showed an overall good agreement between Talisker and Corystes data. Both the gilder and ship observations showed the position of the coastal salinity front at the end of transect 3 and beginning of transect 4. Both data sets also showed the high salinity signature of the slope current and the overspill of high salinity Atlantic water onto the shelf (discussed in chapter 3.4.1). The Islay front was sampled during the Corystes cruise but not during the Talisker mission.

Chlorophyll concentrations recorded by Talisker were generally higher than chlorophyll measured on board Corystes. Note that different methods were used for chlorophyll measures. During the Corystes cruise chlorophyll a was measured using a Turner trilogy fluorometer (Chapter 3.2). Fluorescence emission was measured at 663 to 750 nm. Talisker was equipped with a WET labs Eco-Triplet and fluorescence emission was measured at 470 nm and 695 nm. Differences between measures could also be caused by the patchiness of horizontal chlorophyll distribution. High horizontal resolution of glider measurements was more likely to pick up patches of high chlorophyll while stations 10 km or more apart might miss such patches. The differences in timing of sampling also have to be considered as phytoplankton numbers can change rapidly within days.

The highest chlorophyll recorded during the cruise was 3.8 $\mu$g l$^{-1}$ near the surface at station 12 and 2.1 $\mu$g l$^{-1}$ at 20 m at station 35. Every other chlorophyll sample was below 2 $\mu$g l$^{-1}$. The chlorophyll subsurface maximum at station 35 was also found by Talisker around that location with a maximum of 5.3 $\mu$g l$^{-1}$. Talisker frequently recorded chlorophyll maxima around 5 $\mu$g l$^{-1}$ or higher. Values recorded by Talisker agree with previous chlorophyll concentrations recorded on the Malin shelf in summer with maximum values around 5 $\mu$g l$^{-1}$ (Savidge & Lennon 1987).
and 7 $\mu$g l$^{-1}$ (Gowen et al. 1998).

This study had access to daily chlorophyll images from MODIS and VIIRS satellites. Unfortunately most days cloud cover reduced the quality of satellite images with only four usable images during the two month glider deployment (Figure 4.2). One of the advantages of using gliders is that data collection is not restricted by weather and Talisker was able to collect a much larger dataset than satellite images could provide during the study period. However, satellite images were still useful to support the glider study. On the 22nd of July, satellite data showed part of a high chlorophyll bloom (around 5 $\mu$g l$^{-1}$) in the middle of the study area. The glider was piloted towards it and recorded elevated chlorophyll levels similar to those recorded by satellite. (Figure 4.6, around 50 km). While satellite data could give no information about the vertical distribution, Talisker data revealed that chlorophyll was restrained to the surface layer (between 20 and 60 m depending on the location) with highest concentrations at, or close to, the surface.

4.4.3 Optical properties

Chlorophyll data from glider or satellite can provide useful information about phytoplankton distribution and changes in abundance. Identification of phytoplankton groups or species from chlorophyll signatures alone is currently impossible. However the use of IOPs that can be easily measured alongside chlorophyll is promising (Vaillancourt et al. 2004, Cannizzaro et al. 2009). Optical signatures of laboratory mono cultures are distinguishable between phytoplankton species (Vaillancourt et al. 2004). Natural phytoplankton assemblages in the field present a greater challenge. However Cannizzaro et al. (2009) and Cunningham et al. (2003) showed that high density blooms comprised of mostly one species can have recognisable optical signatures. Here, we explore the use of routinely collected optical parameters in studying natural mixed phytoplankton assemblages.

CDOM concentrations found in this study fall within the range of CDOM measured in the Clyde Sea (Bowers & Brett 2008) and other coastal waters (Kowalczuk et al. 2006). CDOM measured by Zhao et al. (2013) during a glider mission near the coast of Florida was approximately 2 to 3 time higher, even during bloom conditions. Terrestrial input is considered to be the major source of CDOM in estuaries, leading to a strong negative relationship between salinity and CDOM in estuaries and near coastal waters (e.g. Bowers & Brett 2008). During transects 1, 4, 5 and 6 there was a significant strong relationship present, suggesting that even at a relatively large distance from the coast, CDOM can still be linked to terrestrial input. Other studies that relate changes in CDOM to terrestrial input generally focus on salinity changes from a fresh water source (Bowers & Brett 2008, Castillo et al. 2010). In Transects 2 and 3 salinity was always above 35.0, indicating that any
terrestrial input was highly diluted and salinity cannot be used as a good indicator for land run off for these transects.

In oceanic waters, where land run off is considered low, production by phytoplankton is considered a major source of CDOM (Kowalczuk et al. 2006, Stedmon et al. 2000, Castillo et al. 2010). Here, the relationship between chlorophyll and CDOM was weak (Figure 4.9, Table 4.2), showing that the production of CDOM was not proportional to phytoplankton abundance in this case. Previous studies have suggested that in some cases CDOM production from phytoplankton material or slow degradation of material to CDOM can take longer than the span of a bloom. This means high CDOM signature might be present weeks after the bloom has died (Bricaud et al. 1981, Kalle 1966). It is also possible that other CDOM pools are present from bacteria or zooplankton (Steinberg et al. 2004, Ortega-Retuerta et al. 2009).

Bb can have a wide variety of sources including dissolved organic matter, suspended particulate matter, colloids, viruses, bacteria, phytoplankton, detritus and bubbles (reviewed by Stramski et al. 2004). Behrenfeld et al. (2005) found two distinct patterns in oceanic surface waters when bb was plotted against chlorophyll; in regions of low productivity (below 0.2 µg chl l\(^{-1}\)) changes in chlorophyll do not relate to changes in bb. In regions of higher (above 0.2 µg chl l\(^{-1}\)) productivity, bb showed a strong linear correlation to chlorophyll, suggesting that in regions of high chlorophyll, most backscatter is caused by phytoplankton (Behrenfeld et al. 2005). Here, bb concentrations were considerably low (up to 0.0013 m\(^{-1}\) sr\(^{-1}\)) compared to Behrenfeld et al. (2005) even though chlorophyll in the surface area was generally above 0.2 µg chl l\(^{-1}\). Despite the relatively low bb found in this study, bb and chlorophyll were still found to have a positive relationship for transects 1 to 4 (Figure 4.9, Table 4.2). The relationships for transect 5 and 6 were not determined as they were likely influenced by bio-fouling.

To see if different phytoplankton communities can be linked to a different bb to chlorophyll ratio, bb was plotted against chlorophyll for glider dives that were close to cruise stations (Figure 4.11). Stations 21 and 23 have a very similar bb to chlorophyll relationship. However, similarity analysis suggest that the sites were over 50% dissimilar in terms of species composition (Chapter 3, Figure 3.7). The regression line between stations 20 and 14 were different, even though full species counts suggest a similar species composition (Appendix B, Table B.1). In conclusion, during this study it was not possible to relate bb to chlorophyll ratios to phytoplankton community. Several limitations to this approach were that the glider was not at the exact location at the exact time as data was collected on-board the Corystes, so community might have changed between ship and glider measures. Moreover other non living particles might have contributed to the bb pool.
4.4.4 Limitations to the use of gliders

A very common problem for long term glider deployment is that of bio-fouling (Zhao et al. 2013, English et al. 2009). During this study the optical sensors operated without any indication of bio-fouling until transect 5. Satellite images suggested a high chlorophyll bloom of up to 5 $\mu g \cdot l^{-1}$ close to the glider track, and samples from the Corystes cruise in the area found *Phaeocystis* concentrations of up to 1 million cells $l^{-1}$. The high chlorophyll signature found by the glider to the end of transect 5 showed the extent and depth structure of the *Phaeocystis* bloom. Bio-fouling in this case is likely linked to the *Phaeocystis* as this genus is known to produce a sticky polysaccharide mucus that might stick to the optical sensors (Schoemann et al. 2005).

High chlorophyll readings throughout the water column during the bloom might be explained by sinking material. However, all three optical sensors reported a simultaneous and rapid increase in readings; this suggests that sensor readings were negatively influenced by bio-fouling. Bb increased quickly to sensor saturation values. This is possible for blooms with a high bb to chlorophyll ratio, but the fact that sensors remained at saturation level after the bloom makes bio-fouling a more likely explanation. CDOM and chlorophyll did not reach sensor saturation and readings decrease again during transect 6 but remained higher than expected. Chlorophyll measures decreased from 7 $\mu g \cdot l^{-1}$ to 2 $\mu g \cdot l^{-1}$, but remain above 2 $\mu g \cdot l^{-1}$ for the rest of the mission. High background levels of chlorophyll can be expected in coastal waters in summer, however the observed pattern suggests that chlorophyll and bb in transect 6 were most likely overestimated due to bio-fouling. Interestingly, Zhao et al. (2013), who used a similar Wetlab Eco-triplet sensor, reported a similar pattern of bio-fouling, where the bb sensor reached saturation while other sensors remained functional.

Currently, the best way of dealing with bio-fouling is glider recovery and manual cleaning in frequent intervals; anti-fouling coating cannot be used on optical sensors as it would interfere with readings (English et al. 2009). Seegers et al. (2015) decided to use bio-fouling as an additional source of data collection; barnacles growing on the glider were tested for domoic acid as an additional measure for the presence of toxin producing *Pseudo-nitzschia* cells in the water.

Even in the absence of bio-fouling, sensor calibration can drift with time (Hemsley et al. 2015). Additional measurements, e.g. ship based are needed to be able to correct glider drift (Hemsley et al. 2015). Here we found an overall good agreement between ship and glider data for temperature, but higher salinities recorded by the glider compared to ship measurements. Another issue addressed by Hemsley et al. (2015) was fluorescence quenching during daylight hours. Surface chlorophyll
measured during sunlight hours is likely to be underestimated due to fluorescence inhibition by high irradiance.

4.5 Conclusion

This study reports the first use of sea gliders to survey phytoplankton on the Malin shelf. Glider measurements offer robust, high resolution three dimensional chlorophyll data, that can be used, together with satellite and other data, to characterise shelf sea phytoplankton. The glider recorded a higher resolution data set than is possible during a research cruise. Satellite images have the potential to cover a greater area but are limited by cloud cover and cannot provide information on three dimensional chlorophyll distribution. Glider data showed the variation of chlorophyll with depth and its strong relationship to temperature. Horizontal patchiness of chlorophyll suggests that high chlorophyll patches might be missed by ship sampling with larger distances between stations.

A high biomass bloom of the potentially harmful species *Phaeocystis* was successfully recorded by Talisker towards the end of the mission. This suggests that gliders could be routinely used for offshore surveillance of phytoplankton with the possibility of early detection of high biomass blooms that could potentially be harmful to coastal economy.

Phytoplankton identification from glider measurements remains challenging. IOPs provide robust and easily available data that can be used to study phytoplankton as shown for laboratory monocultures (Vaillancourt et al. 2004) and high density single species blooms in the field (Cannizzaro et al. 2009). However, the relation between phytoplankton and IOPs are not always straight forward and further work to address such relationships is needed. Newly developed sensors might allow species identification from imagery (Ziccarelli et al. 2016), however this would increase battery use and thereby reduce glider deployment time. Bio-fouling also became a problem after about 1 month deployment, suggesting that if gliders will be used for monitoring, frequent recovery would be necessary.
5  An individual-based model for high biomass HAB transport

Part of the analysis presented here was published in:

5.1 Introduction

Chapter 4 described the first application of sea gliders for the detection and surveillance of high density phytoplankton blooms in Scottish waters. Once high density blooms are detected offshore, bio-physical computer models offer the potential to predict growth and advection of the bloom. This will potentially allow estimation and early warning of harmful phytoplankton densities at coastal sites and an assessment of the potential damage blooms could cause to coastal aquaculture. Once this information is available counter steps can be taken, i.e. early harvest of shellfish or relocation of cages used in finfish aquaculture or the deployment of tarpaulins to protect cages from harmful blooms.

In this chapter, a computer model with potential predictive capacity for HAB transport is presented and discussed. The model couples a hydrodynamic model with a phytoplankton growth and transport model. Here, *Karenia mikimotoi* was used as a model species for HAB transport and development. *K. mikimotoi* is a dinoflagellate common in British waters that can cause extensive fish mortalities under high density bloom conditions (Jones et al. 1982, Davidson et al. 2009). *K. mikimotoi* is suitable as a model species as it is monitored in parallel with regulatory sampling by Food Standards Scotland (FSS), providing a good temporal and spatial dataset for model verification, with several high biomass bloom examples for the west coast of Scotland.

High biomass blooms of *K. mikimotoi* can cause low oxygen conditions and increased H$_2$S following bloom decay (Robin et al. 2013). Other studies also show that *K. mikimotoi* can produce several bioactive compounds which can be hemolytic and ichtyotoxic (Brand et al. 2012). In UK waters, *K. mikimotoi* has lead to the loss of over 3000 farmed salmon in the Firth of Clyde in 1980 (Jones et al. 1982). Gills were damaged and dead fish showed a complete necrosis of lamellar tissues (Jones et al. 1982). In 2003, 53000 fish died in Orkney and Shetland as a consequence of a bloom (Davidson et al. 2009).

In 2005, up to 3.7 million *K. mikimotoi* cells l$^{-1}$ were observed during a prolonged bloom in coastal waters in west of Ireland. Between mid June to mid September,
discolouration of seawater and foam formation near the coast was reported (Silke et al. 2005). The intense bloom caused mortalities of marine organisms including fish, benthic invertebrates and farmed bivalves. The following year, in 2006, an exceptional bloom of \textit{K. mikimotoi} was recorded around the west and north coast of Scotland over several months (Davidson et al. 2009). The extent of the bloom, both spatial and temporal, was the greatest ever recorded in UK waters. Fish mortalities were few, however mortalities of multiple benthic species were reported (Davidson et al. 2009). \textit{K. mikimotoi} was originally found near the islands of Mull, Harris and Lewis in July and subsequently further north near Skye, Orkney and Shetland (Davidson et al. 2009). The rapid increase of cells at coastal locations suggested that high concentrations were unlikely to be caused by local growth alone and at least some percentage of blooms were caused by advection of cells to the coast (Davidson et al. 2009). Since 2006 high densities of \textit{K. mikimotoi} have been found in a number of years, but a bloom with the extent of that in 2006 has not been repeated.

High biomass blooms such as \textit{K. mikimotoi} have the potential to be detected remotely via satellite imagery or through the use of new technology for surveillance such as gliders, as proposed in chapter 4. After offshore bloom detection, prediction of bloom transport and development is necessary to provide early warning for coastal sites. The model presented here has the potential to provide such predictions by modelling growth and advection of a remotely detected seed population of the target species. This was done by coupling a hydrodynamic model with an individual based phytoplankton model included the biology of \textit{K. mikimotoi}, with no other species being described by the model (see chapter 1.6). \textit{K. mikimotoi} cells are subjected to growth, mortality, motility and advection driven by the hydrodynamic model.

In this chapter the model is used to address the following research questions:

Q1) Can the model explain the exceptional \textit{K. mikimotoi} blooms that occurred in 2006, 2010 and 2011 by a combination of advection and growth?

Q2) Is it necessary to include biological growth and behaviour to simulate \textit{K. mikimotoi} blooms?

Q3) How does the inclusion of direct wind forcing influence model prediction?

Q4) Can cell densities calculated from satellite imagery be used to initialise such models?

Q5) Can initialising the model with single discrete seed populations provide information about bloom origin?

Q6) Is it possible that the bloom in 2006 was seeded by overwintering cells from the exceptional \textit{K. mikimotoi} bloom near Ireland in 2005?

Q7) What is the role of the European Slope Current (ESC) in \textit{K. mikimotoi} bloom advection.
Q8) How will using different hydrodynamic models affect predicted bloom advection?

5.2 Methods

5.2.1 *K. mikimotoi* Data

*K. mikimotoi* was enumerated from water samples collected as part of the biotoxin producing phytoplankton monitoring programme overseen by FSS. Water samples were collected from about 40 coastal sites in Scotland (Figure 5.1) and *K. mikimotoi* were enumerated using the Utermöhl method as described in detail in Davidson et al. (2009).

During summer and early autumn 2006 concentrations of over 3 million *K. mikimotoi* cells $l^{-1}$ were found around the Scottish coast (Davidson et al. 2009). Cells were first found near Mull and Lewis in July and subsequently near Skye and Orkney in August (Figure 5.2 a). In September cell concentrations decreased at most sites, except for Shetland where cell concentrations rapidly increased to nearly 0.5 million cells $l^{-1}$ (Figure 5.2 a). The rapid increase of cells at coastal locations suggested that high concentrations were unlikely to be caused by local growth alone and that at least some parts of the cells were advected clockwise around the coast (Davidson et al. 2009).

In 2010 and 2011, *K. mikimotoi* reached concentrations of over 200 000 cells $l^{-1}$ at multiple sampling stations around the west Scottish coasts with peaks of up to 1 million cells $l^{-1}$. During 2010, elevated *K. mikimotoi* concentrations were found near Mull in July, near the isle of Skye and north Scotland in August and finally at some monitoring stations on Sheltand (Figure 5.2 b). During 2011, around 1 million cells $l^{-1}$ were recorded near the isle of Skye in August and subsequently in lower concentrations around Mull, Lewis and Orkney (Figure 5.2 c).

Satellite images from summer 2006 were useful to study bloom development (Figure 5.3). High chlorophyll concentrations were visible near the west Scottish coast throughout July. The bloom was observed to move towards Shetland mid August with high chlorophyll around Shetland during late August and early September.

In 2010 and 2011 coverage of the Scottish coast was extremely limited by cloud cover, making it difficult to track the *K. mikimotoi* bloom via satellite remote sensing. For each year only one usable image was available and hence this was used as initial seed population in the model (Figure 5.4).
Figure 5.1: Map of FSS sampling locations (red).
Figure 5.2: Development of *K. mikimotoi* at selected sites from July to August for (a) 2006, figure redrawn from Davidson et al. (2009) b) 2010 and c) 2011.
Figure 5.3: Chlorophyll ($\mu g \, l^{-1}$) from Modis aqua satellite data as weekly median composite maps from July to September 2006.
5 IBM for HAB transport

(a) 16.07.2010

(b) 18.08.2011

Figure 5.4: Chlorophyll (µg l⁻¹) from Modis aqua satellite data obtained from the National Oceanic and Atmospheric Administration data service for (a) 16.7.2010 and (b) 18.8.2011.

5.2.2 The Model

The model used here is a coupled bio-physical model. The model runs offline, which means the hydrodynamic model output is produced before being coupled with the biological individual based model (IBM). The biological growth and transport model only responds to the hydrodynamic model output, i.e. the biological model does not give any feedback to the hydrodynamic model. The biological model consists of a particle tracking model that uses the velocities produced by the hydrodynamic model to move phytoplankton cells, treated as particles, around the model domain. On top of the particle transport model the biological model also includes a formulation for cell growth, mortality and migration. Each component of the model is explained in more detail below and specific parameter values are presented in Table 5.1.

Hydrodynamic models POLCOMS and NEMO

The hydrodynamic models POLCOMS (Proudman Oceanographic Laboratory Coastal Ocean Modelling System) and NEMO (Nucleus for European Modelling of the Ocean) are physical models describing currents and other oceanographic parameters such as temperature and salinity of the North West European Shelf Sea. POLCOMS was designed to specifically look at shelf sea process and shelf-ocean interactions. In 2008, the Met Office replaced POLCOMS with NEMO as an operational forecast model for the North West European Shelf (O’Dea et al. 2008). This was done as NEMO can be easily used with the Forecasting Ocean Assimilation Model 7km Atlantic Margin model, which is nested to the global ocean model used by Met Office.
Table 5.1: Model parameters, table adapted from Gillibrand et al. (2016). Switches could be set to 1 = yes/on, 0 = no/off.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of particles</td>
<td>457954</td>
</tr>
<tr>
<td>Time step of particle model (s)</td>
<td>600</td>
</tr>
<tr>
<td>Start day of simulation for 2006</td>
<td>1st July</td>
</tr>
<tr>
<td>Start day of simulation for 2010</td>
<td>16th July</td>
</tr>
<tr>
<td>Start day of simulation for 2011</td>
<td>17th August</td>
</tr>
<tr>
<td>Start day of simulation for 2012</td>
<td>20th July</td>
</tr>
<tr>
<td>Start time of simulation (hh:mm:ss)</td>
<td>15:00:00</td>
</tr>
<tr>
<td>Length of simulation (h)</td>
<td>2208</td>
</tr>
<tr>
<td>Output frequency (h)</td>
<td>24</td>
</tr>
<tr>
<td>Duration of mobile stage (d)</td>
<td>200</td>
</tr>
<tr>
<td>Upwards swimming speed (UPSS, m h(^{-1}))</td>
<td>2.2</td>
</tr>
<tr>
<td>Downwards swimming speed (m h(^{-1}))</td>
<td>0</td>
</tr>
<tr>
<td>Maximum depth for upwards swimming behaviour (m)</td>
<td>30</td>
</tr>
<tr>
<td>Switch for cell growth</td>
<td>1</td>
</tr>
<tr>
<td>Switch for cell mortality</td>
<td>1</td>
</tr>
<tr>
<td>Mortality constant K</td>
<td>4x10(^{-8})</td>
</tr>
<tr>
<td>Minimum velocity shear (s(^{-1}))</td>
<td>0.001</td>
</tr>
<tr>
<td>Number of cells per virtual particle</td>
<td>5.0x10(^{12})</td>
</tr>
<tr>
<td>Switch for vertical diffusion</td>
<td>1</td>
</tr>
<tr>
<td>Switch for horizontal diffusion</td>
<td>1</td>
</tr>
<tr>
<td>Switch for wind forcing</td>
<td>1</td>
</tr>
<tr>
<td>Depth to which wind causes advection (zC)</td>
<td>30m</td>
</tr>
<tr>
<td>Cell density resolution (cells l(^{-1}))</td>
<td>113</td>
</tr>
<tr>
<td>Conversion rate from satellite chlorophyll to K. mikimotoi cell numbers (µg l(^{-1}) per cell)</td>
<td>1.89x10(^{-5})</td>
</tr>
</tbody>
</table>


For this chapter, three dimensional fields for temperature and velocity were obtained for the study area (-10 °W to 3.2 °E and 54 °N to 61 °N) from 0 to 30 m depth in 5 m intervals. For 2006, three dimensional data fields were obtained for both models to allow comparison and sensitivity analysis between models. For NEMO, additional files for 2010 and 2011 were downloaded, but were unavailable for POLCOMS. Values produced by both models are daily means and do not account for tidal forcing. POLCOMS fields were obtained from the Environmental System Science Centre data server Godiva. NEMO fields were obtained from the Marine Environment Monitoring Service Copernicus. Both models have a similar horizontal resolution of around 0.1 degree or 6 to 7 km for the study area.

**Biological model**

The biological model is written in Fortran and consists of a particle tracking model and biological growth model. For the particle tracking model three dimensional
velocity fields were linked to the model which represents numbers of phytoplankton cells as ‘particles’ (sometimes referred to as ‘super-individuals’, Hellweger & Bucci 2009). The particles are moved through the model domain by the three dimensional velocity fields and vertical and horizontal diffusion. The model uses a fourth-order Runge-Kutta integration for advection (Ross & Sharples 2004) and a random walk displacement for diffusion (Proctor et al. 1994).

In addition to advection by currents, particles are additionally moved by direct wind stress near the surface (Proctor et al. 1994, Elliott 1986). The influence of direct wind was modelled to a depth of 30 m, whereby the direct effect of wind decreases with depth (Elliott 1986). Wind data was obtained from the British Atmospheric Data Centre (BADC) as hourly measurements of wind speed and directions from stations on the islands Tiree, Lewis (Stornoway) and Shetland (Lerwick). For each data point wind from the closest station was used.

In contrast to passive particles that would be only subjected to advection and diffusion, phytoplankton particles were also given a species specific formulation for growth, mortality and vertical migration following Gentien et al. (2007). Biological formulation for *K. mikimotoi* solely depend on physical features and cell densities and are therefore suitable to be used in this IBM. The model can be easily coupled with the hydrodynamic model, while complexity of the biological model is kept to a minimum as no other factors such as grazing and competition have to be included. Growth and mortality were expressed as:

\[
\frac{\delta C}{\delta t} = \mu(T)C - K\gamma C^2 
\]  

(1)

with C being cell concentration (cells l\(^{-1}\)) and K the mortality constant (Table 5.1). Following laboratory and numerical experiments, Gentien et al. (2007) established a growth formulation for *K. mikimotoi* that is solely depended on temperature, which can be easily obtained from hydrodynamic model output. Temperature (T) dependent growth \(\mu(T)\) in divisions day\(^{-1}\) was described as

\[
\mu(T) = 2.5 \times 10^{-3}T^3 - 0.15T^2 + 2.8775T - 17.27
\]

(2)

Auto-toxicity was established as the main driver of mortality and population density control in *K. mikimotoi* laboratory cultures (Gentien et al. 2007). In the model, the likelihood of cell encounter rate, and thereby the effect of auto-toxicity and aggregation and sinking, increases with turbulent shear velocity, which is included in the mortality function as \(\gamma\) (Gentien et al. 2007). As model output did not provide
turbulent velocity shear, large scale velocity shear was calculated:

$$\gamma = \frac{U_j - U_{j+1}}{\Delta z_j}$$  \hspace{1cm} (3)

with $U_j$ being the velocity at depth $j$ and $\Delta z_j$ the vertical distance (m) between depth $j$ and $j+1$.

### 5.2.3 Model sensitivity

Biological parameters for *K. mikimotoi* growth and migration were calculated from strains isolated from French coastal waters. It is possible that 'local' parameters for Scottish strains could be slightly different, but without cultures of Scottish strains of *K. mikimotoi*, no such parameters were available. It is therefore helpful to know the sensitivity of the model to those parameters. Model sensitivity analysis is simply testing the effect that changes in parameters would have on model output. This can be assessed using a one-parameter at a time approach as suggested by Fasham et al. (1990) or a more complex approach testing the effect of changes in multiple parameters during one model run (e.g. Baklouti et al. 2006). The biological model used here has relatively few parameters and we therefore chose to use the one-parameter-at-a-time approach which is robust and easy to use and well established in the literature (e.g. Fasham et al. 1990, Anderson 1992, Jamu & Piedrahita 2002, Yoshie et al. 2007). We used normalised sensitivity as proposed by Fasham et al. (1990). The model was run with the original values (Table 5.1) and total predicted cell density was then compared to the output of a model run where one parameter was changed. The model was considered sensitive to any parameter that had a standardised sensitivity value higher than 1 or lower than -1 as suggested by Fasham et al. (1990).

The normalised sensitivity was calculated as

$$S(p) = \frac{(E(p) - E_s)/E_s}{(p - p_s)/p_s}$$ \hspace{1cm} (4)

with $E_s$ being the total cell density if model is run with original parameters, $E(p)$ being total cell density after a single parameter $p$ was changed, $p$ being the value of the original parameter and $p_s$ being the changed value of the parameter.

### 5.2.4 Model Runs

A suite of model runs was designed to test the hypotheses stated above. Distribution and concentration of cells predicted by the model was compared to satellite
data (when available) and phytoplankton counts from coastal monitoring stations to determine if the model could be used to hindcast exceptional blooms observed in 2006, 2010 and 2011 (Q1). The model was run without the inclusion of biological behaviour (runs 19, 22, 23, Table 5.2) to test if *K. mikimotoi* cells can be modelled as passive particles and occurrence of blooms can be explained by advection alone (Q2). Several model runs were repeated with and without the inclusion of direct wind forcing (runs 1 and 2, Table 5.2, runs 25 to 42, Table 5.3) to evaluate the role of wind driven advection in *K. mikimotoi* bloom transport (Q3). For 2006, 2010 and 2011, the model was initialised with seed populations calculated from satellite chlorophyll (Q4) and several single initial seed populations (Q5) in order to study possible bloom origins and advection of seed populations (run 1, Table 5.2, runs 39 to 42, Table 5.3, runs 79 to 84, Table 5.5). The model was further initialised with seed populations near the coast of Northern Ireland (Q6) and the ESC (Q7) for the 2006 bloom (runs 25 to 38, Table 5.3). Model runs for 2006 that used POLCOMS data were repeated with NEMO data to allow comparison of model output (Q8, runs 43 to 60, Table 5.4).

**Initial seed populations from satellite imagery for 2006**

The 2006 *K. mikimotoi* bloom was first observed in early July (Figure 5.2) with good satellite coverage available for the week of the 1st July (Figure 5.3). Therefore, the model was initialised at a location estimated from that satellite image. Estimated values from literature (Jones et al. 1982, Vanhoutte-Brunier et al. 2008, Dahl et al. 1987) for chlorophyll a per *K. mikimotoi* cell were used to calculate initial cell density from satellite chlorophyll a images (Table 5.1). It is not yet possible to identify *K. mikimotoi* and discriminate it from other phytoplankton from satellite imagery, with identification algorithms currently in development (Kurekin et al. 2014). With high numbers of *K. mikimotoi* recorded at coastal monitoring stations (Figure 5.2) and no offshore data available it was therefore assumed that remotely recorded chlorophyll was representative of a mono-specific bloom of *K. mikimotoi*.

After calculating cell densities, the model was initialised with numerical particles, each representing a cluster of *K. mikimotoi* cells (Table 5.1). The model calculated changes in cell density and location every 600 s and model output was produced in 24 h intervals from the 1st July to the 30th September. There was no additional influx of cells into the model domain and cell numbers in the model therefore only changed as a result of cell growth and mortality of existing cells. Cells were also removed from the model domain by sinking (below 30 m) or advection outside of the model domain.

The model was run with different parameters to assess model sensitivity to changed parameters (Table 5.2). The model was run with different wind forcing con-
ditions (runs 2 to 8) to determine the role of direct wind forcing on cell transport. Changes to the biological model assessed the importance of accurately modelling biological behaviour to be able to model bloom events (runs 9 to 23). This included changes to temperature, which directly affected cell growth.

Table 5.2: List of the first set of model runs (1 to 24). All model runs were initialised with cell concentrations calculated from satellite and run with POLCOMS temperature and velocity fields for 2006. Values that were modified from Table 5.1 are given in the right column (see Table 5.1 for abbreviations). For certain runs temperature (T) and wind speed (ws) were changed.

<table>
<thead>
<tr>
<th>Run</th>
<th>Model description</th>
<th>Changed parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Model run with no change in parameters</td>
<td>none</td>
</tr>
<tr>
<td>2</td>
<td>Model run without wind forcing</td>
<td>switch = 0</td>
</tr>
<tr>
<td>3</td>
<td>Decrease in depth to which wind forcing is applied</td>
<td>zC=10 m</td>
</tr>
<tr>
<td>4</td>
<td>Decrease in depth to which wind forcing is applied</td>
<td>zC=20 m</td>
</tr>
<tr>
<td>5</td>
<td>10% increase in wind speed</td>
<td>ws = ws+0.1ws</td>
</tr>
<tr>
<td>6</td>
<td>10% decrease in wind speed</td>
<td>ws = ws-0.1ws</td>
</tr>
<tr>
<td>7</td>
<td>5% increase in wind speed</td>
<td>ws = ws+0.05ws</td>
</tr>
<tr>
<td>8</td>
<td>5% decrease in wind speed</td>
<td>ws = ws-0.05ws</td>
</tr>
<tr>
<td>9</td>
<td>Increase in mortality constant</td>
<td>K=2x10^{-8}</td>
</tr>
<tr>
<td>10</td>
<td>Decrease in mortality constant</td>
<td>K=8x10^{-8}</td>
</tr>
<tr>
<td>11</td>
<td>Increase in mortality constant</td>
<td>K=4x10^{-7}</td>
</tr>
<tr>
<td>12</td>
<td>Decrease in mortality constant</td>
<td>K=4x10^{-9}</td>
</tr>
<tr>
<td>13</td>
<td>10% increase in temperature</td>
<td>T = T+0.1T</td>
</tr>
<tr>
<td>14</td>
<td>10% decrease in temperature</td>
<td>T = T-0.1T</td>
</tr>
<tr>
<td>15</td>
<td>5% increase in temperature</td>
<td>T = T+0.05T</td>
</tr>
<tr>
<td>16</td>
<td>5% decrease in temperature</td>
<td>T = T-0.05T</td>
</tr>
<tr>
<td>17</td>
<td>Increase in max. depth of migration</td>
<td>max. depth = 60 m</td>
</tr>
<tr>
<td>18</td>
<td>Decrease in max. depth of migration</td>
<td>max. depth = 15 m</td>
</tr>
<tr>
<td>19</td>
<td>No upwards swimming of cells</td>
<td>UPSS = 0 m h^{-1}</td>
</tr>
<tr>
<td>20</td>
<td>Decrease in upwards swimming speed</td>
<td>UPSS = 1.1 m h^{-1}</td>
</tr>
<tr>
<td>21</td>
<td>Increase in upwards swimming speed</td>
<td>UPSS = 4.4 m h^{-1}</td>
</tr>
<tr>
<td>22</td>
<td>No cell growth or mortality</td>
<td>switches = 0</td>
</tr>
<tr>
<td>23</td>
<td>No cell growth, mortality or motility</td>
<td>UPSS = 0 m h^{-1}</td>
</tr>
<tr>
<td>24</td>
<td>No diffusion</td>
<td>switches = 0</td>
</tr>
</tbody>
</table>

Discrete initial seed populations for 2006

To determine possible origin populations that could have initiated the 2006 *K. mikimotoi* bloom in Scotland, the model was initialised with a selection of different discrete initial seed populations (ISPs, Table 5.3). The model was used to test whether the full extent of the 2006 *K. mikimotoi* bloom could have been caused by advection of a single, discrete seed population (runs 25 to 34). Model runs 35 and 36 tested the potential of a seed population from the coast of Northern Ireland to reach the Scottish west coast and initialise a bloom. The positions of ISPs for model runs
37 and 38 were designed to study the potential of seed populations from the shelf break to initiate the observed bloom in 2006. It was further tested if the observed bloom progression along the coast could be modelled by initialising the model with multiple ISPs close to the locations the bloom was first observed (runs 39 to 42). For each ISP location the model was run with and without direct wind forcing to determine the role of wind in cell advection and coastal bloom development.

Table 5.3: List of the second set of model runs (25 to 42) with discrete ISPs. The model was run with POLCOMS temperature and velocity fields for 2006. No parameters were changed from Table 5.1, except for wind forcing.

<table>
<thead>
<tr>
<th>Run</th>
<th>Model description</th>
<th>Wind forcing</th>
</tr>
</thead>
<tbody>
<tr>
<td>25/26</td>
<td>Single ISP near Mull, w/out wind</td>
<td>switch = 1/ 0</td>
</tr>
<tr>
<td>27/28</td>
<td>Single ISP near south Lewis w/out wind</td>
<td>switch = 1/ 0</td>
</tr>
<tr>
<td>29/30</td>
<td>Single ISP near north Lewis ISP w/out wind</td>
<td>switch = 1/ 0</td>
</tr>
<tr>
<td>31/32</td>
<td>Single ISP near Kyle of Tongue w/out wind</td>
<td>switch = 1/ 0</td>
</tr>
<tr>
<td>33/34</td>
<td>Single ISP near Shetland w/out wind</td>
<td>switch = 1/ 0</td>
</tr>
<tr>
<td>35/36</td>
<td>Multiple ISP near Ireland w/out wind</td>
<td>switch = 1/ 0</td>
</tr>
<tr>
<td>37/38</td>
<td>Multiple ISP near the ESC w/out wind</td>
<td>switch = 1/ 0</td>
</tr>
<tr>
<td>39/40</td>
<td>2 ISP near Mull and Lewis</td>
<td>switch = 1/ 0</td>
</tr>
<tr>
<td>41/42</td>
<td>3 ISP near Mull, Lewis and shelf break</td>
<td>switch = 1/ 0</td>
</tr>
</tbody>
</table>

Model runs using NEMO as a hydrodynamic model for 2006

As POLCOMS was replaced by NEMO as an operational oceanographic forecast model (O’Dea et al. 2008) the biological growth and transport model was coupled to NEMO for the next set of model runs (Table 5.4). The temperature and velocity fields from NEMO had the same spatial and temporal specification as data fields used from POLCOMS. The coupled model using NEMO was tested for sensitivity of parameters in the same manner as for the coupled model using POLCOMS (Table 5.2) to allow comparison of sensitivity of those factors between the different hydrodynamic models. Model runs 61 to 78 were designed to test differences in predicted transport of cells when using NEMO data fields with the biological model.
Table 5.4: List of model runs using NEMO temperature and velocity fields for 2006. Runs 43 to 60 were initialised with cell concentrations and locations calculated from satellite images, Runs 61 to 78 were initialised with 3 discrete ISPs as in run 42. Values that were modified from Table 5.1 are given in the right column (see Table 5.1 for abbreviations). For certain runs temperature (T) was changed to evaluate small changes in this important parameter.

<table>
<thead>
<tr>
<th>Run</th>
<th>Model description</th>
<th>Changed parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>43</td>
<td>Model run with no change in parameters</td>
<td>none</td>
</tr>
<tr>
<td>44</td>
<td>Model run without wind forcing</td>
<td>switch = 0</td>
</tr>
<tr>
<td>45</td>
<td>Increase in mortality constant</td>
<td>K=2x10^{-8}</td>
</tr>
<tr>
<td>46</td>
<td>Decrease in mortality constant</td>
<td>K=8x10^{-8}</td>
</tr>
<tr>
<td>47</td>
<td>Increase in mortality constant</td>
<td>K=4x10^{-7}</td>
</tr>
<tr>
<td>48</td>
<td>Decrease in mortality constant</td>
<td>K=4x10^{-9}</td>
</tr>
<tr>
<td>49</td>
<td>10% increase in temperature</td>
<td>T = T+0.1T</td>
</tr>
<tr>
<td>50</td>
<td>10% decrease in temperature</td>
<td>T = T-0.1T</td>
</tr>
<tr>
<td>51</td>
<td>5% increase in temperature</td>
<td>T = T+0.05T</td>
</tr>
<tr>
<td>52</td>
<td>5% decrease in temperature</td>
<td>T = T-0.05T</td>
</tr>
<tr>
<td>53</td>
<td>Increase in max. depth of migration</td>
<td>max. depth = 60 m</td>
</tr>
<tr>
<td>54</td>
<td>Decrease in max. depth of migration</td>
<td>max. depth = 15 m</td>
</tr>
<tr>
<td>55</td>
<td>No motility</td>
<td>UPSS = 0 m h^{-1}</td>
</tr>
<tr>
<td>56</td>
<td>Decreased motility</td>
<td>UPSS = 1.1 m h^{-1}</td>
</tr>
<tr>
<td>57</td>
<td>Increased motility</td>
<td>UPSS = 4.4 m h^{-1}</td>
</tr>
<tr>
<td>58</td>
<td>No cell growth or mortality</td>
<td>growth and mortality off</td>
</tr>
<tr>
<td>59</td>
<td>No cell growth, mortality or motility</td>
<td>biology off</td>
</tr>
<tr>
<td>60</td>
<td>No diffusion</td>
<td>diffusion off</td>
</tr>
<tr>
<td>61</td>
<td>ISP near Mull, Lewis and Shelf</td>
<td>none</td>
</tr>
<tr>
<td>62</td>
<td>no wind</td>
<td>no wind</td>
</tr>
<tr>
<td>63</td>
<td>Increase in mortality constant</td>
<td>k=2x10^{-8}</td>
</tr>
<tr>
<td>64</td>
<td>Decrease in mortality constant</td>
<td>k=8x10^{-8}</td>
</tr>
<tr>
<td>65</td>
<td>Increase in mortality constant</td>
<td>k=4x10^{-7}</td>
</tr>
<tr>
<td>66</td>
<td>Decrease in mortality constant</td>
<td>k=4x10^{-9}</td>
</tr>
<tr>
<td>67</td>
<td>10% increase in temperature</td>
<td>T = T+0.1T</td>
</tr>
<tr>
<td>68</td>
<td>10% decrease in temperature</td>
<td>T = T-0.1T</td>
</tr>
<tr>
<td>69</td>
<td>5% increase in temperature</td>
<td>T = T+0.05T</td>
</tr>
<tr>
<td>70</td>
<td>5% decrease in temperature</td>
<td>T = T-0.05T</td>
</tr>
<tr>
<td>71</td>
<td>Increase in max. depth of migration</td>
<td>max. depth = 60 m</td>
</tr>
<tr>
<td>72</td>
<td>Decrease in max. depth of migration</td>
<td>max. depth = 15 m</td>
</tr>
<tr>
<td>73</td>
<td>No upwards swimming of cells</td>
<td>UPSS = 0 m h^{-1}</td>
</tr>
<tr>
<td>74</td>
<td>Decrease in upwards swimming speed</td>
<td>UPSS = 1.1 m h^{-1}</td>
</tr>
<tr>
<td>75</td>
<td>Increase in upwards swimming speed</td>
<td>UPSS = 4.4 m h^{-1}</td>
</tr>
<tr>
<td>76</td>
<td>No cell growth or mortality</td>
<td>switches = 0</td>
</tr>
<tr>
<td>77</td>
<td>No cell growth, mortality or motility</td>
<td>switches = 0,</td>
</tr>
<tr>
<td>78</td>
<td>No diffusion</td>
<td>UPSS = 0 m h^{-1}</td>
</tr>
</tbody>
</table>

*Model runs using NEMO as a hydrodynamic model for 2010 and 2011*

After the model was successfully linked to NEMO data fields, it was used to study K.
mikimotoi blooms post 2008. FSS monitoring detected the presence of high density blooms of *K. mikimotoi* at several points on the West Scottish coast during the years 2010 and 2011 (Figure 5.2). Therefore, the model was used to study the origin and development of these blooms (Table 5.5). Several possible ISPs were tested for both years to find potential origins and pathways of advective transport for these years. The model was initialised with cell densities calculated from satellite images (runs 79 and 82) and potential single or multiple ISPs around the stations the bloom was first recorded (runs 80, 81, 83, 84).

Table 5.5: List of model runs, the location of the initial seed population (ISP) using data fields for 2010 and 2011 from the hydrodynamic model NEMO. No parameters were changed from Table 5.1.

<table>
<thead>
<tr>
<th>Run</th>
<th>ISP</th>
<th>Model description</th>
</tr>
</thead>
<tbody>
<tr>
<td>79</td>
<td>satellite</td>
<td>ISP from satellite</td>
</tr>
<tr>
<td>80</td>
<td>1 ISP</td>
<td>ISP near Mull</td>
</tr>
<tr>
<td>81</td>
<td>2 ISP</td>
<td>ISP near Mull and shelf</td>
</tr>
<tr>
<td>82</td>
<td>satellite</td>
<td>ISP from satellite</td>
</tr>
<tr>
<td>83</td>
<td>2 ISP</td>
<td>ISP near Skye and Lewis</td>
</tr>
<tr>
<td>84</td>
<td>3 ISP</td>
<td>ISP near Skye, Lewis and Mull</td>
</tr>
</tbody>
</table>

5.3 Results

5.3.1 Satellite seeding of the 2006 bloom

The first set of model runs (Table 5.2) were initiated with varying cell concentration throughout the model domain, estimated from satellite images (Figure 5.5 and 5.6). As mentioned above, all satellite derived chlorophyll was converted into *K. mikimotoi* cells. It is therefore possible that the total number of *K. mikimotoi* used to initialise the model was an overestimation as other species could have added to the observed chlorophyll. This has to be considered when comparing model predictions to numerical counts from coastal monitoring stations. While assumptions like this are necessary to initialise the model, and might affect the absolute prediction of cell density, it does not affect model predictions of advection and changes in relative abundance of cells. Here, the model work is focused on studying the transport of *K. mikimotoi* and changes in relative abundance at sites caused by temperature dependent growth and physical advection.

Figure 5.5 a) shows model output in 14 day time steps for model run 1. *K. mikimotoi* were predicted to be present throughout the domain with some part of the population remaining near the Scottish west coast for the duration of the model run. The model simulated an increase in cell concentration throughout the domain
after 4 weeks. After 6 weeks, the model predicted that cells in the north and east accumulated around the coast, while cells near the west were transported away from the coast and towards the shelf edge.

Monitoring data showed that cell concentrations on the west coast decreased rapidly in mid August as correctly simulated by this model run; however, the model struggled to recreate bloom timing and intensity for the Orkney and Shetland islands in the north of Scotland. The model predicted an earlier bloom onset and blooms
lasted for a longer duration than observed at monitoring stations. The modelled *K. mikimotoi* densities did not reach the over 1 million cells l$^{-1}$ that were recorded at Orkney monitoring stations.

The effects of physical advection of cells were tested with a number of changes to direct wind forcing (runs 2 to 8) and both vertical and horizontal diffusion (run 24). The model run without direct wind forcing (Figure 5.5 b, run 2) predicted a similar distribution of cells in the first month compared to the model run that included direct wind forcing (Figure 5.5 a, run 1). After 2 months, cells showed a stronger accumulation around the west coast compared to the model run that included direct wind forcing. The model was subsequently run with changes in wind strength (run 3 to 8). Predicted cell concentrations and distribution for these runs were similar to run 1 and model output is therefore not shown. Including horizontal and vertical diffusion was important for the model to accurately determine bloom advection. Running the model without diffusion (run 24) led to a rapid change in cell distribution and concentration. Cells were distributed in high densities around the coast with a reduced prediction of transport and bloom progression and low cell densities in offshore areas.

The model was also run with different parametrisation of the biological growth model or factors that directly influence growth and mortality, such as temperature and shear (runs 9 to 23). The detailed analysis of model sensitivity can be found in chapter 5.3.3. The inclusion of biological growth and vertical swimming behaviour was important for the model to predict bloom densities of *K. mikimotoi* (Figure 5.6). If there is no upwards swimming (run 19) cell loss by diffusion strongly reduces total number of cells and bloom densities cannot be sustained (Figure 5.6 a). Like motility, growth and mortality are crucial components of the biological model and need to be included for the model to be able to produce bloom densities (run 22, Figure 5.6 b). If growth, mortality and upwards swimming are not included, predicted cell concentrations rapidly decrease to zero (run 23, model output not shown).
5.3.2 Discrete seed locations for the 2006 bloom

The model was run with discrete initial seed populations to determine possible bloom origins and their advective transport (runs 25 to 42, Figure 5.7). To determine if overwintering populations near Ireland could have initiated the *K. mikimotoi* bloom along the Scottish west coast, the model was run with several ISPs around the...
Northern Ireland coast (Figure 5.7 a). The model predicted cell transport from the
Northern Ireland coast to the Scottish west coast within a week, with bloom densities
predicted near the islands of Mull and Skye. After two month cells were predicted

![Figure 5.7](image.png)

Figure 5.7: Modelled bloom development for *K. mikimotoi* from discrete initial seed populations from (a) North Ireland, (b) South Lewis, (c) North Lewis, (d) North Scotland and (e) Shetland. Direct wind forcing was included.

Northern Ireland coast to the Scottish west coast within a week, with bloom densities predicted near the islands of Mull and Skye. After two month cells were predicted
to be advected as far north as the islands of Lewis and Harris. This run showed that cells originating near the Northern Ireland coast can be advected towards the Scottish west coast where cells were predicted in harmful densities. However, coastal monitoring reported cells as far north as the Orkney and Shetland islands. The model output showed that cells originating from the Northern Ireland coast were not advected this far north during the model simulation and thus suggested that an additional input of *K. mikimotoi* was necessary further north in the model domain to recreate the observed cell distributions.

It is possible that cells are transported clockwise around the coast within the ESC (Holt & Proctor 2008) and additional input of *K. mikimotoi* might have been a result from cells crossing over from the ESC into shelf waters. Seeding from the ESC was therefore tested for multiple locations close to the shelf break to see if the model could predict transport of cells to the Scottish north coast including the Orkney and Shetland Islands (Figure 5.7 b-e). Input of cells from the shelf break near the islands Lewis and Harris lead to a predicted advection of cells to the north coast of the Scottish mainland and the Orkney islands (Figure 5.7 b and c). Direct wind forcing reduced predicted cell advection towards the Shetland islands and only the northernmost ISP (Figure 5.7 e) was predicted to reach the islands. Shelf input between the outer Hebrides and Shetland Islands (Figure 5.7 d) was advected towards the north sea and Scottish east coast without reaching Orkney or Shetland.

For model run 39, two ISPs were set close to Mull and Lewis, where cells were first monitored in elevated concentrations in early July (Figure 5.8 a). This was done to determine if it was possible that *K. mikimotoi* recorded after the 1st of July around the coast could originate from the same population that was first observed at this location. The model predicted the observed northwards and clockwise progression of the bloom, however an additional ISP was necessary for cells to reach the northernmost Shetland islands where cells were found at monitoring stations in September (Figure 5.8 b and c). Model runs for discrete ISPs were conducted with and without direct wind forcing. For model runs without wind forcing cells were predicted to be transported further north than for model runs with direct wind forcing. This suggests that wind forcing can be an important factor determining the final location of discrete ISP and can enhance or, in this case, reduce the advection predicted by current transport alone.
5.3.3 Model sensitivity analysis

The algal growth model was found to be sensitive to temperature changes. This was true when embedded in either hydrodynamic model, with a 10% decrease in temperature (approx. 1°C) leading to a decrease of 63% and 87% of predicted cell numbers for POLCOMS and NEMO simulations respectively (Table 5.6). A 10% decrease in temperature caused a greater percentage change in cell numbers than a 10% increase. The bio-physical model coupled with NEMO was more sensitive to a decrease in temperature but less sensitive to an increase in temperature than when compared to POLCOMS.

Motility had to be included in the model for the successful simulation of the development of a *K. mikimotoi* bloom. Upwards swimming behaviour of cells was important to counteract loss from vertical diffusion of cells (Table 5.6). If upwards swimming was included, the model was not very sensitive to the changes in parameters governing motility (speed of upwards swimming, maximum depth for
Table 5.6: Sensitivity analysis of parameters for the biological model coupled with POLCOMS or NEMO data fields.

<table>
<thead>
<tr>
<th>Parameter (new value)</th>
<th>% Increase/ decrease of Parameter</th>
<th>Increase/ decrease in Density POLCOMS NEMO</th>
<th>Normalised Sensitivity POLCOMS NEMO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (90%)</td>
<td>-10%</td>
<td>-63% -87%</td>
<td>6.28 8.66</td>
</tr>
<tr>
<td>Temperature (110%)</td>
<td>10%</td>
<td>56% 33%</td>
<td>5.56 3.47</td>
</tr>
<tr>
<td>Motility (0)</td>
<td>-100%</td>
<td>-62% -61%</td>
<td>0.62 0.61</td>
</tr>
<tr>
<td>Motility (2.1)</td>
<td>-50%</td>
<td>-0% -19%</td>
<td>-0.005 0.39</td>
</tr>
<tr>
<td>Motility (4.4)</td>
<td>100%</td>
<td>6% -25%</td>
<td>0.06 0.26</td>
</tr>
<tr>
<td>Maximum depth (0)</td>
<td>-100%</td>
<td>-24% -52%</td>
<td>0.24 0.52</td>
</tr>
<tr>
<td>Maximum depth (15)</td>
<td>-50%</td>
<td>3% -5%</td>
<td>-0.058 0.092</td>
</tr>
<tr>
<td>Maximum depth (60)</td>
<td>100%</td>
<td>10% -16%</td>
<td>0.10 -0.16</td>
</tr>
<tr>
<td>Mortality (2x10^{-8})</td>
<td>-50%</td>
<td>121% 69%</td>
<td>-2.41 -1.38</td>
</tr>
<tr>
<td>Mortality (8x10^{-8})</td>
<td>100%</td>
<td>-45% -58%</td>
<td>-0.45 -0.58</td>
</tr>
<tr>
<td>Mortality (4x10^{-7})</td>
<td>900%</td>
<td>-89% -93%</td>
<td>-0.1 -0.1</td>
</tr>
<tr>
<td>Mortality (4x10^{-9})</td>
<td>-90%</td>
<td>1003% 746%</td>
<td>-11.14 -8.29</td>
</tr>
<tr>
<td>Diffusion off</td>
<td></td>
<td>-39% -83%</td>
<td></td>
</tr>
<tr>
<td>Biology off</td>
<td></td>
<td>-98% -98%</td>
<td></td>
</tr>
<tr>
<td>Growth (0.4 div/day)</td>
<td>3%</td>
<td>-15%</td>
<td></td>
</tr>
<tr>
<td>Growth (1 div/day)</td>
<td>186%</td>
<td>159%</td>
<td></td>
</tr>
</tbody>
</table>

Changes in the value of the mortality constant lead to drastic changes in total biomass predicted by the model (Table 5.6). Cell death is a central part of the biological model and lower mortality will lead to a nearly proportional increase in cell concentrations. If the mortality constant K was halved, total cell concentrations at the end of the model run were 20% higher. If K was reduced by an order of magnitude, cells increased 10 times. When K was doubled, cell concentration was 45% lower and when K was increased by an order of magnitude, cell concentration was 89% lower. Including both growth and mortality was important for the model to run, showing that cells cannot be treated as passive particles.

5.3.4 Differences in predicted growth and advection between model simulations using POLCOMS or NEMO data

While NEMO and POLCOMS both cover the North West European shelf sea with a similar model resolution, NEMO has a larger model domain including the shelf break and adjacent oceanic waters. Here, it was tested how coupling temperature and velocity fields from different hydrodynamic models to the IBM would affect the prediction of growth and advection of cells. Running the coupled bio-physical model with cell densities calculated from satellite (run 1 and 43, Figure 5.9) showed differences in predicted cell distribution when output from the different hydrodynamic models was used. Both models predicted accumulation of cells near north Ireland upwards swimming, Table 5.6).
and mid North Sea after 2 weeks. After 6 weeks, the model coupled with NEMO predicted a higher concentrations of cells around the west Scottish coast while POLCOMS simulated a higher accumulation of cells around the east coast and the ESC. After 8 and 10 weeks coastal accumulation intensified if current velocities predicted by POLCOMS were used, while NEMO predicted a more even distribution of cells.

Differences in transportation became more evident when three discrete ISP were used, with and without wind (Figures 5.10 and 5.11). Seed populations from Mull
and Lewis developed around the west coast of Scotland. POLCOMS simulated a larger extent of cell distribution with cells spreading around the north coast. ISP from the shelf edge were predicted to reach Shetland with or without wind when using NEMO, suggesting that the effect of the ESC on cell transport is stronger in that model. When wind was included, POLCOMS did not predict that cells reached Shetland.
5.3.5 Modelling *K. mikimotoi* blooms for 2010 and 2011

For these model runs the IBM was coupled with NEMO as POLCOMS was no longer operational with model output not available post 2008. To study the *K. mikimotoi* bloom in 2010, the model was initiated with cell concentrations estimated from satellite (Figure 5.12) as well as one (Figure 5.13 a) or two (Figure 5.13 b) ISPs.

As the bloom was only recorded at monitoring stations on the west coast, elevated chlorophyll recorded from satellite near the east coast was unlikely to be
related to the *K. mikimotoi* bloom. Therefore, when ISP were calculated from satellite chlorophyll, (run 79) only the relevant section of the satellite image was used to reduce the high background concentrations of cells. Chlorophyll from satellite (Figure 5.4 a) showed elevated chlorophyll on the Scottish west coast south of the outer Hebrides and between Mull and the isle of Skye. Coastal monitoring suggested that the bloom was first present near Mull and Skye before it was recorded further north. After being initialised from satellite chlorophyll, the model simulated cell growth and spread of cells along the west coast (Figure 5.12). Unlike field observations, model simulations predicted bloom concentrations around Orkney but not Shetland. The predicted, but not observed, bloom around Orkney could be caused by the overestimation of bloom seed population related to the assumption that all satellite chlorophyll was caused by *K. mikimotoi*.

![Figure 5.12: Modelled bloom development for *K. mikimotoi* for 2010 with ISP from a satellite image from the 16.7.2010.](image)

The bloom in Shetland might have been caused by an additional input of cells from the shelf edge as observed in 2006. To test this, the model was initialised with discrete seed populations (Figure 5.13). Discrete ISP was near Mull and Skye, where the bloom was first observed (run 80, Figure 5.13 a), were predicted to be advected northwards, past the outer Hebrides, the isle of Ewe and up to the Kyle of tongue. Cells were not predicted to be advected towards Shetland during the model run. For the next model run (run 81) a second ISP was set to represent additional input of cells from the shelf edge (Figure 5.13 b). Despite the model being initialised with an ISP close to Orkney, model simulations did not predict bloom densities near Orkney in agreement with monitoring results (Figure 5.2). The model predicted cell advection towards Shetland within a month.
Figure 5.13: Modelled bloom development for *K. mikimotoi* for 2010 with ISP (a) near Mull and (b) near Mull and an additional input from the ESC.

To study the 2011 *K. mikimotoi* bloom, the model was seeded with a section from a satellite image as was done for the previous year (run 82, Figure 5.14). Elevated chlorophyll from satellite was highest south of Skye and west of the outer Hebrides. The model predicted cell concentrations to quickly increase and spread along the west coast. However advection during this year was not as strong as in 2006 and 2010. Simulated northwards transport of cells was lower than for other years, with a predicted advection time of nearly two month between the north west coast and Orkney. In agreement with field data the model predicted that cells would not reach
Shetland, even if cells would have been present within the slope current.

Figure 5.14: Modelled bloom development for *K. mikimotoi* for 2011 with ISP from a satellite image from the 18.8.2011.

For model run 83 two discrete ISP were introduced near Skye and north Lewis where cells were first recorded from coastal monitoring (Figure 5.15). Cells from Skye were advected towards the Isle of Ewe, while cells from Lewis reached Orkney by the end of the model period. The effect of adding another ISP near Mull was tested but the results showed little difference in cell advection to the previous run (run 84, model output not shown).

Figure 5.15: Modelled bloom development for *K. mikimotoi* from for 2011 with ISP near the islands Lewis and Skye.
5.4 Discussion

5.4.1 Model hindcast capacity

Coupled bio-physical models can provide information on HAB development and transport (see chapter 1.6). Here, we test the ability of a coupled bio-physical model consisting of a Lagrangian particle tracking model, a biological growth model and a three dimensional hydrodynamic model, to hindcast bloom events of exceptional *K. mikimotoi* blooms in 2006, 2010 and 2011 (Q1). To assess the model’s hindcast capacity, cell distribution predicted by the model was compared to available satellite images and cell counts from coastal monitoring stations.

Satellite data could provide an estimate of total chlorophyll present in the surface layer. However, satellite data cannot provide information about the vertical bloom structure or species composition. Algorithms for species discrimination from satellite images are currently being developed for *K. mikimotoi* (Kurekin et al. 2014, Miller et al. 2006), and will potentially greatly improve the use of satellite data. *K. mikimotoi* contains specific, remotely identifiable pigments (Brand et al. 2012), that were recently used to distinguish high biomass blooms of *K. mikimotoi* from other blooms (Sourisseau et al. 2016). During the years 2010 and 2011 high cloud cover further limited the use of satellite chlorophyll data. To improve validation of model hindcasts a better surveillance of offshore areas would be desirable as suggested in chapter 4.

The model successfully predicted the clockwise transport of cells around the Scottish coast as observed from field samples in 2006 (Davidson et al. 2009). There is, however, a mismatch between observed bloom onset, duration and termination between modelled and observed *K. mikimotoi* blooms. Especially the rapid bloom decline observed from monitoring stations was not recreated by the model. The same was true for model runs in 2010. The model could hindcast the bloom development within the Minch and inner Hebrides and, given suitable ISPs, Orkney and Shetland. However the mismatch of bloom timing and the observed rapid bloom decline remained a challenge. Rapid termination of HABs is often observed in the field and various factors such as environmental conditions, viral infection, grazing, competition and cell age have been suggested as possible explanations for cell death (e.g. Escalera et al. 2012, Velo-Surez et al. 2014, Hense 2010, Diaz et al. 2013, Fehling et al. 2006). Rapid decline of cell numbers might also be caused by a change to sexual reproduction and cyst formation rather than changes in cell mortality. The role of these factors in rapid cell decline of *K. mikimotoi* are, unfortunately, not fully understood yet. This suggests that the constant mortality rate used in this model might be insufficient, but further research on *K. mikimotoi* mortality would be necessary for improvements.
Cross-validation of modelled and observed *K. mikimotoi* from coastal stations is further limited by the low model resolution of the complex, diverse Scottish coastline. Monitoring sites were often located in sea lochs that have a unique and highly dynamic circulation pattern that is not captured by the 6 km to 7 km horizontal resolution of the hydrodynamic model. While models might be suitable to show the overall advection pattern of blooms, insufficient coastline resolution of hydrodynamic model output can lead to discrepancies between model prediction and field measurements which are all taken from coastal locations within or close to sea lochs (Pinto et al. 2016, Silva et al. 2016). Moreover, the hydrodynamic model does not resolve for tides, which can be a determining factor of HAB development and transport in coastal areas (Raine 2014, Dabrowski et al. 2016). To solve this problem, hydrodynamic models with high coastal resolution need to be developed and nested in shelf-ocean models as demonstrated by Aleynik et al. (2016).

The bloom in 2011 was of much smaller extent and modelled results showed a connectivity between blooms observed in Lewis at the end of August and around Orkney in September, with a mismatch of timing of exact bloom onset and bloom densities. As the model was successful in generating a qualitative agreement, it can provide important information about bloom development that can be helpful for coastal HAB management. At the moment, the model can be considered a tool to study likely pathways of *K. mikimotoi*, rather than providing a fully functional forecast model. The model can be used to study some aspects of exceptional blooms such as advection between sites and the overall pattern of bloom development. However, there are several areas with room for improvement, such as including a high resolution coastline model (Aleynik et al. 2016) or adjusting the biological formulation of the model (discussed below).

### 5.4.2 Does life really matter?

Lagrangian particle tracking models, similar to the one presented here, have been used to study advection of HABs in Vietnam (Dippner et al. 2011), Ireland (Pinto et al. 2016), and the Iberian shelf (Moita et al. 2016, Silva et al. 2016, Ruiz-Villarreal et al. 2016). These studies concluded that passive transport of particles alone can often be useful to explain HAB transport. Prediction of wind and current strength and direction have recently been included in a short term early warning bulletin in several countries including Scotland, Spain and Portugal (Ruiz-Villarreal et al. 2016, Cusack et al. 2016).

Regional oceanography and the predicted movement of passive particles is a fundamental part of modelling HAB advection; however, the development of species specific biology could improve model capacity to better predict cell numbers. This is important as many harmful species are considered harmless below certain cell
densities. In addition, biological swimming behaviour could directly change physical advection by changing the position of cells in the water column. Current strength and direction can change with depth and thereby changing the advection of cells in dependence of their position in the water column.

The model presented here includes a simple biological behavioural model including temperature dependent growth, shear dependent mortality and vertical migration behaviour during day time (Gentien et al. 2007). Without growth or migration, the model was not able to predict densities in the order of magnitude observed from field samples (Q2).

Modelled growth of *K. mikimotoi* was solely determined by temperature (Gentien et al. 2007) and the predicted cell density is hence very sensitive to temperature changes. Temperature dependent growth was simulated following Gentien et al. (2007), who used laboratory studies on *K. mikimotoi* isolated from French coastal waters. Growth formulation could therefore be improved by growth studies on Scottish strains of *K. mikimotoi* to adjust growth to local conditions. However, attempts to isolate *K. mikimotoi* from Scottish waters have been unsuccessful so far. Temperature dependent growth can help explaining seasonal bloom formation and decline; during spring and early summer increasing temperatures would lead to higher growth, while decreases in temperature at the end of summer would lead to a decrease in growth and eventually termination of the bloom.

As timing of bloom onset and termination was not always correctly simulated by the model it might also be necessary to consider other factors that might influence *K. mikimotoi* growth. A phototactic vertical migration behaviour was observed for *K. mikimotoi* (Gentien et al. 2007, Horiguchi et al. 1999) and implemented in the model as a constant upwards swimming speed during day time hours. Inclusion of vertical migration was necessary to model *K. mikimotoi* blooms, in agreement with Milroy et al. (2008), who found that a positive phototaxis was a crucial part of modelling blooms of *K. brevis*. Contrary to the model approach described by Milroy et al. (2008), phytoplankton growth was not directly limited by light availability in this model.

Nutrient deficiency is another factor often used to explain harmful bloom termination (Fehling et al. 2006). However, *K. mikimotoi* might be able to access nutrients from deeper layers due to their motile behaviour as suggested for *K. brevis* (Sinclair et al. 2006). Remineralisation from previous blooms can also provide enough nutrients to sustain elevated numbers of *K. mikimotoi* (Yamaguchi 1994, Le Corre et al. 1993). Harmful high density *Karenia* blooms have previously been reported in oligotrophic waters (Stumpf et al. 2008). During the *K. mikimotoi* bloom in Scotland in 2006, for example, nutrient conditions were too low to support the observed cell densities (Davidson et al. 2009). Moreover, including nutrient limita-
tion in the model would also increase the model complexity. It would be necessary to couple the model to an ecological nutrient or water-quality model (e.g. as done by Vanhoutte-Brunier et al. 2008), which would not only increase model complexity and thereby risk of error, but also increase computing time of the model as nutrients could not be modelled offline as phytoplankton growth would have a direct feedback on nutrient concentrations. For these reasons nutrient limitation was not included in the growth model.

Sourisseau et al. (2016) suggested that modelling of *K. mikimotoi* should include species competition with the dinoflagellate *Lepidodinium chlorophorum*, which form high biomass blooms under similar conditions as *K. mikimotoi*. To include the interspecies interactions such as competition and grazing, population based models are more suitable than IBMs as used here. Vanhoutte-Brunier et al. (2008) described a population model (PLM) that included a *K. mikimotoi* compartment separate from other phytoplankton compartments, with a species specific growth and mortality description. Growth was determined by temperature, nutrients and light, while mortality was dependent on shear, temperature and cell density. The model also assumes that growth of other phytoplankton groups is reduced by *K. mikimotoi* due to production of allelo-chemicals (Vanhoutte-Brunier et al. 2008).

The model described by Vanhoutte-Brunier et al. (2008) could hindcast overall observed patterns during a *K. mikimotoi* bloom in English channel in 2003 and revealed that bloom development was caused by the development of suitable environmental conditions, rather than advection from adjacent areas. Modelled cell densities were, however, lower than field observations. The timing of modelled bloom initiation and termination was also different between observation and model prediction. Despite the complex and detailed formulation of *K. mikimotoi* growth and mortality, the model could not explain the observed rapid bloom decline (Vanhoutte-Brunier et al. 2008).

Introducing new compartments to model the behaviour of a specific species increases model complexity and the potential for introducing error into the model (Hense 2010, Fulton et al. 2003). The interaction between the new species specific compartment and other compartments has to be described mathematically; this can be difficult for species such as *K. mikimotoi*, as little it known about the interaction between *K. mikimotoi* and other phytoplankton or grazers. Waterborne chemical cues from *K. mikimotoi* can reduce growth of competitors (Yang et al. 2011) but can also control densities of *K. mikimotoi* by auto-toxicity (Gentien et al. 2007). Grazers feed on toxic *K. mikimotoi* and non-toxic *Gymnodinium* at the same rate in monospecific prey cultures but prefer non-toxic species over toxic once in mixed cultures (Schultz & Kirboe 2009). While the studies mentioned above were done under controlled laboratory conditions, evidence for any competitive or anti grazing
capacity of \textit{K. mikimotoi} in the field has yet to be found. Including such biological interaction would also further increase model complexity.

In summary, to keep model complexity low and in recognition of the limited amount of data suitable to support more complex model parametrisation, an IBM with simple growth and behaviour description for \textit{K. mikimotoi} was used in this chapter. Growth was modelled solely as a function of temperature, leading to a high model sensitivity to temperature changes. Different to the population based model approach of Vanhoutte-Brunier et al. (2008), this model focuses on bloom advection with individual cell parcels treated as discrete units coupled with a Lagrangian framework following individual cells through the fluid motion, making it easier to study the effect of advection on bloom development. An even simpler approach to study physical advection of HABs is to describe cells as passive particles (Dippner et al. 2011, Pinto et al. 2016, Moita et al. 2016, Silva et al. 2016). However, here we conclude that biological description is necessary to simulate bloom progression realistically.

5.4.3 Model initiation

Lack of species specific offshore data can pose a challenge to bloom initiation. With no regular offshore monitoring, the model described here can be used to study potential locations and advective transport of seed populations to increase our understanding of bloom events (Q4-7).

One possibility is to use cell densities calculated from satellite derived chlorophyll to initialise the model (Q4). As mentioned above when using satellite data for model validation, a major drawback is the lack of species discrimination. Using satellite images could introduce a high number of non target species in the model, leading to overall high chlorophyll throughout the model domain. High densities of \textit{K. mikimotoi} found at coastal sites do, however, suggest that most of the observed chlorophyll was likely to be attributed to that species. Model initialisation from satellite images would also benefit from laboratory studies to obtain a better calculation to convert chlorophyll to cell numbers. Values from literature can vary by an order of magnitude (e.g. between Jones et al. 1982 and Dahl et al. 1987), and a better description of the relationship between chlorophyll and cell numbers for Scottish strains of \textit{K. mikimotoi} would be desirable to improve model initialisation, but are limited by a lack of culture.

Here, satellite images from 2006, 2010 and 2011 were successfully used for model initiation. The large spatial extent of cell distribution derived from satellite images allowed to study wind and current driven physical accumulation of cells. During the 2006 bloom initiation with satellite images showed strong accumulation of cells near coastal regions. This suggests that physical accumulation can help to explain
the observed rapid increase of cells observed at coastal sites (Davidson et al. 2009). A drawback of using satellite images for model initiation was that the overall large number and wide spatial extent of modelled particles made it difficult to study the advection of specific high density populations that might have been present during the bloom. Using discrete ISPs can help to study such advective pathways (Q5). Model simulations using discrete ISPs were successfully used to determine bloom origin and transport of populations along the west Scottish coast.

5.4.4 Pathways of bloom progression

Model simulations with discrete ISPs was useful to determine if *K. mikimotoi* cells originating from the Northern Ireland coast could have reached the west coast of Scotland and initiated the bloom observed in 2006 (Q6). The model was initialised with several discrete ISPs near the Northern Ireland coast, where an extensive *K. mikimotoi* bloom was observed in 2005. Model simulations suggested that cells present near the Northern Ireland coast were predicted to be advected to the west Scottish coast. Seed populations on the shelf near Northern Ireland would have been able to initialise the observed bloom in Scotland in 2006. There were no high density blooms of *K. mikimotoi* in Northern Ireland prior to the 2010 and 2011 bloom in west Scotland. It is possible that a seed population from 2010 overwintered and is linked to the bloom the next year. Unfortunately, the overwintering strategy of *K. mikimotoi* is not fully understood yet, with the formation of cysts possible but not yet confirmed. Other species of *Karenia* are known to have benthic stages in their life cycle (Brand et al. 2012) or form ‘cyst-like structures’ (Roth et al. 2008). However, without further evidence for *K. mikimotoi*, it is also possible that low densities of free swimming *K. mikimotoi* overwinter in the water column, which would allow a much quicker response of *K. mikimotoi* to a change to favourable environmental conditions.

Results of model simulations for 2006 indicated that cells located near the Northern Ireland coast could cause blooms along the west coast of Scotland but not the north coast or the Orkney and Shetland islands, where the bloom was observed in September 2006. Additional seed populations that might have entered the shelf from the ESC near the north of Scotland had to be included in model initiation to explain the full extent of the bloom (Q7). The same was true for 2010, when an additional ISP had to be included in the model simulation to hindcast the observed bloom in Shetland.

Exchange between oceanic waters and shelf waters across the ESC is complex and determined by seasonal and inter-annual differences in circulation and wind driven exchange of surface waters (Chapter 2, Ellett et al. 1986, Jones 2016, Holt & Proctor 2008, Burrows & Thorpe 1999). Several authors suggest that cells can be
transported along the ESC and subsequently be injected onto the shelf if there is an overspill of Atlantic water as observed in chapter 3 and 4 (Davidson et al. 2009, Holt & Proctor 2008, Holt et al. 2012). Model results of this chapter suggested that cells were present within the ESC and their incursion onto the shelf would explain the 2006 and 2010 bloom events.

5.4.5 The effect of hydrodynamic model output on cell advection

It was demonstrated that the IBM model can be coupled with physical data fields produced by either NEMO or POLCOMS (Q8). However, simulating *K. mikimotoi* growth and advection with data produced by different hydrodynamic models led to noticeable differences in model prediction. When the model was initialised with cell concentrations calculated from satellite, model simulations coupled to NEMO velocity fields resulted in less physical accumulation of cells in coastal regions compared to simulations coupled to POLCOMS velocity data. For model scenarios using three discrete ISP to initialise the model, simulations using NEMO output predicted a smaller spatial extent of the bloom; however, the model still reproduced the same pattern of clockwise advection predicted by simulations linked to POLCOMS. Model predictions for cell distribution along the Scottish west coast was similar between hydrodynamic models, with the most noticeable differences for distribution of cells at the Scottish north coast, especially when comparing model runs with and without direct wind forcing (Q3).

Wind forcing data was obtained from weather monitoring stations and was therefore independent of the hydrodynamic model used. When POLCOMS output was coupled to the IBM, cells accumulated along the north coast of the Scottish mainland. Without wind forcing cells were transported from ISPs near the ESC towards the Shetland islands, the northernmost stations where *K. mikimotoi* was recorded. When direct wind forcing was included, simulation of cell advection did not transport cells as far north as Shetland. The difference between inclusion or exclusion of direct wind forcing was less pronounced for model simulations using NEMO data; when direct wind forcing was not included in the model, cells were advected towards Shetland and Orkney after 2 to 4 weeks. Including wind forcing affected the path of advection to a small degree, with cells still being predicted to reach the same locations at approximately the same time. The effect of wind forcing when using NEMO data might be due to predictions of higher current velocity of the ESC by NEMO compared to POLCOMS. This was also translated into a further and faster predicted transport of cells along the ESC for model simulations using NEMO hydrodynamic velocities.
5.5 Conclusion

In this chapter the following 8 research questions were addressed:

Q1) Can the model explain the exceptional *K. mikimotoi* blooms that occurred in 2006, 2010 and 2011 by a combination of advection and growth?

Here, the model was used to study high density *K. mikimotoi* blooms as observed at the Scottish west coast in 2006, 2010 and 2011. The model could reproduce patterns of bloom advection and could be used to test hypotheses about possible bloom origins and transport of *K. mikimotoi* populations. The model was also useful to explain combined effects of physical accumulation and biological growth. However, limitations, such as coastline resolution and lack of offshore species data leave room for further model development to improve simulations.

Q2) Is it necessary to include biological growth and behaviour to simulate *K. mikimotoi* blooms?

Biological growth and migration behaviour had to be included in the model to allow simulation of bloom densities of *K. mikimotoi*.

Q3) How does the inclusion of direct wind forcing influence model prediction?

The effect of direct wind forcing on cell advection was different between model simulations using hydrodynamic data provided from POLCOMS and NEMO. When the IBM was coupled with current data produced from POLCOMS, direct wind forcing could cause differences in physical accumulation of cells near the coast and advective transport along the ESC. The effect of wind was less pronounced in model simulations using current data produced by NEMO. This is most likely due to a stronger representation of the ESC in NEMO compared to POLCOMS.

Q4) Can cell densities calculated from satellite imagery be used to initialise such models?

The model could be initiated with satellite images and model predictions could be used to draw conclusions about physical accumulation and cell growth. However, high background chlorophyll concentrations made interpretation of results difficult. Moreover, species discrimination of satellite chlorophyll and updated calculations to convert chlorophyll to cell numbers for Scottish strains of *K. mikimotoi* would be desirable to improve confidence in simulations.

Q5) Can initialising the model with single discrete seed populations provide information about bloom origin?
Discrete ISPs were successfully used to determine bloom origin and transport of populations along the west Scottish coast.

Q6) Is it possible that the bloom in 2006 was seeded by overwintering cells from the exceptional *K. mikimotoi* bloom near Ireland in 2005?

Model simulations confirm that it would have been possible for overwintering cells from the Northern Ireland to be advected towards the west Scottish coast. However, cells were not predicted to reach as far as the Scottish north coast, Orkney or Shetland.

Q7) What is the role of the European Slope Current (ESC) in *K. mikimotoi* bloom advection.

To simulate bloom occurrence in the north of Scotland, an additional input of cells from the ESC was necessary, suggesting that the ESC played a crucial part in bloom development and extent of *K. mikimotoi*.

Q8) How will using different hydrodynamic models affect predicted bloom advection?

The IBM can simulate *K. mikimotoi* blooms using either hydrodynamic model output. However, using predicted current data from NEMO lead to a stronger effect of advection of cells by the ESC and thereby reduced the effect of direct wind forcing.

In summary, the model presented here is useful as a tool explaining different aspects of observed blooms, such as the role of advection, biological growth and possible bloom origins. While the model currently cannot provide an operational HAB forecast, it is of value to improve our understanding of HAB transport and the combination of biological behaviour and physical drivers such as wind, currents and temperature. Further work is needed for the development of reliable species discrimination from satellite imagery (Kurekin et al. 2014, Sourisseau et al. 2016), models with a high resolution for coastal areas (Aleynik et al. 2016) and culturing Scottish strains of *K. mikimotoi* to allow the development of a mathematical growth formulation adjusted to local parameters. Better knowledge of species distribution and concentrations on the shelf would also be desirable to allow model initiation and validation.
Inter-annual differences in wind and currents and their effect on high biomass HAB transport

6.1 Introduction

Negative effects of HABs are often only noticed if they affect coastal areas. Foam events or mass mortalities of fish are most visible in coastal areas but go largely unnoticed when happening offshore. The majority of aquaculture and shellfish harvesting sites are also located close to the coast, with regulatory monitoring in Scotland limited to coastal sites. It is possible that local conditions at coastal sites cause rapid cell growth and the development of HABs. However, during numerous bloom events, a rapid increase of numbers of harmful phytoplankton cells at coastal sites has been recorded (e.g. Davidson et al. 2009, Whyte et al. 2014). The increase of cell numbers exceeding possible \textit{in situ} growth can be explained by advection of high cell densities to monitoring sites.

For example, a rapid increase of \textit{K. mikimotoi} in coastal areas was recorded in summer 2004 in west India (Robin et al. 2013). Hindcast analysis of that bloom suggested it first developed offshore, where a combination of upwelling and strong thermal stratification provided optimal growth conditions for \textit{K. mikimotoi} (Robin et al. 2013). Onshore advection, promoted by the current regime and a sudden change in wind direction, could then explain the rapid increase of cells in coastal areas (Robin et al. 2013). Similar observations were made for \textit{K. mikimotoi} in North West European shelf waters; in summer 1991, warm weather and strong thermal stratification were linked to a high density \textit{K. mikimotoi} bloom that developed in offshore shelf waters near Ireland. Onshore advection was then caused by changes in winds and upwelling relaxation leading to an onshore flow (Raine et al. 1993).

Advection of cells was also suggested to explain the rapid increase of cell numbers observed during the exceptional Scottish \textit{K. mikimotoi} boom in 2006 (Davidson et al. 2009). Hindcast modelling (chapter 5) showed that cells present at offshore locations on the shelf were likely to be advected towards the coast. Domain wide model initialisation from satellite images showed a strong accumulation of cells near the coast (Figure 5.5) and ISPs from various locations on the shelf were predicted to be transported towards coastal areas (Figure 5.7).

A possible location for the seed population for the 2006 bloom are the waters north of the Northern Ireland coast, where an extensive bloom was observed the previous year (Davidson et al. 2009). Modelling confirmed that cells present near the Northern Ireland coast would indeed have been advected towards the west Scottish coast (Figure 5.7 a). This observation gives rise to the question of whether blooms at the west coast of Scotland could be predicted from a knowledge of previous blooms in
Northern Ireland. However, the combination of an exceptional bloom near the north coast of Northern Ireland or the Republic of Ireland followed by an extensive bloom in Scotland seems to be the exception. For example, high densities of *K. mikimotoi* were recorded near the coast of Northern Ireland during a regulatory monitoring cruise in 2012, with no bloom of *K. mikimotoi* being observed in Scotland in the same or the following year.

Should a seed population have been present in 2006 and 2012 it is possible that inter-annual differences in advection could have transported cells towards Scotland in 2006 but away from the coast in 2012. Inter-annual differences in advection, either by wind or currents, were recently linked to HAB occurrence in the north of Scotland (Whyte et al. 2014). In this case, two exceptional blooms of toxin producing *Dinophysis* were explained by sudden onshore advection of cells caused by rapid changes in wind direction in summer 2006 and 2013. As a result in 2013, 70 people were reported to suffer from shellfish poisoning after consumption of mussels harvested in Shetland (Whyte et al. 2014). A similar link between sudden changes in wind direction and onshore advection of *Dinophysis* was also observed for Ireland (Raine et al. 2010b). In this situation, weather forecasts can be are used as an index for HAB likelihood: Sudden changes from wind directed towards the shore, to wind directed seawards generally lead to increasing surface water flow in an onshore direction. This leads to a coastal influx of deeper, nutrient rich waters. If wind directions change rapidly, it would lead to a sudden onshore transport of warm surface waters, creating optimal growth conditions for *Dinophysis*. This index has a good accuracy in summer, but is limited to the time span of a reliable weather forecast (Raine et al. 2010b).

Such observations have lead to a recent improvement of short term HAB prediction for the European Atlantic coast. Weekly risk assessments of HAB likelihood now utilise weather forecasts and predictions of currents and water temperature (Silva et al. 2016, Cusack et al. 2016). Using this information together with available information of coastal HAB counts, there was a 86% success rate of HAB prediction in Portugal up to 3 day in advance (Silva et al. 2016). Such predictions are most accurate when information about harmful cells is present at other coastal or offshore locations, making it possible to predict the path of advection for such cells. For some areas it might even be possible to predict HAB occurrence based on physical factors alone. Dippner et al. (2011) suggested that a permanent seed population for HABs was present in Vietnamese offshore waters during periods of upwelling high riverine nutrient input. If the relevant cells are present during these conditions, coastal HABs could be predicted by wind speed and direction linked to inter-annual differences in monsoon strength (Dippner et al. 2011).

In this chapter, the relationship between onshore advection and occurrence of
coastal \textit{K. mikimotoi} blooms in Scotland is explored.

The first aim of this chapter is to simulate pathways for \textit{K. mikimotoi} cells near the Malin Shelf in 2006 and 2012. It is possible that differences in wind and current conditions between the years would lead to advection of cells towards the Scottish coast during 2006 and away from the Scottish coast during 2012. To determine whether this is the case, the IBM model introduced in chapter 5 was run with different modelled seed populations and environmental conditions from 2006 and 2012.

The second aim of this chapter is to determine whether there could be permanent seed population for \textit{K. mikimotoi} offshore or within the ESC, and inter-annual differences in wind and currents could lead to on or off shore transport of such seed populations, explaining why \textit{K. mikimotoi} blooms occur only during some years but not others. To address this aim, the IBM described in the previous chapter was used to simulate bloom advection of an initial seed population within the ESC for the years 2000 to 2015. Model results were compared to results from regulatory \textit{K. mikimotoi} monitoring to validate model output.

\section{6.2 Methods}

\subsection{6.2.1 The model and data acquisition}

See chapter 5.2.1 and 5.2.2 for model description and data acquisition. The model was not modified from its original parameters (chapter 5, Table 5.1). NEMO was used as the hydrodynamic model for all model runs and temperature and velocity fields for years 2000 to 2015 were obtained from the Marine Environment Monitoring Service Copernicus. Daily wind data for the same time period was obtained for BADC weather stations on Tiree, Stornoway and Lerwick.

Additional to cell data from FSS (as described in chapter 5.2.1), \textit{K. mikimotoi} cell counts were obtained from an AFBI regulatory monitoring cruise to the Malin shelf in 2012. Surface water samples were collected from approximately 50 stations across the Malin shelf (chapter 3, Figure 3.2). Samples were fixed with Lugol’s iodine and \textit{K. mikimotoi} were enumerated using the Utermöhl method as described in detail in Gowen et al. (1982) and chapter 3. Satellite data for 2012 for the time of data collection is shown in Figure 6.1. High densities of \textit{K. mikimotoi} were found in samples taken on the 20th July 2012. Around the same time (23rd to 30th July) the satellite image indicated a high chlorophyll concentration at approximately the same location. Satellite images indicated that the bloom was advected towards the north coast of Ireland but not the Scottish west coast (Figure 6.1).
Model runs were designed to determine if advection of cells was different between years and if that could explain why there was a bloom in Scotland in 2006 but not 2012 (Table 6.1, runs 1 to 12). Predicted temperature and velocity fields for 2006 and 2012 are given in Figures 6.2 and 6.3. For model output for other years see Appendix F.

For runs 1 and 2 ISP were estimated from satellite chlorophyll from the 23rd July 2012 as described in chapter 5.2. Discrete ISPs (runs 3 and 4), were located at the original AFBI sampling points and model simulations were conducted with and without direct wind forcing. The model was run with wind and current conditions for 2012 (runs 3 and 4) and 2006 (runs 5 and 6) to determine if inter-annual changes in wind and current regimes would lead to different predictions of advective transport. For the same reason the model was initialised with three discrete ISPs thought to be the seed populations for the bloom in 2006 (chapter 5) and run with wind and current conditions for 2012 (runs 7 and 8). For runs 9 to 12, the model was initialised...
with a theoretical seed population near the shelf break and run for 2006 and 2012, with and without direct wind forcing.

To further test the role of inter-annual differences in wind and currents we modelled the path of a theoretical seed population located at the shelf edge for the years 2000 to 2015 (Table 6.1, runs 13-28). Recorded *K. mikimotoi* cell densities from regulatory monitoring sites in Scotland for these years are presented in Figure 6.4.

Table 6.1: List of model runs. The second column shows the year for current, temperature and wind data that was coupled to the IBM. Column 3 and 4 describe the initial seed population (ISP) used for model initiation and the switch for direct wind forcing (1 = on, 0 = off) respectively.

<table>
<thead>
<tr>
<th>Run</th>
<th>Year</th>
<th>ISP</th>
<th>switch for wind</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2012</td>
<td>satellite (whole domain)</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>2012</td>
<td>satellite section</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>2012</td>
<td>ISP from Coryste cruise 2012</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>2012</td>
<td>ISP from Coryste cruise 2012</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>2006</td>
<td>ISP from Coryste cruise 2012</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>2006</td>
<td>ISP from Coryste cruise 2012</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>2012</td>
<td>ISP from 2006 monitoring</td>
<td>1</td>
</tr>
<tr>
<td>8</td>
<td>2012</td>
<td>ISP from 2006 monitoring</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>2012</td>
<td>Shelf input</td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td>2012</td>
<td>Shelf input</td>
<td>0</td>
</tr>
<tr>
<td>11</td>
<td>2006</td>
<td>Shelf input</td>
<td>1</td>
</tr>
<tr>
<td>12</td>
<td>2006</td>
<td>Shelf input</td>
<td>0</td>
</tr>
<tr>
<td>13-28</td>
<td>2000-2015</td>
<td>Shelf input</td>
<td>1</td>
</tr>
</tbody>
</table>
6 Inter-annual differences in HAB transport

(a) June 2006

(b) June 2012

(c) July 2006

(d) July 2012
Figure 6.2: Average surface water temperature obtained from NEMO for June to September for 2006 and 2012.
6 Inter-annual differences in HAB transport

(a) June 2006  (b) June 2012

(c) July 2006  (d) July 2012
Figure 6.3: Average surface currents obtained from NEMO for June to September for 2006 and 2012.
6 Inter-annual differences in HAB transport

(a) 2000  
(b) 2001  
(c) 2002  
(d) 2003  
(e) 2004  
(f) 2005  
(g) 2006  
(h) 2007  
(i) 2008  
(j) 2009  
(k) 2010  
(l) 2011
Figure 6.4: Maps showing peak presence of *K. mikimotoi* in 2000 to 2015 (blue = 5000 to 100000 cells l$^{-1}$, green = 100000 to 500000 cells l$^{-1}$, orange = 500000 to 1 million cells l$^{-1}$, red = above 1 million cells l$^{-1}$).

6.3 Results

6.3.1 Patterns in advection during 2006 and 2012

To study the transport of the *K. mikimotoi* bloom observed in 2012 near the north Irish coast, the model was initialised with cell densities calculated from a satellite image from the 20th July 2012 (run 1, Figure 6.5 a). As *K. mikimotoi* were only observed near the Northern Ireland coast, only that section from the satellite image was used as an ISP (run 2, Figure 6.5 b). The model predicted advection of cells northward along the west coast of the outer Hebrides. Noticeably, no cells were advected along the strait between the outer Hebrides and the Scottish mainland, an area that is known as the Minch (Figure 6.5 b).
Figure 6.5: Modelled bloom development for *K. mikimotoi* from initial positions from a) domain wide satellite chlorophyll b) a satellite section limited to the area of bloom observation.

As all satellite derived chlorophyll was converted into *K. mikimotoi* cell numbers, it might overestimate the density and extent of the present bloom (discussed in more detail in chapter 5). Therefore, for the next model run, it is assumed that cells were only present at the exact location at which they were found during the monitoring cruise (run 3,4, Figure 6.6). The model simulated cell advection with (Figure 6.6 a) and without direct wind forcing (Figure 6.6 b) to differentiate between advection caused by currents and by direct wind forcing. In both cases the model again
predicted cell transport towards the outer Hebrides but not along the Minch.

Figure 6.6: Discrete ISPs from AFBI monitoring cruise data (2012) a) with direct wind forcing and b) without direct wind forcing.

To determine whether inter-annual changes in wind and current conditions transported *K. mikimotoi* cells towards the Scottish west coast in 2006 but not 2012, the model was next run with wind, current and temperature data from 2006 (run 5,6, Figure 6.7). The predicted advection for this simulation was noticeably different to the one using 2012 wind forcing and hydrodynamic data. Simulating cells with 2006 conditions with (Figure 6.7 a) and without (Figure 6.7) direct wind forcing predicted cell advection from north Ireland towards the Scottish west coast, including Mull,
the Isle of Skye and along the Minch.

(a)

Figure 6.7: Discrete ISPs from AFBI monitoring cruise data (2012) using hydrodynamic conditions for 2006 together a) with direct wind forcing recorded in 2006 and b) without direct wind forcing.

To further explore the effect of inter-annual differences in oceanographic conditions, the model was initialised with the ISPs used to study the 2006 bloom (chapter 5) and coupled to wind and oceanographic conditions for 2012 (run 7,8, Figure 6.8). Despite different forcing conditions, model simulations predicted coastal bloom of *K. mikimotoi*. This might be due to the close proximity of ISPs to the coast, suggesting that under such conditions a bloom would be unavoidable.
For the next model simulations ISPs were located at several positions within the ESC to determine if different meteorological and oceanographic conditions would lead to different patterns of advection of cells and hence different predictions of bloom occurrence in coastal areas (Figure 6.9 and 6.10). The model was run with and without direct wind forcing for both scenarios. These simulations showed a marked difference in predicted cell advection. Assuming a seed population for *K. mikimotoi* was present in the ESC in both years, model simulations predicted onshore advection
and enhanced growth during 2006, while growth was less in 2012, with no onshore advection simulated by the model.

Figure 6.9: Model simulations with ISPs located in the ESC and hydrodynamic conditions for 2012 together a) with direct wind forcing recorded in 2012 and b) without direct wind forcing.
Figure 6.10: Model simulations with ISPs located near the shelf edge and ESC and hydrodynamic conditions for 2006 together a) with direct wind forcing recorded in 2006 and b) without direct wind forcing.

6.3.2 Inter-annual differences in advection of shelf populations

Model simulations showed clear differences in predicted advection and cell growth between 2006 and 2012 for a given seed population of *K. mikimotoi*. To further explore the role of inter-annual differences in currents, the model was initialised with a theoretical seed population of *K. mikimotoi* in the ESC and coupled with physical data (wind, currents, temperature) for years 2000 to 2015 (Figure 6.11). Model predictions were then compared to results from regulatory monitoring. Results are
summarised in Table 6.2
During all years the model predicted the development of a *K. mikimotoi* bloom on the shelf if the model was initialised with a seed population in the ESC. However, model predictions showed strong variations of location and intensity of predicted blooms between years, with onshore cell advection only being predicted for some years. Model simulations with physical conditions from 2012 predicted the lowest density and bloom extent of *K. mikimotoi* compared to all other years. Cells were predicted to remain within the ESC with no onshore advection simulated by the model. The model simulation for 2006 showed the opposite trend, and predicted bloom densities and a spacial extent of the bloom that was greater than for other years. There is a general qualitative agreement between model predictions and
observed cells from coastal monitoring for both 2006 and 2012.

Table 6.2: Summary of *K. mikimotoi* model predictions for coastal regions and agreement with monitoring observations for 2000 to 2015. Discrepancy 1 (Modelled but not observed bloom) was marked with D1 and Discrepancy 2 (Observed but not modelled) was marked with D2.

<table>
<thead>
<tr>
<th>Year</th>
<th>Model prediction</th>
<th>Agreement to observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>No cells near the coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2001</td>
<td>Bloom near the north coast</td>
<td>No. D1</td>
</tr>
<tr>
<td>2002</td>
<td>Bloom near the north coast</td>
<td>No. D2*</td>
</tr>
<tr>
<td>2003</td>
<td>Bloom near the north coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2004</td>
<td>Bloom near the north coast</td>
<td>No. D1</td>
</tr>
<tr>
<td>2005</td>
<td>Bloom near the north coast</td>
<td>No. D1</td>
</tr>
<tr>
<td>2006</td>
<td>Bloom around the coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2007</td>
<td>Bloom around the coast</td>
<td>No. D1</td>
</tr>
<tr>
<td>2008</td>
<td>No cells near the coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2009</td>
<td>No cells near the coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2010</td>
<td>Bloom around the coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2011</td>
<td>No cells near the coast</td>
<td>No. D2</td>
</tr>
<tr>
<td>2012</td>
<td>No cells near the coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2013</td>
<td>Bloom near the north coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2014</td>
<td>No cells near the coast</td>
<td>Yes</td>
</tr>
<tr>
<td>2015</td>
<td>No cells near the coast</td>
<td>Yes</td>
</tr>
</tbody>
</table>

* Modelled bloom (north coast) was observed, but blooms were also observed around the west coast.

For simulation with year 2000 conditions, the model predicted a large bloom on the shelf, but little advection of cells towards the coast. Monitoring stations recorded low *K. mikimotoi* densities, except for one high density bloom with over 0.5 million cells l$^{-1}$ at the Isle of Skye.

*K. mikimotoi* bloom predictions from year 2001 simulations were similar to those for 2000. However, during 2001 cells were predicted to be advected closer to the west coast and bloom densities were predicted around the north coast and Orkney and Shetland. Regulatory monitoring indicated that only low numbers of *K. mikimotoi* were present during 2001, with no elevated cell levels being recorded in the north of Scotland.

Model prediction and observed cell numbers showed little agreement for 2002. Model simulations predicted a strong northwards advection of cells close to Orkney and Shetland with no cells being predicted close to the west coast. Monitoring recorded elevated cell numbers of *K. mikimotoi* in Shetland as simulated by the model. However elevate cell numbers were also recorded around Skye and the outer Hebrides, in contrast to the model simulation.
Model simulations for 2003 predicted a high growth of *K. mikimotoi*, probably due to elevated water temperature in July (Appendix F). Advection was predicted to transport cells towards the north Scottish coast. The model simulation agreed with field data from monitoring stations with elevated cell densities observed around Orkney and Shetland and further down the east coast.

In 2004 and 2005 recorded numbers of *K. mikimotoi* from monitoring stations were low, while the model predicted advection of cells towards Shetland in 2004 and the north coast of the Scottish main land in 2005. Interestingly, during 2005, the model simulated a strong advection of a *K. mikimotoi* population towards the Northern Ireland coast, where a bloom was recorded in that year (Silke et al. 2005).

In 2007, 2008 and 2009 regulatory monitoring suggested there were only low numbers of *K. mikimotoi* present in coastal waters. The model simulated advection of cells towards the coast for 2007, resulting in differences between observed and predicted coastal blooms. Model simulations run for 2008 and 2009 predicted advection in onshore direction without prediction of blooms at the coast during the period of the model run in agreement with field data.

Modeled and observed *K. mikimotoi* blooms showed some agreement in 2011; The model simulated high growth of *K. mikimotoi* and advection of cells along the Minch and towards Shetland, while bloom densities were recorded at several locations around the coast during that year. To the contrary, the model predicted no onshore advection of cells during 2011, while high numbers of cells were recorded at several monitoring points. It is possible that bloom occurrence during 2011 was fuelled by overwintering cells from the bloom the previous year as suggested for the blooms in 2005 in Northern Ireland and 2006 in Scotland.

In 2013 high numbers of cells were recorded north of Lewis and around Orkney, which partly agreed with model prediction of onshore advection of cells towards Lewis and Shetland.

During 2014 and 2015, agreement between model simulations and field data was good, with no elevated numbers of *K. mikimotoi* recorded at monitoring station or predicted by the model.

### 6.4 Discussion

#### 6.4.1 Differences in advective transport between 2006 and 2012

Model simulations suggested that differences in bloom occurrence on the Scottish west coast in 2006 and 2012 were linked to differences of current regimes between the years. During 2012, high densities of *K. mikimotoi* were recorded near the Northern Ireland coast and during 2006, model simulations indicated that a seed population for the observed bloom in Scotland was also present near the Northern Ireland coast.
Model simulations in this chapter suggest that, if cells were present in the same location at the same density for both years, inter-annual differences in current regimes would have caused different advective transport of cells between the years.

Onshore advection towards the Scottish west coast was stronger in 2006 than 2012. However, advection of *K. mikimotoi* towards the west coast of Scotland predicted by the model depended strongly on the location of the initial population of cells. Model simulations with ISPs close to the Northern Ireland coast predicted a strong onshore advection for 2006 conditions with predicted cell transport towards the coast of the Scottish mainland and the inner and outer Hebrides (Figure 6.7). For 2012, the model simulated some level of transport of cells towards the west Scotland, but mainly towards the outer Hebrides, not the inner Hebrides or the coast of the mainland (Figure 6.6). For model simulations with ISPs located on the shelf, but closer to the Islands, the model predicted bloom densities of *K. mikimotoi* at coastal sites for both years (Figure 6.8 and 5.11). This highlights the importance of the location of ISPs in simulating bloom occurrence. Modelling approaches such as this one have the potential to be used in HAB prediction, however, to be able to do so, more information about offshore populations of *K. mikimotoi* has to be available. The potential for model predictions would, therefore, be greatly improved with the development of better methods for offshore HAB surveillance by satellite discrimination (Kurekin et al. 2014) or glider deployment as described in chapter 4.

In chapter 5 the importance of cells being introduced to the shelf from the ESC was discussed. Here, model simulations show that cells within the ESC were advected towards the coast in 2006 conditions, but stayed within the ESC in 2012. The ESC and shelf break can act as a barrier for water exchange between the shelf and adjacent oceanic waters (Huthnance 1995). However, during some years (e.g. as observed in 2015, chapter 3 and 4) Atlantic water is advected across the shelf break onto the Malin shelf (Gowen et al. 1998, Inall et al. 2009, Davies & Xing 2003, Xing & Davies 2001). Unfortunately, the underlying physical drivers for inter-annual variability in the strength of the ESC and overspill of oceanic surface water onto the shelf are still poorly understood (Jones 2016 and references therein). Better understanding of the conditions that lead to Atlantic overspill and thereby introducing cells onto the shelf would be desirable for HAB prediction, as the results from this chapter suggest that hydrodynamic conditions, together with offshore data to determine the presence of seed populations, could potentially be used as an index for the likelihood of coastal *K. mikimotoi* blooms.

Growth of *K. mikimotoi* cells was less under environmental conditions for 2012 than for 2006 under the same seed conditions (Figure 6.6 and 6.7). Water temperature was generally lower during 2012 compared to 2006 (Figure 6.2) which might,
given the high model sensitivity to temperature found in chapter 5, explain the lower growth during this year. However, running the model with current and wind conditions from 2006 but temperature fields from 2012 (data not shown) revealed that, in this case, differences in growth caused by temperature were minimal. This suggests that current conditions in 2006 lead to a stronger physical accumulation of cells, while current conditions in 2012 were more likely to lead to cell dispersion (Figure 6.3). Stronger current speed of coastal currents (Figure 6.3) might have also lead to higher shear and hence increased cell mortality (Gentien et al. 2007).

Local currents, especially close to the surface, can be strongly influenced by wind patterns, which can even lead to a reversal of smaller surface currents in extreme cases (Ellett et al. 1986). However, running the model with and without direct wind forcing showed that the main differences in advection between years was caused by different current strength and direction rather by differences in direct wind forcing (Figures 6.6 to 6.10). Here we found that including direct wind forcing did make a difference to phytoplankton advection, but main inter-annual differences in advection were mostly explained by differences in currents.

### 6.4.2 Inter-annual differences in advection

Model simulations were run using direct wind forcing from weather stations and hydrodynamic conditions obtained from NEMO for years 2000 to 2015, to study the effect of inter-annual differences in current regimes on predicted *K. mikimotoi* transport. All model simulations included direct wind forcing recorded hourly from weather stations (Appendix E). Model results, however, suggested that the advective transport caused by wind only caused minimal changes to advection solely predicted by current advection and diffusion. Current velocity and directions produced by NEMO (Appendix F) showed inter-annual variation of the strength of the ESC and smaller coastal currents.

Differences in the current regime caused differences in predicted onshore advection between years (Figure 6.11). The prediction of presence or absence of high density (above 0.1 million cells l$^{-1}$) *K. mikimotoi* blooms at the coast was then compared to results from coastal monitoring. To accurately simulate cell numbers and timing of the bloom, a better knowledge of the seed population would be necessary. Here, following the example from Dippner et al. (2011), it was assumed that there is a permanent seed population offshore and presence or absence of cells can be predicted by physical advection. Model prediction and field observations agreed for some years, but not all: modelled and observed presence or absence of *K. mikimotoi* agreed for 10 out of 16 years used for model simulations (62.4 %). For years 2000, 2008, 2009, 2012, 2014 and 2015 observed and predicted cell densities of *K. mikimotoi* were low. Model simulation of cells did not reach coastal areas which
suggests that even if a seed population of *K. mikimotoi* was present offshore it would not necessarily be advected towards the Scottish coast. For years 2003, 2006, 2010 and 2013, the predicted presence of *K. mikimotoi* near coastal sites agreed with field observations. For these years it is possible that observed coastal *K. mikimotoi* originated from the shelf edge, however, further field data is needed to validate that.

For 6 years predicted location of *K. mikimotoi* was in disagreement with field data. For 2001, 2004, 2005 and 2007 the model predicted advection of cells towards the north coast, however, cell counts from the north coast, Orkney and Shetland indicated overall low numbers or absence of *K. mikimotoi*. During these years, current regimes favoured onshore advection of cell populations in the north of the ESC. It is possible that seed populations were simply not present during these years, at least not as far north. This is in agreement with results from chapters 2 and 3, where no *K. mikimotoi* cells were found during offshore cruises, suggesting that a seed population might not be permanently present. It is also possible that blooms predicted by model simulations were indeed present around the coast, but missed by monitoring if blooms were not present near coastal monitoring sites. Model simulations for 2005 and 2007 suggested that seed populations in the south of the model domain would have been advected towards Northern Ireland. Elevated concentrations of *K. mikimotoi* were recorded near the coast of Northern Ireland in 2005 (Silke et al. 2005) but not in 2007.

For 2002 and 2011, blooms were observed around the west coast, however no onshore advection was predicted by the model. Model simulations for 2002 predicted onshore advection of cells, however, cell advection was predicted towards the north coast of Scotland, not the west coast where cells were recorded. The observed bloom in 2011 might have been caused by overwintering cells from the *K. mikimotoi* bloom the previous year. However, more information about overwintering strategies of *K. mikimotoi* would be needed to confirm that.

Inter-annual differences in currents and winds can be caused by a multitude of factors, some of which are natural, while others are linked to anthropogenic climate change. Large scale oceanographic patterns like the North Atlantic Oscillation (NAO), caused by changes in the pressure differences between the north and south of the North Atlantic, can lead to inter-annual variations in physical factors (Flatau et al. 2003, Hurrell et al. 2013). For example, the NAO index showed a strong correlation with the latitude of the Thermohaline Overturning Circulation (Taylor & Stephens 1998). A high NAO index was associated with a northwards expansion of the North Atlantic current system with a two year time lag (Taylor & Stephens 1998).

Inter-annual differences in oceanography in the North East Atlantic (North West European Shelf sea) were also linked to a weakening trend in the strength of the
subpolar gyre (Johnson et al. 2013). The strength of the subpolar gyre determines how much nutrient rich water enters the channel from the north. During periods of a weak gyre surface waters can be nearly exclusively from a southern origin (Johnson et al. 2013). Anthropogenic climate change was also linked to inter-annual and inter-decadal changes in regional oceanographic features; time series of mooring data reaching back to the 1980s showed an overall warming trend of the sea surface temperature with an increase of 0.57 °C per decade while timing of the maximum temperature in summer is becoming earlier by 12 days per decade (Inall et al. 2009). Changes in temperature are ultimately linked to the North Atlantic current system which is largely driven by temperature and salinity.

6.5 Conclusion

The first aim of this chapter was to determine whether differences in wind and current conditions between 2006 and 2012 would lead to different patterns of advection of *K. mikimotoi* populations on the shelf. Model simulations suggested that this was the case. To address the second aim, whether coastal *K. mikimotoi* blooms could be explained by inter-annual differences in advective transport, the model was run with theoretical seed populations offshore for years 2000 to 2015. Model simulations suggest that onshore advection of *K. mikimotoi* was a possible explanation for bloom occurrence in some years, but not all. The results presented here show that modelled current conditions can help explain observed *K. mikimotoi* patterns, however, better information of offshore populations would be needed to allow a higher confidence in model results.
7 Preliminary model development to study *Phaeocystis* bloom advection

7.1 Introduction

The model presented in chapter 5 was written with a species specific growth formulation for *Karenia mikimotoi*. However, no *K. mikimotoi* cells were found during the field work undertaken in chapters 2 to 4. During the research cruise in autumn 2014 (chapter 2), cell concentrations were generally low; however, during the cruise (chapter 3) and glider mission (chapter 4) in summer 2015, a high density bloom of *Phaeocystis* was found on the Malin shelf. The elevated chlorophyll concentration, caused by the around 1 million cells l$^{-1}$, was also visible from satellite imagery (chapter 4). High density blooms of *Phaeocystis* have previously been linked to fish and shellfish mortalities caused by anoxia following bloom decay (Rogers & Lockwood 1990, Peperzak & Poelman 2008). Foam produced by *Phaeocystis* can be an additional nuisance when accumulating at beaches or coastal areas (Schoemann et al. 2005). Therefore, it would be desirable to predict the advective transport of such blooms.

The potential link between coastal *Phaeocystis* blooms and onshore advection by wind and currents around the European coast has been addressed by several studies. It was initially hypothesized that high density *Phaeocystis* blooms in coastal areas were caused by eutrophication (Lancelot et al. 1987). On the contrary, *Phaeocystis* distribution and relative abundance from continuous plankton recorder (CPR) data collected since 1948 showed no apparent link between *Phaeocystis* occurrence and areas or periods of high eutrophication (Gieskes et al. 2007). Instead, CPR data revealed that there was a persistent population of *Phaeocystis* present in mid Atlantic oceanic regions that are generally unaffected by coastal eutrophication. Based on these records, Gieskes et al. (2007) suggested that *Phaeocystis* occurrence in the North Sea could be linked to advection and influx of oceanic waters, containing seed populations of *Phaeocystis*. Similar links have already been established between occurrence of certain zooplankton species in the North Sea and influx of Atlantic water (Reid et al. 2003, Lindley et al. 1990). Unfortunately, not enough data of *Phaeocystis* is available to establish such a link for this genus (Gieskes et al. 2007).

Studies focussing on the Dutch coast also showed a link between offshore growth and onshore advection of high density *Phaeocystis* blooms. For example, a high density bloom of *Phaeocystis*, responsible for the loss of 10 million kg of mussels within a Dutch coastal estuary in 2001, was thought to be advected towards the commercially important shellfish harvesting sites by a sudden change in wind direction (Peperzak & Poelman 2008). In support of this hypothesis, there was an apparent
link between observed foam events at the Dutch coastline and onshore wind direction (Blauw et al. 2010). Operational *Phaeocystis* forecasts in the Netherlands are, therefore, supported by detection of high chlorophyll signatures visible from satellite and model simulations of growth and advection of those observations (Woerd et al. 2006).

In Vietnam waters, occurrence of high density *Phaeocystis* blooms near the coast appeared to be linked to the strength and direction of monsoon winds and circulation (Hai et al. 2010). Model simulations suggested that harmful blooms in coastal areas were transported alongshore with the coastal jet when wind strength and circulation patterns from south westerly monsoons were weak. When wind and south westerly monsoon circulation were strong, cells were advected offshore (Hai et al. 2010). The Lagrangian transport model treated cells as passive particles with no biological formulation of cells included (Hai et al. 2010).

As discussed in chapter 5, there are limitations when treating cells as passive particles in Lagrangian transport models. Including species specific biological formulations is often desirable but difficult, either due to the lack of knowledge about the biology of the target species or due to the complex nature of the target species’ life cycle and food web interactions (Hai et al. 2010, Pinto et al. 2016, Moita et al. 2016, Silva et al. 2016, Sourisseau et al. 2016). Conceptual models for biology that include several life cycle stages for *Phaeocystis* have been suggested (Hai et al. 2010, Whipple et al. 2005); however, there are still unknown factors in these models. Because of this, and their complexity, they have not yet been included in numerical modelling.

Complex population based models (PLMs) with a separate *Phaeocystis* compartment, phytoplankton competitors, grazers and different nutrients have been used successfully to study the effect of grazing pressure (Verity 2000) and nutrient requirements (Lancelot et al. 2005, Gypens et al. 2007) for *Phaeocystis* dominance and bloom development. However, such complex models are still limited by the lack of information on the effect of colony and aggregate formation on grazing and nutrient uptake (Verity 2000, Lancelot et al. 2005). While these models are undoubtedly useful to study specific elements of *Phaeocystis* bloom development, they are generally unsuitable to study advection of high density blooms.

In this chapter, with the main focus on bloom advection, the individual based model (IBM) introduced in chapter 5 was used with a species specific temperature dependent growth formulation for *Phaeocystis* (Schoemann et al. 2005). The aim of this chapter was to use the model to hindcast bloom development and advection of the *Phaeocystis* bloom observed during the field work discussed in chapter 3 and 4. To assess the model’s hindcast capacity, this chapter was designed to test the following research questions:
Q1) Is the model capable of simulating observed *Phaeocystis* bloom densities if growth is modelled as a temperature-dependent growth function?
Q2) Can the model provide information about advective transport of *Phaeocystis* blooms?
Q3) Can information collected from scientific cruises and glider deployment be used for model initiation?

### 7.2 Methods

#### 7.2.1 *Phaeocystis* Data

As *Phaeocystis* does not pose a direct threat to human health, the genus is not included in regulatory monitoring in the UK. Records of *Phaeocystis* blooms are therefore poor, which makes it difficult to find information of abundance and distribution of cells that would be desirable for model initialization and verification. For some occasions, however, good records of *Phaeocystis* are available and can be used in this study. Extremely high densities (10 million cells l\(^{-1}\)) of *Phaeocystis* were recorded on the Scottish east coast near Aberdeen in 2005. Samples were collected by Marine Scotland and *Phaeocystis* was enumerated (International Council for the Exploration of the Sea 2006). Cell concentrations between 5 to 10 million cells l\(^{-1}\) were found in 4 samples taken between the 25th April 2005 and 5th May 2005, with no counts available before or after that period. Therefore, satellite images were used to identify potential bloom pathways from high chlorophyll signatures (Figure 7.1). Elevated chlorophyll near the east coast was visible from the 11th April until the 5th May. Satellite imagery suggested that the high chlorophyll area might have developed north of Aberdeen and expanded southwards.

Another high density *Phaeocystis* bloom, with up to 1 million cells l\(^{-1}\), was observed during a research cruise and glider mission in summer 2015 (see chapter 3 and 4 for details). Unfortunately, there were no *Phaeocystis* cell counts made at coastal stations during or after the observed bloom. However, on the 24th August 2015, a high presence of *Phaeocystis* was noted in samples collected from Shetland and the east coast of Skye.

#### 7.2.2 Model

See chapter 5.2.2 for a description of the model. Modified parameter values are presented in Table 7.1. The ocean circulation model NEMO was used as the hydrodynamic model (chapter 5.2.2). The Lagrangian particle tracking model described in chapter 5.2.2 was not modified for these simulations. The biological model was modified to incorporate the growth of *Phaeocystis* as described by Schoemann et al.
Figure 7.1: Chlorophyll (µg l\(^{-1}\)) from Modis aqua satellite data obtained from the National Oceanic and Atmospheric Administration data service from the 2.3.2005 to the 29.5.2005. Aberdeen, where the bloom was recorded, is marked with a green circle.

Values (as set by Schoemann et al. 2005) for the maximal growth rate (\(\mu_{\text{max}}\)), the optimal temperature for growth (\(T_{\text{opt}}\)) and the temperature interval (\(dT\)) are given.

\[
\mu = \mu_{\text{max}} \times EXP[-(T - T_{\text{opt}})^2 / dT^2]
\]
Table 7.1: Model parameters. Switches could be set to 1 = yes/on, 0 = no/off.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of particles</td>
<td>457954</td>
</tr>
<tr>
<td>Time step of particle model (s)</td>
<td>600</td>
</tr>
<tr>
<td>Start day of simulation for 2005</td>
<td>25th April</td>
</tr>
<tr>
<td>Start day of simulation for 2015</td>
<td>15th July</td>
</tr>
<tr>
<td>Start time of simulation (hh:mm:ss)</td>
<td>15:00:00</td>
</tr>
<tr>
<td>Length of simulation(h)</td>
<td>2208</td>
</tr>
<tr>
<td>Output frequency (h)</td>
<td>24</td>
</tr>
<tr>
<td>Duration of mobile stage (d)</td>
<td>200</td>
</tr>
<tr>
<td>Upwards movement caused by positive buoyancy (m h^{-1})</td>
<td>1</td>
</tr>
<tr>
<td>Maximum depth for upwards swimming behaviour (m)</td>
<td>30</td>
</tr>
<tr>
<td>Switch for cell growth</td>
<td>1</td>
</tr>
<tr>
<td>Switch for cell mortality</td>
<td>1</td>
</tr>
<tr>
<td>Mortality constant K</td>
<td>$4 \times 10^{-8}$</td>
</tr>
<tr>
<td>Minimum velocity shear (s^{-1})</td>
<td>0.001</td>
</tr>
<tr>
<td>Maximal growth rate</td>
<td>$\mu_{max} = 1.3$</td>
</tr>
<tr>
<td>Optimal temperature for growth</td>
<td>$T_{opt} = 16.3$</td>
</tr>
<tr>
<td>Temperature interval</td>
<td>$dT = 13.7$</td>
</tr>
<tr>
<td>Number of cells per virtual particle for 2005</td>
<td>$5.0 \times 10^{13}$</td>
</tr>
<tr>
<td>Number of cells per virtual particle for 2015</td>
<td>$5.0 \times 10^{12}$</td>
</tr>
<tr>
<td>Switch for vertical diffusion</td>
<td>1</td>
</tr>
<tr>
<td>Switch for horizontal diffusion</td>
<td>1</td>
</tr>
<tr>
<td>Switch for wind forcing</td>
<td>1</td>
</tr>
<tr>
<td>Depth to which wind causes advection (zC)</td>
<td>30m</td>
</tr>
<tr>
<td>Cell density resolution (cells l^{-1})</td>
<td>113</td>
</tr>
</tbody>
</table>

in Table 7.1. Vertical motility for *Phaeocystis* was set to 1 m h^{-1} to account for positive buoyancy observed for this genus (Skreslet 1988).

A list of model runs is given in Table 7.2. Model runs 1 to 11 assessed the the effect of changes in the biological growth description on predicted cell numbers for the high density bloom observed in 2005. Model runs 12 to 14 and 15 to 16 were designed to test the role of advection in bloom transport during 2005 and 2015 respectively. Model sensitivity was calculated as described in chapter 5.2.3.
Table 7.2: List of model runs, year of the run (physical data), initial seed population (ISP) and biological growth formulation used.

<table>
<thead>
<tr>
<th>Run</th>
<th>Year</th>
<th>ISP</th>
<th>growth</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2005</td>
<td>Aberdeen</td>
<td>No biology</td>
</tr>
<tr>
<td>2</td>
<td>2005</td>
<td>Aberdeen</td>
<td>No biology, positive buoyancy (1 m h$^{-1}$)</td>
</tr>
<tr>
<td>3</td>
<td>2005</td>
<td>Aberdeen</td>
<td>Growth and mortality</td>
</tr>
<tr>
<td>4/5</td>
<td>2005</td>
<td>Aberdeen</td>
<td>$\mu_{\text{max}} \pm 0.1$</td>
</tr>
<tr>
<td>6/7</td>
<td>2005</td>
<td>Aberdeen</td>
<td>$dT \pm 1.6$</td>
</tr>
<tr>
<td>8/9</td>
<td>2005</td>
<td>Aberdeen</td>
<td>$T_{\text{opt}} \pm 1$</td>
</tr>
<tr>
<td>10/11</td>
<td>2005</td>
<td>Aberdeen</td>
<td>Temperature±1°C</td>
</tr>
<tr>
<td>12</td>
<td>2005</td>
<td>North east coast</td>
<td>biology switches=1</td>
</tr>
<tr>
<td>13</td>
<td>2005</td>
<td>Shelf</td>
<td>biology switches=1</td>
</tr>
<tr>
<td>14</td>
<td>2005</td>
<td>North Sea</td>
<td>biology switches=1</td>
</tr>
<tr>
<td>15</td>
<td>2015</td>
<td>Satellite</td>
<td>biology switches=1</td>
</tr>
<tr>
<td>16</td>
<td>2015</td>
<td>Malin Shelf (field observation)</td>
<td>biology switches=1</td>
</tr>
</tbody>
</table>

7.3 Results

7.3.1 Biological growth

The model was initialised with cell concentrations of 10 million cells l$^{-1}$ at a single ISP near Aberdeen (Figure 7.2, runs 1 to 3). When cells were treated as passive particles (Figure 7.2 a) or without growth and mortality but with a positive buoyancy (Figure 7.2 b), the model was unable to sustain the observed bloom densities of over 1 million cells l$^{-1}$. Only by including biological growth, the model was able to simulate cell densities similar to those recorded around Aberdeen (Figure 7.2 c).

The model sensitivity to changes in the growth formulation was tested by changing values for the parameters used in the growth formulation to the upper and lower limits suggested by (Schoemann et al. 2005). Small changes in the maximal growth rate $\mu_{\text{max}}$ had no effect on cell density predicted by the model. Changes in water temperature or temperature related parameters had little effect on the total cell density predicted by the model (Table 7.3). Changes in $T_{\text{opt}}$ had normalised sensitivity values over 1, suggesting that the model is only sensitive to changes in this value (based on sensitivity established by Fasham et al. 1990).
Figure 7.2: Model simulations treating cells as (a) passive particles (b) particles with motility but no growth or mortality (c) particles with biological growth (Schoemann et al. 2005), mortality and motility.

Table 7.3: Model sensitivity to changes in the biological growth.

<table>
<thead>
<tr>
<th>Parameter (new value)</th>
<th>% Increase/decrease of Parameter</th>
<th>Increase/ decrease in Density</th>
<th>Normalised Sensitivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu_{max}$ (1.4)</td>
<td>7%</td>
<td>100%</td>
<td>0</td>
</tr>
<tr>
<td>$\mu_{max}$ (1.2)</td>
<td>-7%</td>
<td>100%</td>
<td>0</td>
</tr>
<tr>
<td>$dT$ (15.3)</td>
<td>12%</td>
<td>106%</td>
<td>-0.57</td>
</tr>
<tr>
<td>$dT$ (12.1)</td>
<td>-12%</td>
<td>92%</td>
<td>-0.61</td>
</tr>
<tr>
<td>$T_{opt}$ (17.3)</td>
<td>6%</td>
<td>92%</td>
<td>1.43</td>
</tr>
<tr>
<td>$T_{opt}$ (15.3)</td>
<td>-6%</td>
<td>108%</td>
<td>1.18</td>
</tr>
<tr>
<td>Temperature (90%)</td>
<td>-10%</td>
<td>93%</td>
<td>-0.66</td>
</tr>
<tr>
<td>Temperature (110%)</td>
<td>10%</td>
<td>107%</td>
<td>-0.76</td>
</tr>
</tbody>
</table>

7.3.2 Bloom advection

To determine the potential role of advection in the accumulation of *Phaeocystis* near the Aberdeen coast in 2005, the model was initialised with high cell concentrations near the north east Scottish coast, where high chlorophyll was visible from satellite
images prior to the bloom in Aberdeen (Figure 7.3, run 12). Model simulation predicted advection of cells towards the central North Sea, but away from Aberdeen where the bloom was observed.

![Model prediction of advection for initial seed populations near the North coast.](image)

Figure 7.3: Model prediction of advection for initial seed populations near the North coast.

Further model simulations were initialised with seed populations originating from the shelf (Figure 7.4 a, run 13) and the North Sea (Figure 7.4 b, run 14). In both cases the model predicted advection of cells towards the central North Sea rather than the Aberdeen coast.
To study potential advection of *Phaeocystis* in 2015, the model was initialised with satellite images taken on the 3rd July (Figure 7.5 a, run 15). Cell numbers from satellite chlorophyll were calculated using cell counts from *Phaeocystis* collected during the Corystes research cruise (chapter 3). Only the satellite section where the bloom was observed was used for model initialisation. Benefits and limitations of using satellite imagery for model initiation were discussed in chapter 5. The model predicted advection of cells towards and clockwise along the west and north coast (Figure 7.5 a). Cells were predicted to be transported as far north as the Orkney islands within six weeks. For the next model run, the model was initialised with a smaller ISP where cells were found during field work on the 15th July (chapter 3). Advection was predicted to transport cells towards the Scottish west coast and along the Minch (Figure 7.5 b, run 16).
Figure 7.5: Model prediction of advection for a) satellite observations from the 3rd July 2015 and b) the initial seed population observed during field data collection.

7.4 Discussion

7.4.1 Model development with *Phaeocystis* specific growth

Under optimal light and nutrient conditions, *Phaeocystis* growth can be modelled as a function of temperature alone (Schoemann et al. 2005). These assumptions are frequently unrealistic in natural environments and will limit the ability of model
simulations to predict the onset or termination of blooms. However, the model simulations described in this chapter did not aim to describe the response of *Phaeocystis* to changing environmental conditions. Instead, this work can be seen as a preliminary study to determine the potential of Lagrangian particle tracking models to be used in understanding progression of high density *Phaeocystis* blooms.

The model successfully simulated observed blooms with realistic bloom densities observed in 2005 and 2015. The *K. mikimotoi* specific biological model introduced in chapter 5 was altered to simulate *Phaeocystis* growth. Both *K. mikimotoi* and *Phaeocystis* specific growth were modelled as a function of temperature. As a result the *K. mikimotoi* biological model was found to be very sensitive to temperature changes (chapter 5.3.3). The model was less sensitive to temperature changes when simulating *Phaeocystis* specific growth, which can be due to the stronger direct impact of temperature changes on *K. mikimotoi* growth formulation compared to the *Phaeocystis* growth formulation (Figure 7.6).

![Figure 7.6: Temperature dependent growth for *Phaeocystis* (Schoemann et al. 2005) and *K. mikimotoi* (Gentien et al. 2007).](image)

The *Phaeocystis* model introduced here used the same mortality description as for *K. mikimotoi*. Shear and cell density were the main drivers of *K. mikimotoi* mortality as cell encounter rate, and therefore aggregate formation and sinking, would increase with these factors (Gentien et al. 2007). Sinking of *Phaeocystis*
colonies was also linked to cell aggregation and colony size (Skreslet 1988) and the mortality formulation was therefore adapted from *K. mikimotoi*. However, further model development would possibly benefit from a *Phaeocystis* specific growth and mortality formulation.

In contrast to *K. mikimotoi* blooms, which have been found to be able to grow on remineralised nutrients alone (Yamaguchi 1994, Le Corre et al. 1993), enhanced nutrient availability has been strongly linked to the occurrence of high density *Phaeocystis* blooms (Lancelot et al. 1987, 2005, Gypens et al. 2007). As discussed in chapter 5, coupling a nutrient model to this IBM would be difficult as it would significantly increase model complexity and be very difficult to parametrise. Even model frameworks that specifically consider the role of nutrient availability on *Phaeocystis* bloom dynamics can struggle to find an appropriate formulation for *Phaeocystis* specific nutrient uptake. *Phaeocystis* growth has been shown to depend on the concentrations of various nutrients, including nitrate, phosphate, iron and manganese (see Schoemann et al. 2005 and references therein). Nutrient requirement and uptake can vary greatly between colonies, which can store excess nutrients in the extracellular mucus present.

Biological models that include several nutrient pools, grazing, competition and different *Phaeocystis* life stages (single cells and colonial) successfully recreated observed bloom patterns, bloom succession and nutrient cycles for *Phaeocystis* dominated environments (Verity 2000, Lancelot et al. 2007, Gypens et al. 2007). However, such models are not capable of studying the potential effect of advection. Other models, designed to study advection of *Phaeocystis* blooms struggle to adequately simulate *Phaeocystis* biology (Blauw et al. 2010) or treat cells as passive particles (Hai et al. 2010).

In this chapter, a specific growth formulation for *Phaeocystis* had to be included to allow the model to recreate the high cell numbers observed in the field (Q1). As the model suggests that high cell numbers are most likely caused by *in situ* growth, rather than physical accumulation, further modelling work should focus on improving the biological growth equation for *Phaeocystis*, while keeping model complexity as low as possible.

### 7.4.2 Model initiation and hindcast capacity

The model aimed to hindcast bloom events of *Phaeocystis* observed in 2005 and 2015. Specifically, model simulations were designed to study possible locations of bloom origins and potential advective pathways of bloom transport. Model simulations could recreate observed cell densities when biological temperature dependent growth was included. However, the model did not simulate bloom termination, which is likely linked to changing nutrient loads, competition and grazing as discussed above.
Validation of model simulations for 2005 is difficult due to the limited amount of field data. The model suggests that advection might not have played a central role in the development of the bloom observed in 2005. ISP from the shelf, the Scottish north coast or the North Sea were not predicted to be advected towards Aberdeen by model simulations. This suggests that the bloom might have developed \textit{in situ}, due to favourable growth conditions.

In 2015, model simulations predicted the advection of \textit{Phaeocystis} towards the west coast of Scotland. However, with high cloud cover and no categorical cell counts for \textit{Phaeocystis} available after the observed bloom it is impossible to say if model predictions are correct. However, model simulations show that it would be possible that the \textit{Phaeocystis} occurrence noted in Skye in late August was caused by advection from cells previously observed on the shelf. However, model simulations suggest that advection as far as Shetland would be impossible within the 6 weeks between cell observations on the shelf and Shetland islands. Due to the general lack of validation data, questions on the model capacity to simulate bloom advection can therefore not be answered (Q2).

Model simulations for 2015 were initialised with satellite data or data collected from field work (Figure 7.5). Field data can provide useful information that can be combined with model simulations. As the bloom was present during the 2015 research cruise (chapter 3), information about bloom location and cell numbers was available. Biological data collected during the glider deployment (chapter 4) provided additional information about the extent and three dimensional structure of the bloom. In this chapter, field data was successfully used to initialise the model (Q3), however, a continuous data set covering the bloom would have been necessary for model validation. Some of the benefits and challenges of combining different sets of data were also discussed in chapter 4.4.2. Here I expand the discussion to include modelling as an additional source of data with the ability to fill gaps in knowledge such as the role of advection in HAB transport.

### 7.5 Conclusion

Here, a preliminary model for growth and advection of high density \textit{Phaeocystis} blooms was introduced. This chapter described an initial attempt of combining field data collected for this thesis with modelling approaches. Results of this chapter suggest that a biological growth formulation for \textit{Phaeocystis}, rather than treating cells as passive particles, was necessary to simulate high cell densities observed in the field (Q1). Field data could be used for model initialisation (Q2), demonstrating the benefits of combining different approaches to data collection. Without the inclusion of nutrient limitation in the model, it was not possible to simulate bloom
termination, which might require a different model approach all together and is not within the scope of this PhD project. Without more detailed records of Phaeocystis blooms, it is impossible to validate model hindcast capacity (Q2).
8 Summary and general conclusion

This PhD project was designed to study the role of environmental drivers on, and advective transport of, harmful phytoplankton in North West European shelf seas. The results of this study were designed to be used to improve detection and early warning of such harmful events. Such early warning would allow us to mitigate economic losses to aquaculture; for example, so shellfish can be harvested early and finfish cages can be relocated or protected with tarpaulins. In order to address gaps in knowledge relating to drivers of harmful phytoplankton and the role of advection in bloom transport, this project addressed the following points:

1) Assessment of the phytoplankton community
Baseline information on phytoplankton community structure in the North West European shelf sea is limited. This study contributed to closing this gap by collecting data on phytoplankton and their physical environment on two research cruises (chapter 2 and 3) to the shelf sea, shelf break and adjacent oceanic waters. This data collection also provided much needed information of the role of the shelf break and the European Slope Current (ESC) in structuring phytoplankton community.

2) Offshore phytoplankton surveillance using gliders
Offshore phytoplankton data is generally limited to sporadic research cruises. In Scotland, no offshore waters are currently monitored for harmful phytoplankton species or toxins. Collecting such data routinely would offer opportunities to establish an early warning system for harmful algal blooms (HABs) in combination with bio-physical modelling. To begin to address this issue, a sea-glider was deployed (chapter 4), providing the first study of the application of this technology for phytoplankton surveillance and potential detection of high density blooms in UK waters.

3) Model development
After an early bloom detection, modelling can potentially supply information about likely bloom path and development. In chapters 5 to 7, an Individual-Based Model (IBM) coupled with a hydrodynamic model was introduced. The model has the potential to predict advection and biological growth of a single target species and provide information on bloom origins and subsequent development.

4) Environmental drivers of phytoplankton
Throughout this thesis, environmental drivers of phytoplankton in the North West European Shelf sea were discussed with a focus on harmful species. The main drivers that were identified were stratification, nutrient concentrations and light conditions.
5) **Advective transport of HABs**
The important role of advection was established during field work and modelling. Advection in the region is strongly linked to the shelf break and the ESC, which can play a crucial part in the onshore or offshore transport of offshore blooms. Interannual differences in current strength and the potential for overspill of Atlantic water onto the shelf might help explain observed patterns of high density HABs in coastal waters.

6) **Research questions**
The three research questions outlined in chapter 1.7 were addressed based on information collected and analysed during this PhD project.

7) **Further work**
Areas that would benefit from further research were identified and directions of further work were suggested.

Each of the above points is discussed in more detail in the following sections.

### 8.1 Assessment of the phytoplankton community and its environment in North West European shelf seas

#### 8.1.1 Phytoplankton assessment and impact of data

The hydrography of the area is relatively well studied (Ellett et al. 1986, Proctor et al. 2003, Hill et al. 2008, Inall et al. 2009, Jones 2016). The Malin and Hebridean Shelves are characterised by a diverse and unique coastline to the east, and a steep continental slope to the west. Water can enter the shelf from the Atlantic or the Irish Sea, creating permanent and seasonal frontal systems on the shelf. The ESC is a strong, permanent current that is steered along the steep continental shelf edge and it is a key driver of advective transport in the area (see chapter 1.1). Conversely, phytoplankton distribution in relation to these hydrodynamic features is less well studied in the area. The most recent study on phytoplankton distribution on the North West European Shelf sea was based on samples collected over a decade ago in shelf and adjacent oceanic areas, with no sample collection near the shelf edge and the ESC which are potentially important in governing phytoplankton structure (Fehling et al. 2012).

Chapter 2 and 3 provide an updated assessment of phytoplankton in the area with data collection from the shelf break and the ESC. Phytoplankton abundance in late autumn was low, but with two distinct communities present on the shelf
and shelf break/oceanic stations (chapter 2). During summer, the phytoplankton community could also be divided into two groups present in coastal waters and shelf waters including adjacent oceanic areas. Community differences were related to light and nutrient conditions in autumn and salinity, temperature and nitrate conditions in summer (chapter 2 and 3), which are discussed in more detail in chapter 8.4.

In autumn, communities were separated by the shelf edge and in summer by the Islay and Irish coastal fronts. The lack of a division of phytoplankton between shelf water and oceanic water in summer could have been linked to a large overspill of Atlantic water onto the shelf observed during the research cruise. No coastal stations were sampled in autumn.

Information on phytoplankton distribution, seasonality and inter-annual variation collected during this project can help to provide the information necessary to assess GES of British shelf seas, as required by the Marine Strategy Framework Directive MSFD. The phytoplankton life form approach currently used by Tett et al. (2008), only reports detailed information about phytoplankton in coastal areas and sea lochs. The information collected here will therefore help to accurately expand the MSFD assessment to shelf areas and provide a baseline on which changes over time can be assessed.

In addition, nutrients and phytoplankton biomass information can be used as indicators for the assessment of eutrophication required for the MSFD and OSPAR (OSlo and PARis Convention) regulations (Claussen et al. 2009, Ferreira et al. 2011). The Malin and Hebridean Shelves represent environments that are relatively unaffected by eutrophication with most nutrients entering the shelf from adjacent oceanic water rather than riverine and terrestrial input (Proctor et al. 2003). Data collected here can therefore be used as a representative environment of waters with low anthropogenic nutrient input. Further data collection in the area would benefit integrated monitoring programmes required by the MSFD to address GES targets, enabling better understanding of seasonal dynamics and changes over time.

8.1.2 Implications for HAB monitoring

There are multiple examples of HAB occurrence near continental shelves being strongly linked to certain hydrodynamic conditions. On the Iberian shelf, for example, elevated densities of *Dinophysis* were often found in strongly stratified upwelling areas (Escalera et al. 2010, Reguera et al. 2012, Diaz et al. 2013). Information about upwelling could therefore potentially be used as an indicator for *Dinophysis* (Velo-Surez et al. 2014). Another example is the strong association between *Pseudo-nitzschia* bloom formation and eddy development near Washington state (Horner et al. 2000, Trainer et al. 2002, Adams et al. 2006). Onshore advection of eddies, such as the Juan de Fuco eddy, often lead to onshore advection of *Pseudo-nitzschia*
blooms, which had previously developed in the eddy (Horner et al. 2000, Trainer et al. 2002).

In the North West European Shelf sea, the major hydrodynamic feature of the ESC was previously suggested as a possible origin of harmful algae blooms (Davidson et al. 2009, chapter 5 and 6). During autumn, stations within the ESC had approximately 90% similarity in phytoplankton community to each other. This suggests that data collections from single points within the ESC can be representative for a large section of the ESC. During summer, a large overspill of Atlantic water onto the shelf was recorded. Phytoplankton communities associated with this water could be grouped together with 60% or higher similarity between stations.

These results suggests that in Scotland, the strength of the ESC and the potential for overspill of Atlantic water onto the shelf could be used to determine if harmful species present in the ESC would be separated from the shelf and consequently coastal areas, or if cells are likely to be advected towards the coast. Numerical modelling could be used to support predictions of onshore HAB advection based on hydrodynamic conditions (see chapter 8.3). To successfully establish an early warning system based on predictions of HAB advection, frequent monitoring of the ESC would be required. A potential new approach for doing this is discussed below.

8.2 Gliders as a tool for offshore surveillance

One of the challenges of HAB prediction in Scotland is the lack of early detection, with no monitoring of offshore waters. Satellite imagery can provide an estimate of offshore phytoplankton biomass, but is strongly limited by cloud cover. In chapter 4, an alternative method for offshore data collection was introduced. The chapter described the successful deployment of a sea glider and the potential to detect and survey high biomass phytoplankton blooms. The glider recorded phytoplankton distribution with a high vertical and horizontal resolution that would be impossible to obtain from satellites, which is limited to viewing the sea surface, or research cruises, which generally record data with a lower horizontal resolution.

Giders would be a suitable tool for routine offshore surveillance, with battery life lasting up to several months. Using gliders would also be less expensive than financing scientific cruises for the same data coverage. The results from chapter 4 suggest that gliders may be utilised to detect harmful high density blooms. Early detection, together with modelling approaches, can then be used to determine the risk of onshore advection of such blooms (chapter 7).

Next to HAB surveillance, routinely collected glider data could be used to assess changes in the environment in accordance with MSFD and OSPAR requirements (Johnson 2008). Long term data on phytoplankton biomass can be used as an
indicator for environmental changes such as eutrophication (Johnson 2008, Ferreira et al. 2011). Currently, this kind of data is unavailable due to the lack of resources and costs associated with ship based sampling. Glider data could overcome these issues and solve the current data acquisition problem.

Glders can be programmed to run a fixed transect repeatedly. A transect should include boundary areas such as frontal systems and the shelf break. As these areas are not fixed in space and vary over time, the glider path can be easily adjusted to include such features. These can be determined from satellite imagery and the real time water temperature and salinity data collected from the glider. Monitoring boundary conditions will allow an estimate of the extent of phytoplankton community groups as observed in previous cruises. Such estimates could also be supported with satellite chlorophyll imagery.

The limitations to using such technologies include the risk of bio-fouling on glider instruments, which would require frequent recovery of the glider for maintenance. Results from chapter 4 suggest that this would be necessary every 1 to 2 months with battery replacements every 3 to 4 months if chlorophyll is measured within the top 150 m of the water column only. As it takes the glider roughly a week to cover the distance from the shelf break to coastal areas, where the glider can be recovered, at least two gliders would need to be deployed to ensure a continuous data coverage of the ESC and shelf seas. Assuming monthly recovery for maintenance, gliders could record a transect similar to transect 1 in chapter 4 across the Malin shelf, in the first week of deployment, and a transect along the ESC, similar to transect 2 in chapter 4, in the second week before returning the same path for recovery after approximately a month of deployment.

Another limitation that should be considered is the lack of species specific data obtained from gliders. New in situ instruments for phytoplankton identification, such as deployable flow-cytometers are currently being tested in combination with glider deployment, however issues with turbulence and glider battery life still need to be resolved (McLane Research Laboratories 2016 and personal communication, Feb. 28th, 2017). Species specific identification from satellite images is also currently being developed for potentially harmful high density bloom forming species such as K. mikimotoi and Phaeocystis (Miller et al. 2006, Kurekin et al. 2014).

Another methodology for phytoplankton discrimination is offered by the use of Inherent Optical Properties (IOPs) that can be measured routinely alongside chlorophyll. In chapter 4 a preliminary attempt to use this information for species discrimination was presented. It has to be noted that for this study the information of phytoplankton taxonomy was limited to cruise data collected in proximity to the glider measurements with spatial and temporal differences in collection.
8.3 Model development

8.3.1 Model framework and biological model

Model studies can vary greatly in their basic framework and level of complexity (see chapter 1.6). Here, a relatively simple biological model, coupled with a Lagrangian transport model, was chosen to study the role of advective transport in harmful bloom progression. IBMs like this one are generally better suited to study advection than Eulerian ecosystem models. Relative low model complexity reduces error and accounts for the mathematical formulation of biological interactions.

Lagrangian transport models have successfully been used to study HAB advection by treating cells as passive particles (Hai et al. 2010, Dippner et al. 2011, Pinto et al. 2016, Moita et al. 2016, Silva et al. 2016). This allows the prediction of advective HAB pathways, even when information about their exact species composition and their biology is limited. Dippner et al. (2011), for example, used this kind of model to determine the possibility of onshore advection for generic HABs that might develop offshore without fitting the model to a specific species. The obvious limitation of this approach is that the model cannot appropriately simulate cell numbers without growth and mortality formulation. This is important as many harmful species are considered harmless below certain cell densities.

Here, *Karenia mikimotoi* was used as a model species. *K. mikimotoi* is well recorded as it is enumerated during regulatory monitoring, providing good data sets for model validation. For some simulations (run 25 to 40, chapter 5) data from coastal monitoring was also used for model initiation to test hypothesis of connectivity of coastal blooms. As *K. mikimotoi* is only harmful in high densities, cell growth and mortality was included. *K. mikimotoi* also has a positive phototaxis which was also included in the biological model.

Model simulations with and without biological cell growth, mortality and motility showed that these biological formulations greatly improved model prediction. Many phytoplankton transport models do not include such behaviour. This suggests that development of operational forecast models should focus on including key biological features as physical advection alone could not explain observed bloom patterns for *K. mikimotoi* in Scottish waters. While including biology was found to be essential for *K. mikimotoi* bloom simulation, there was some mismatch between modelled and observed cell numbers, indicating that further development of the biological model could increase model accuracy.

Growth of *K. mikimotoi* has previously been shown to be strongly temperature dependent (Gentien et al. 2007) and including only temperature to govern biological growth allowed the development of a low complexity model with a strong focus on physical advection. However, this resulted in a high model sensitivity to temper-
nature changes (chapter 5). It would therefore be important for further studies to investigate how changing sea temperature could affect *K. mikimotoi* blooms. This should consider short term acclimatisation and long term adaptation of cells.

Currently, the model cannot simulate the rapid bloom decline that is observed from coastal monitoring. This is a common problem and model development would therefore benefit from a better mathematical formulation for cell death. For this model, cell death was assumed to be caused by shear induced collision and auto-toxicity alone. Possible improvements to this could be made if the life cycle of *K. mikimotoi* was better understood. Future laboratory studies should therefore focus on changes between sexual and asexual reproduction, the potential for cyst formation and environmental or biological conditions related to such changes. A better knowledge of cell loss from grazing, bacterial competition and viral infection would also be helpful to explain observations and improve modelling.

In chapter 7, the biological growth model was modified to simulate *Phaeocystis*, which was observed during the work reported in chapter 3 and 4. The model successfully simulated observed bloom numbers despite the extremely simplified temperature dependent growth formulations. However, the model was again not able to recreate bloom decline, which is possibly linked to nutrient limitation and cannot be modelled with the IBM used here.

### 8.3.2 Model simulations

There are several options for model initialisation. Information of initial cell distribution can, for example, be extracted from satellite chlorophyll. This approach calculates cell numbers from observed surface chlorophyll by assuming a monospecific bloom in the area. This assumption is reasonable, as *K. mikimotoi* (chapter 5 and 6) and *Phaeocystis* (chapter 7) were observed in very high densities, suggesting they would contribute to a significant part, if not all, of the observed chlorophyll. Limitations to using satellite data are that cloud cover can reduce data availability and chlorophyll is only available for the sea surface. Calculating cell numbers from satellite chlorophyll could be improved by further laboratory studies to better describe the relationship between *K. mikimotoi* numbers and chlorophyll signatures. Further development of algorithms for species discrimination from satellite images (Miller et al. 2006, Kurekin et al. 2014) would also improve this approach of model initialisation.

To test the hypothesis about bloom origin and advective pathways and connections between sites, the model was initialised with single discrete seed populations. This approach to model initialisation revealed the 2006 bloom could have been linked to overwintering cells from a previous bloom near the Irish coast. The role of cell transport along the ESC and overspill of cells onto the north Hebridean shelf was
also explored by the model. The model realistically predicted the clockwise advec- 
tion observed for the *K. mikimotoi* bloom in 2006. Similarly, the model could 
simulate bloom development along the west Scottish coast observed in 2010. For 
the observed *K. mikimotoi* bloom in 2011, model simulations suggested a connec-
tion between blooms observed in Lewis at the end of August and around Orkney 
in September. This confirms the importance of advective transport in HAB pro-
gression and demonstrates the usefulness of IBMs in HAB management and early
warning.

Overall, results from model simulations suggest that the model can predict the 
approximate time and location of blooms, if the bloom origin is known. The model 
could therefore potentially be integrated into HAB monitoring in the near future. 
Even though the model is not currently an operational forecast, it can provide useful 
information about bloom development and likelihood of bloom transport towards 
coastal areas. For this, offshore blooms have to be detected early, e.g. from satellite 
imagery or from routine monitoring, which is currently not in place, but discussed in 
chapter 8.2. Without the use of such models, early detection of blooms has limited 
ability to provide early warning of coastal bloom occurrence. The potential to 
combine modelling approaches with offshore detection of blooms was demonstrated 
in chapter 7.

### 8.4 Environmental drivers of phytoplankton

#### 8.4.1 Stratification

Results from the glider mission (chapter 4) showed a strong link between phyto-
plankton biomass and thermal stratification. Vertically, phytoplankton distribution 
was limited to the surface waters when the water was thermally stratified with 
early no phytoplankton present below the thermocline. In regions where thermal 
stratification weakened, phytoplankton could extend further through the water col-
umn. The only exception to this was during the high density *Phaeocystis* bloom 
that was observed near the end of the glider mission. Despite thermal stratification, 
chlorophyll was recorded throughout the water column. It was possible that this ob-
servation was caused by a high number of sinking cells. However, continuously high 
background readings from optical sensors suggested that bio-fouling also affected 
sensor readings.

The frontal systems, that were identified on the Malin shelf in summer, divided 
the thermally stratified Malin shelf from vertically mixed coastal and Irish sea water 
(chapter 3 and 4). Phytoplankton communities were grouped accordingly into two 
different groups: One group was present in stratified waters and had higher cell 
counts and chlorophyll a, while the other group was present in vertically mixed
waters and had a higher species diversity with more diatoms present. Previous studies in the area also found elevated chlorophyll a at the stratified side of the Islay front compared to the well mixed side (Simpson et al. 1979, Gowen et al. 1998). Higher diatom diversity in well mixed waters could be linked to diatoms being generally better adapted to turbulence than dinoflagellates (Margalef 1978).

High numbers of the potentially harmful genera *Pseudo-nitzschia* and *Phaeocystis* were found on the stratified shelf. Previous work has suggested that stratification is a necessary requirement for the development of harmful dinoflagellate blooms such as *Dinophysis* and *K. mikimotoi* blooms (Raine et al. 2010a, Raine 2004, Farrell et al. 2012). Blooms of the haptophyte *Phaeocystis* and the diatom *Pseudo-nitzschia* have also been observed in vertically mixed surface layers (e.g. Davies et al. 1992, Fehling et al. 2012), suggesting that stratification is not a bloom requirement. Nutrient conditions might therefore help to explain bloom occurrence (discussed in chapter 8.4.2).

The horizontal distribution of phytoplankton recorded by the glider (chapter 4) was very patchy which could not be explained by changes in stratification, water temperature or salinity. This suggests that other factors such as nutrients (discussed in chapter 8.4.2) and light (discussed in chapter 8.4.3) have to be considered to explain observed patterns. These factors were also identified as main drivers linked to phytoplankton community differences in autumn, when lower temperatures combined with stormy weather lead to a deepening or complete breakdown of stratification (chapter 2).

### 8.4.2 Nutrients

For samples collected during cruises, nutrients were significantly related to phytoplankton community differences (chapter 2 and 3). Surface concentrations of nitrate, phosphate and silicate were generally lower in summer compared to autumn, with surface concentrations of silicate and phosphate being close to zero for most coastal stations and some shelf stations (chapter 3, Appendix D). During summer, elevated cell numbers of potentially harmful *Pseudo-nitzschia* and *Phaeocystis* were found in waters with Atlantic signatures and higher nitrate compared to more coastal sites (chapter 3).

The highest concentrations of the diatom *Pseudo-nitzschia* were found in waters with silica concentrations close to zero and nitrate concentrations above 1 mmol N m$^{-1}$, suggesting that silicate was the limiting nutrient. While *Pseudo-nitzschia* numbers were below the HAB threshold for this species, limited availability of silicate and phosphate was found to increase toxin production in *Pseudo-nitzschia* (Fehling et al. 2004a). Previous studies established that nitrate to silicate ratios above 4:1 would lead to silicate limitation and a subsequent shift to a flagellate-dominated
phytoplankton assemblage (Gilpin et al. 2004). In agreement with this study, diatoms were not found to be dominant with high nitrate to silicate ratios present (chapter 3).

Previous studies suggested that coastal *Phaeocystis* blooms were linked to an increase in phosphate availability and a decrease in the nitrate to phosphate ratio (Riegman 1995). However, there is no evidence that decreases in nitrate to phosphate ratios are linked to an increase of *Phaeocystis* bloom occurrence (Davidson et al. 2012). In this study, 1 million *Phaeocystis* cells l$^{-1}$ were found in shelf waters with a nitrate to phosphate ratio around 15:1, suggesting that nutrient concentrations might be low (chapter 3, Figure 3.4), but not necessarily limiting to growth.

Results from this study suggest that occurrence of potentially harmful species might not necessarily be linked to optimal nutrient conditions, as elevated numbers of *Pseudo-nitzschia* were present under silicate limitation and *Phaeocystis* bloomed in the absence of elevated phosphate concentration or nitrate limitation. This is in agreement with Davidson et al. (2012), who concluded that HABs cannot be explained by changes in nutrient ratios alone.

This study also provides an important baseline on which anthropogenic changes in nutrient requirements and availability, and the response of phytoplankton can be assessed. Climate change, for example, could alter nutrient requirements of phytoplankton (Thrane et al. 2017). Temperature data from the Malin shelf, reaching back to the 1980s showed an overall warming trend of the sea surface temperature with an increase of 0.57 °C per decade (Inall et al. 2009). Recent studies revealed that phytoplankton acclimatisation to higher temperatures was linked to a reduced production of ribosomes (Toseland et al. 2013, Thrane et al. 2017). Production of ribosomes has a high phosphorus requirement, and reduced production can therefore lower the phosphate requirement and increase the optimal nitrate to phosphate ratio of phytoplankton cells (Thrane et al. 2017, Hessen et al. 2017). Authors therefore suggested that increasing water temperature could thereby cause a shift from phosphate to nitrate limitations in some regions (Thrane et al. 2017). However, anthropogenic increase of atmospheric nitrogen deposition is likely to increase nitrate (Pennelolas et al. 2013). This increase in supply is thought to exceed the potential higher nitrate demand in response to temperature changes (Pennelolas et al. 2013, Thrane et al. 2017).

8.4.3 Light

In chapter 2, multivariate statistical methods revealed a strong, significant relationship between light (turbidity and light attenuation) and phytoplankton community differences. Near the shelf break and oceanic stations, light conditions were better, with lower turbidity and light attenuation than on the shelf. Coincidently, the
phytoplankton community was different at shelf stations in comparison to other stations. Potentially harmful *Pseudo-nitzschia* and *Dinophysis* were nearly absent in shelf-break and oceanic waters, but present in low numbers at all shelf stations. Even if numbers are too low to be considered harmful, such populations could still provide a potential seed for HABs when conditions change seasonally (Raine 2004, Davidson et al. 2009).

The lower light levels in surface waters on shelf stations is likely linked to the stormy conditions prior to and during sample collection. Strong winds can induce resuspension of sediment from the sea floor and thereby increase turbidity and light attenuation. When phytoplankton are exposed to low light conditions, photoacclimatisation processes generally lead to an increased production of chlorophyll a within a cell (Falkowski & LaRoche 1991). This does not only increase the photosynthetic rate of cells, but also increases the nitrogen requirement of cells for the production of photosynthetic pigments (Thrane et al. 2016). The production of photosynthetic pigments can also increase as a response to increasing temperatures (Thrane et al. 2017). This shows the importance of considering light in combination with other factors such as temperature and nutrients, as done in chapter 2.

The effect of light on HAB development was also assessed when *K. mikimotoi* specific model simulations were run with and without a positive phototaxis (chapter 5). Simulations revealed that including this phototactic behaviour was necessary for the model to realistically simulate blooms of *K. mikimotoi*. It is unclear how changes in visibility might influence this behaviour and thereby HAB dynamics. This information would be important as darkening and decreased clarity of coastal waters is observed as a response to anthropogenic changes such as eutrophication, pollution and increased input of terrestrial waters rich in coloured dissolved organic matter (Aksnes et al. 2009, Dupont & Aksnes 2013, Urtizberea et al. 2013, Capuzzo et al. 2015). Darkening of coastal waters might lead to shallowing of motile dinoflagellates (Urtizberea et al. 2013). The effect this might have on *K. mikimotoi* growth and toxicity are unknown and should therefore be addressed in further studies.

### 8.5 The ESC, coastal currents and phytoplankton advection

The ESC (see chapter 1.1) can act as a mixing barrier (Ellett et al. 1986) but can also facilitate cell transport (Hill et al. 2008, Davidson et al. 2009). In chapter 2, two distinct phytoplankton communities were found, one in shelf waters and another one in waters associated with the ESC. As environmental conditions were not significantly different between sites, this suggests that the ESC could act as a physical barrier for cell exchange. On the contrary, no such community structure was observed during the cruise in summer 2015 (chapter 3), where phytoplankton com-
munities near the shelf edge, adjacent oceanic waters and adjacent shelf waters did not fall into different groups. This is not surprising, as an overspill of Atlantic water onto the shelf was observed during the data collection. Grouping of phytoplankton responded to the extent of overspill, reducing the separation effect observed during autumn the previous year. Overspill of Atlantic water is commonly observed, however, drivers governing the timing and magnitude of Atlantic water entering the shelf can be complex, leading to a high inter-annual variation in the influx of Atlantic water onto the Malin and Hebridean shelf (Jones 2016).

Satellite imagery and counts from coastal monitoring suggested that an observed *K. mikimotoi* bloom in 2006 was advected clockwise around the Scottish coast (Davidson et al. 2009). This was confirmed by numerical modelling (chapter 5). A coupled bio-physical model consisting of a hydrodynamic model, a Lagrangian transport model and a biological growth model for *K. mikimotoi* was used to assess the role of advection in bloom progression. The hydrodynamic models POLCOMS and NEMO were used to provide information about current strength and direction. POLCOMS was discontinued in 2008 and only NEMO could be used for model runs post 2008. Comparing the hydrodynamic model output suggested that NEMO could provide better resolution of the ESC.

Model simulations described in chapter 5 confirmed that initial seed populations could have been advected towards the west Scottish coast from the north Irish coast, where a bloom had been observed the previous year. Simulations also suggested that an additional influx of cells from the shelf edge onto the shelf would have been necessary to explain observed bloom distributions. The same was true for a further bloom in 2010, when additional influx of cells from the shelf edge or ESC was necessary for the model to simulate observed cell distribution.

In the north of Scotland, two exceptional *Dinophysis* blooms in 2006 and 2013 were also linked to changes in advective transport of surface waters. Harmful densities of *Dinophysis* were transported towards the coast of Shetland in 2006 and 2013 during sudden, strong, onshore winds in the area (Whyte et al. 2014). As the importance of advection of harmful cells becomes more and more evident, HAB information bulletins around the European Atlantic coast now include forecasts about wind direction and current regimes (Ruiz-Villarreal et al. 2016, Cusack et al. 2016). This information, together with coastal HAB counts, can be used for a short term HAB prediction up to 3 days in advance (Silva et al. 2016).

Such studies not only highlight the importance of advection, but also the effects inter-annual differences in advection can have on HAB occurrence (Hai et al. 2010, Dippner et al. 2011, Whyte et al. 2014). In chapter 6, the effect of inter-annual variations in wind and current conditions was assessed with the help of model simulations which were then compared to coastal observations. Most noticeable were
differences between 2006 and 2012 between observed and predicted *K. mikimotoi*. During both years *K. mikimotoi* were present on the shelf; however, only during 2006 were cells present in high numbers in coastal regions, while cells were absent or below registration levels during 2012 on the Scottish west coast. Differences in current strength and direction suggested that there was a strong potential for onshore advection during 2006 but not 2012 (chapter 6).

The model was then run with conditions representative of 2000 to 2015. Predicted absence and presence data of *K. mikimotoi* at coastal sites agreed with observation regulatory monitoring for 10 out of 16 years (62.4%). For years where predicted and observed distribution of *K. mikimotoi* disagree, other factors, such as in situ growth and local conditions might be important. It is also unlikely that a seed population is present every year, as no *K. mikimotoi* was found during research cruises in 2014 and 2015 (chapter 2 and 3). This showed again the importance for improved offshore monitoring and their link to coastal blooms.

### 8.6 Research questions

**Research question 1**: What is the role of environmental drivers in structuring phytoplankton communities on the North West European shelf with a focus on potentially important hydrodynamic features such as the shelf edge?

Throughout this thesis the importance of environmental drivers (light, nutrients, water temperature, salinity, stratification) for phytoplankton community structure was shown. In summary, phytoplankton occurrence is often linked to a combination of factors, rather than a single factor, which can be difficult, if not impossible, to untangle. Temperature, for example, is directly linked to thermal stratification, which in turn governs water column stability and nutrient availability. Here, nutrients, as well as nutrient ratios could explain some of the observed distribution patterns, while light (chapter 2), water temperature and salinity (chapter 3) and stratification (chapter 4), were also considered important factors. This thesis provides novel insight of phytoplankton community structure in relation to the shelf edge and environmental differences associated with that. The shelf edge was shown to structure phytoplankton communities (chapter 2); however, this effect was overturned by overspill of Atlantic water onto the shelf as observed in chapter 3 and 4.

**Research question 2**: What is the role of advection in HAB occurrence and development on the shelf?

The importance of advective transport in HAB progression on the North West European Shelf is clearly demonstrated here with a combination of field data and modelling data. The ESC was important to explain observed species distribution
(chapter 2) and clockwise advection (chapter 5). Model simulations could not hindcast observed blooms without accounting for cell transport along the ESC with overspill of cells onto the shelf as observed in chapter 3 and 4. Model simulations from chapter 6 revealed important links between inter-annual variation in advective transport and coastal HAB occurrence, stressing both the importance of better off-shore surveillance and the use of hydrodynamic forecasts and Lagrangian modelling in HAB management and prediction.

**Research question 3):** Can computational models provide information about origin and progression of observed blooms?

The IBM used here could provide important information on bloom origins and potential advective transport pathways. The model combines a Lagrangian particle tracing model with a simple biological growth and behavioural model. Biological behaviour was essential to simulate observed HABs. The model showed potential bloom origin locations for observed *K. mikimotoi* blooms on the west Scottish coast and was able to hindcast the clockwise alongshore transport observed for *K. mikimotoi* in 2006 and 2010. Further model improvements for the biological formulation of *K. mikimotoi* would require the culture of a Scottish strain, which has been unsuccessful to date.

### 8.7 Further work

Throughout this PhD project the importance of interdisciplinary research became evident. Further studies should focus on the combination of physical and chemical environmental factors when considering phytoplankton. This thesis also highlights the benefits of combining different methodologies such as field work, satellite data and modelling. With this in mind, further research is needed to address the following areas:

1) Understanding the effect of seasonality and inter-annual variation on phytoplankton communities would require further data collection on the Malin and Hebridean shelf with focus on the ESC and shelf edge. This is necessary to account for inter-annual variation in current regimes and Atlantic overspill and their direct effect on phytoplankton occurrence and advective pathways, which could help to explain observed inter-annual variations in coastal HAB occurrence. A better description of shelf phytoplankton may enable better monitoring of plankton status for meeting GES targets for the MSFD.

2) Further studies should focus on the improvement of species identification from
IOPs that are routinely collected by satellite and can easily be collected alongside chlorophyll measurements by gliders. Great progress has been made in recent years (Kurekin et al. 2014, Vaillancourt et al. 2004), and further improving this method of remote species identification would provide valuable information for surveillance, management, model simulation and model prediction of HABs.

3) The benefits of glider deployment for offshore data collection is described in chapter 4. Offshore high density bloom detection and surveillance with the potential for species identification from IOPs would strongly improve the predictability of coastal HAB events and efforts should be made to establish an offshore surveillance program using gliders in combination with satellite information.

4) The benefits of using a Lagrangian particle tracking model combined with a simple biological model was demonstrated in chapters 5 to 7. Harmful bloom predictions could be improved by improving the biological model. Further studies should focus on deriving mathematical formulations for cell growth, the effect of changing temperatures on growth, mortality and the effect of changing light conditions on motility and auto-toxicity. Ideally, Scottish strains of K. mikimotoi should be used. Model development could also extend to different species as suggested in chapter 7. The possibility of nesting a hydrodynamic model with a higher coastal resolution into a more general ocean hydrodynamic model as demonstrated by Aleynik et al. (2016) should be considered.
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A Nutrient ratios collected during the Discovery Cruise (chapter 2) and Corystes Cruise (chapter 3)

Table A.1: Nutrient ratios in surface waters of stations collected during the Discovery cruise (chapter 2). N = nitrate, P = phosphate, S = silicate

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Table A.2: Nutrient ratios in surface waters of stations collected during the Corystes cruise cruise (chapter 3). N = nitrate, P = phosphate, S = silicate

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# Appendix B Phytoplankton data from Corystes cruise

## B Full Phytoplankton genera list from Corystes Cruise

Table B.1: Presence and absence data for phytoplankton genera collected during the Corystes cruise for Malin Shelf stations (chapter 3).

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C Salinity-temperature diagram for the Corystes cruise

Figure C.1: Temperature salinity diagram. Colours respond to the groups determined by PCA.
Figure C.2: Temperature salinity diagram. Colours respond to the groups determined by PCA, but stations 6, 12A and 38 are plotted individually.
D Corystes transects for chlorophyll a and nutrient concentrations

For each station three to five measurements were made, one near the surface, one near the bottom and one to three in between, depending on water stratification (Generally one for well mixed waters, tow to three on stratified waters, depending on depth).
Appendix D Nutrient contour plots from COryste cruise

(a)

(b)

(c)

(d)
Figure D.1: Transect 1 for (a) chlorophyll, (b) phosphate, (c) silicate, (d) nitrate, (e) nitrite, (f) ammonium.
Appendix D Nutrient contour plots from Coryste cruise

(a) Chlorophyll a (μg l⁻¹)

(b) Phosphate (nmol m⁻³)

(c) Silicate (nmol m⁻³)
Figure D.2: Transect 2 for (a) chlorophyll, (b) phosphate, (c) silicate, (d) nitrate, (e) nitrite, (f) ammonium.
Figure D.3: Transect 3 for (a) chlorophyll, (b) phosphate, (c) silicate, (d) nitrate, (e) nitrite, (f) ammonium.
Figure D.4: Transect 4 for (a) chlorophyll, (b) phosphate, (c) silicate, (d) nitrate, (e) nitrite, (f) ammonium.
Appendix D Nutrient contour plots from Coryste cruise
Figure D.5: Transect 5 for (a) chlorophyll, (b) phosphate, (c) silicate, (d) nitrate, (e) nitrite, (f) ammonium.
Appendix E Wind data for 2000 to 2015

E Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015

(a) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

(b) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

(c) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

(d) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

(e) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

(f) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

(g) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

(h) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

(i) Wind speed and direction for Tiree, Stornoway and Lerwick for 2000 to 2015.

Figure E.1: Wind strength and direction for 2000 to 2015 from the weather station on Tiree.
Figure E.2: Wind strength and direction for 2000 to 2015 from the weather station on Stornoway.
Figure E.3: Wind strength and direction for 2000 to 2015 from the weather station on Lerwick.
F Surface current and water temperature fields from 2000 to 2015 produced by NEMO

June 2004          July 2004          August 2004         September 2004
Figure F.1: Monthly averages for eastward surface current speed for June to September from 2000 to 2015 as predicted by Nemo.
Figure F.2: Monthly averages for northward surface current speed for June to September from 2000 to 2015 as predicted by Nemo.
Appendix F NEMO current and temperature fields for 2000 to 2015
Figure F.3: Monthly averages for surface temperature for June to September from 2000 to 2015 as predicted by Nemo.