Zooplankton dynamics in winter: A bottom-up analysis of a new zooplankton time series from the English Channel and the Southern Bight of the North Sea

Dissertation

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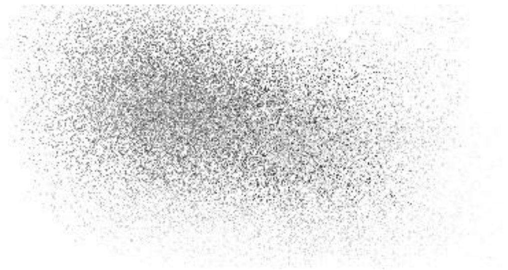
Certification of Written English Quality

I, Rachel Harmer (born in the United Kingdom and native English speaker), hereby confirm that the thesis by Tim Dudeck entitled " Zooplankton dynamics in winter:
A bottom-up analysis of a new zooplankton time series from the English Channel and
the Southern Bight of the North Sea" has been prepared according to excellent written English language standards.

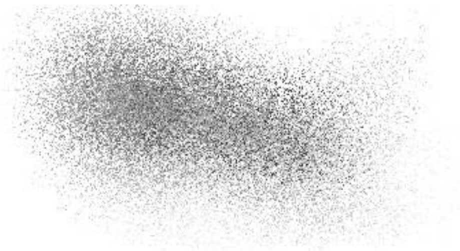
Sincerely,

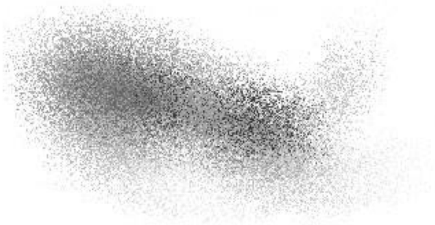
RA Harmer



“White! It serves as a beginning. White cloth may be dyed. The white page can be overwritten; and the white light can be broken.”

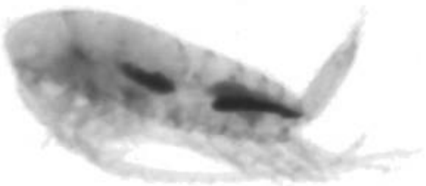
- Saruman





“And he that breaks a thing to find out what it is has left the path of wisdom.”

- Gandalf



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1. Summary

Zooplankton and Phytoplankton form the basis of marine food webs worldwide. In the face of climate change and varying fish predation pressure they are the mediators of energy in ecosystems. Understanding the dynamics and processes of plankton is of greatest importance if we want to address and project problems that may arise in the future. The dynamics of phytoplankton have been studied well and are a key ingredient and mediator in ecosystem models needed to project the consequences of climate change. Not only is the biology of phytoplankton well understood, but it can also be monitored easily, e.g. using satellites, while observing zooplankton abundance from space is so far hardly possible. Yet, zooplankton is the main carbon sink for primary production and the link between autotrophs and higher trophic levels. Many important pelagic fish species and all early life history stages of fish feed on zooplankton. Fish larvae, in particular, are prone to starvation and predation and have varied in abundances and sizes over the past decades. To look at zooplankton dynamics with respect to larval survival has thus been a natural quest in marine science. In most cases however, relevant zooplankton data, abundance and size, was missing. In the present thesis, I try to shed light on zooplankton dynamics during the rarely documented winter season. I provide the first winter time series of zooplankton abundance and size with a wide spatial coverage in the southern North Sea.

Over 1000 zooplankton samples from the eastern English Channel and Southern Bight were examined. Using digital images of the organisms I could measure size, abundance and diversity between 1988 and 2014. For a more detailed analysis using abiotic and chlorophyll values we needed to use modelled data between 1991 and 2013. Over the examined period zooplankton size decreased, overall as well as in certain groups. This is one of a few zooplankton time series documenting the change in size, although the signal is partly masked as small zooplankton groups increased in abundance. In the meantime, zooplankton abundance increased, albeit not continuously. Especially between 2008 and 2011 a strong increase was detected. The sudden increase was mainly observed in the area off the Rhine-Meuse delta in the Southern Bight. Here, the simultaneous elevation in phytoplankton abundance caused a high correlation between zooplankton abundance, zooplankton size and primary production. It indicated a winter phytoplankton bloom and a bottom-up controlled process during winter in this area. Zooplankton was highly correlated with

phytoplankton concentration. Phytoplankton in turn increased most prominently near the Rhine-Meuse delta, suggesting that the vicinity to the estuary provided suitable conditions for primary production. Data for these conditions other than temperature and salinity were not available. Temperature and salinity could not be significantly related due to their rather continuous increase. Nevertheless, the positive relation to zooplankton provided evidence for bottom-up control of phytoplankton too.

The zooplankton samples were collected in the same area where North Sea autumn spawning herring (*Clupea harengus*, L. 1758) lay their eggs. The autumn spawning herring stock suffered from poor recruitment during the 2000s while one part of the stock, the so-called Downs recruitment component gained in importance. Overall recruitment increased again since 2009. I combined data of herring larvae of various different stages, from first-feeding larvae to actual recruitment numbers, to identify potential bottom-up controls that influence herring larvae survival. I could confirm the correlation between numbers of herring larvae at first feeding and the North Atlantic Oscillation index and a decreasing size of herring larvae in a later stage. Further, I could show that there are indeed bottom-up controls of herring larvae, in the form of phyto- and zooplankton density that positively affected herring recruitment. This is despite the fact that both plankton groups mainly showed increased abundances in a relatively small area. Temperature, though only to a small extent, negatively influenced survival. A principal component analysis including all parameters indicated a matching increase of principal component 1 after 2008 and a more continuous trend over time of principal component 2. The former component included zooplankton abundance and size and chlorophyll *a* concentration while the latter included temperature and salinity. These results and the indicated breakpoint around 2009 underline the need for a monitoring of bottom-up controls in the area of larval growth and drift. Although restricted to the Downs component the relevance of local processes, zooplankton abundance and size was highlighted.

When monitoring such alterations in ecosystem state and trophic relations the term “indicator” is inevitable. In efforts to observe changes in good environmental status of the world’s oceans, e.g. due to climate change and overfishing, indicators are being developed that detect change quickly, are easy to apply and easier to monitor. Biodiversity is often the preferred choice of indicator for conservation purposes. At lower trophic levels, taking note of biodiversity changes requires a lot of effort and highly skilled observers that can

distinguish plankton species. Yet, for trophic interactions and energy flow, individual sizes contain information that rivals that of the organism’s identity, but can be easier monitored and applied in projections. These are two main requirements for a good indicator. Using the same zooplankton data from my time series I calculated size diversity and compared it to taxonomic biodiversity. The correlation was highly significant and stable over a wide number of possible size classes and minimum sizes. Looking at different time periods and spatial rectangles with varying number of samples, size diversity was still able to monitor changes in lower trophic levels that occurred only in specific areas. Normalised biomass size spectra were also compared, but did not show a significant correlation with biodiversity. With respect to monitoring and change detection, I discuss the potential of size diversity as an alternative indicator for zooplankton dynamics. Especially in regard to monitoring and projections into the future, size diversity could be easier determined than taxonomic diversity.

Taking the possibility of a winter phytoplankton bloom in 2011 into account the findings could be related to trophic relationships between phytoplankton, zooplankton and fish larvae in the North Sea and other boreal ecosystems. The scarcity of zooplankton size data and winter data provide a loophole for assumptions of models starting in winter. Growth models can be applied without proper data validation using actual zooplankton sizes in the field. This is also true for generalisations in trophic relationships and energy flow at the base of the food web. Predator-prey interactions are often assumed to be only species related. However, I could show that within taxonomic groups, species size can also vary. A clear recommendation for further survey programs and application opportunities with respect to plankton and fish recruitment success is given.

2. Zusammenfassung

Plankton stellt die zwei grundlegenden Ebenen mariner Nahrungsnetze auf der ganzen Welt dar. Im Angesicht von Klimawandel und sich änderndem Fraßdruck durch Fische sind planktonische Organismen die Mediatoren im Energiekreislauf der Ökosysteme. Es gehört zu den wichtigsten Herausforderungen in den Meereswissenschaften, die Dynamiken und Prozesse des Planktons zu verstehen, um zukünftige Probleme analysieren und behandeln zu können. Es wurde zum Beispiel erkannt, dass Phytoplankton ein wichtiger Baustein in Ökosystemmodellen ist und gebraucht wird, um Energieflüsse und Konsequenzen des Klimawandels in Ökosystemen projizieren zu können. Aber nicht nur ist die Biologie des Phytoplanktons schon sehr genau erforscht worden, sondern lässt sich auch einfach beobachten, zum Beispiel durch Satelliten. Zooplankton dagegen kann nicht aus der Ferne observiert werden. Es ist jedoch eine wichtige Kohlenstoffsenke für die Primärproduktion in aquatischen Systemen und das Bindeglied zwischen autotrophen Organismen und höheren trophischen Ebenen. Viele bedeutende pelagische Fischarten und alle frühen Lebensstadien mariner Fische ernähren sich von Zooplankton. Besonders die letzteren sind dem Verhungern und erhöhten Fraßdruck ausgesetzt und variierten in den letzten Jahrzehnten oft stark in Vorkommen und Größe. Das Überleben von Fischlarven unter Berücksichtigung von Zooplanktondynamiken zu studieren war aus diesen Gründen ein wichtiger Bestandteil meeresbiologischer Untersuchungen. Benötigte Daten zu Zooplanktonabundanzen und -größen fehlten jedoch häufig. In dieser Dissertation versuche ich, die Dynamiken des Zooplanktons während der selten dokumentierten Winterperiode zu analysieren. Dafür erstellte ich die erste Zeitreihe für Zooplanktonabundanz und -größe im Winter mit einer räumlichen Auflösung in der südlichen Nordsee.

Über 1000 Zooplanktonproben aus dem östlichen Ärmelkanal und der südwestlichen Nordsee („Southern Bight“) wurden examiniert. Mithilfe von digitalen Bildern der Organismen konnte ich Größe, Abundanz und Diversität des Planktons zwischen 1988 und 2014 messen. Für genauere Analysen mit abiotische und anderen biotischen Faktoren musste die Zeitreihe auf den Zeitraum 1991 bis 2013 beschränkt werden. In diesem Zeitrahmen verringerte sich die mittlere Größe des Zooplanktons. Dies traf jedoch auch für bestimmte taxonomische Gruppen zu. Obwohl der Anteil kleiner Zooplanktongruppen durch eine erhöhte Abundanz dieser zunahm, und dadurch die Abnahme der mittleren Größe der einzelnen Gruppen überschattete, ist es eine der wenigen Zooplanktonzeitreihen, die eine Verringerung der Größe über die Jahre dokumentiert. Währenddessen steigerte sich allerdings auch das Zooplanktonvorkommen, jedoch nicht kontinuierlich, sondern eher sprunghaft, besonders zwischen 2008 und 2011. Die räumlichen Dimensionen dieses Anstiegs beschränken sich größtenteils auf die Region in der Nähe des Rhein-Maas Deltas in der südwestlichen Nordsee. Eine zur gleichen Zeit ebenfalls erhöhte Konzentration an Phytoplankton resultierte in einer signifikanten Korrelation zwischen Zooplanktonabundanz, -größe und Primärproduktion. Es liegt der Verdacht nahe, dass eine frühe Winteralgenblüte und „bottom-up“ Prozesse die Dynamik des Ökosystems im Winter mehr beeinflussen, als früher angenommen wurde. Nichtsdestotrotz konnte durch ihren eher homogeneren Anstieg keine signifikante Verbindung zu Wassertemperatur und Salzgehalt festgestellt werden.

In der Region, in der die Planktonproben gesammelt wurden, laicht auch der Herbstlaicherbestand des Nordseeherings (*Clupea harengus*, L. 1758). Der Herbstlaicherbestand litt unter sehr schwachen Rekrutierungserfolgen Anfang und Mitte der letzten Dekade. Die Downs Komponente, die im gleichen Gebiet laicht, in der die Planktonproben erfasst wurden, gewann allerdings an Bedeutung gegenüber den anderen Laichkomponenten. Anfang des Jahrzehnts gab es allerdings wieder ein paar starke Rekrutierungsjahrgänge. Um die Beziehung zwischen den Überlebenschancen der Heringslarven und “bottom-up“ Prozessen zu untersuchen, sammelte ich Daten verschiedener Heringslarvenstadien, von frühesten Larvenstadien bis zu finalen Rekrutierungszahlen der Assessments. Ich konnte die Beziehung zwischen der Anzahl der frühesten Stadien und dem Nordatlantischen Oszillationsindex und die Verringerung der Größe der späten Larvenstadien bestätigen. Zusätzlich konnte ich zeigen, dass „bottom-up“ Prozesse wie Phyto- und Zooplanktonvorkommen die Anzahl an späten Heringslarven und die Überlebenschance positiv beeinflussen. Obwohl die „bottom-up“ Prozesse vorwiegend lokal waren, hielt die Korrelation dennoch stand. Erhöhte Wassertemperaturen verringerten die Überlebenschance, obwohl der Effekt nur marginal war. Durch die Anwendung der Principal Component Analyse war es mir möglich, Variablen, die eher einen sprunghaften Trend seit 2008 zeigten und solche, die sich relative stetig verhielten, in Komponenten zu vereinen. Dadurch ist es möglich, diese Komponenten vermehrt für Beobachtung einzusetzen und zu zeigen, dass die „bottom-up“ Prozesse in den Verdriftungen und im

Wachstum der frühen Lebensstadien des Nordseeherings eine wichtige Rolle spielen. Trotz des Bezugs auf den Downs Komponenten des Nordseeherings könnten sich ähnliche lokale Prozesse und Beziehungen zu Plankton auch in den anderen Komponenten wiederfinden lassen.

Um Änderungen in solchen trophischen Beziehungen und Ökosystemzuständen großskalig zu beobachten wird oft der Term „Indikator“ genannt. Indikatoren werden seit einigen Jahren entwickelt, um den „good environmental status“ der Ozeane in Zeiten des Klimawandels und der Überfischung zu observieren. Diese Indikatoren sollten Trends schnell aufspüren, unkompliziert anzuwenden sein und noch einfacher zu dokumentieren sein. Das macht Biodiversität zu einen der meistbenutzten Indikatoren der Ökologie. Im unteren Bereich des Nahrungsnetzes jedoch erfordert die Ermittlung der Biodiversität viel Arbeit und gut ausgebildete Taxonomen, um die einzelnen Planktonarten zu unterscheiden. Für trophische Interaktionen und Energieflüsse im Ökosystem eignet sich auch die Größe der Organismen und diese kann einfacher ermittelt werden als die Spezies und gleichzeitig auch für Modellprojektionen verwendet werden. Dies sind zwei Hauptmerkmale eines guten Indikators.

Mit meiner neuen Zooplanktondatenreihe errechnete ich deswegen die Größendiversität in den Proben und verglich diese mit der Biodiversität. Die Korrelation zwischen beiden Indikatoren war hoch signifikant und stabil über eine weite Bandbreite an möglichen Größenklassen und Mindestgrößen. Um die Anzahl der Proben künstlich zu limitieren und somit die Stabilität der Korrelation weiter zu untersuchen verglich ich die Indikatoren in bestimmten Zeitabschnitten und räumlichen Konfigurationen. Selbst in lokalen Regionen mit wenigen Proben hielt die Beziehung stand. Ich errechnete auch das „Normalised biomass size spectrum“ und setzte es in Kontrast zu Größendiversität. Es entstand jedoch keine signifikante Korrelation mit der Biodiversität. Für Monitoringprogramme und Einschätzung von unteren trophischen Ebenen eignet sich Größendiversität durchaus, hat aber einige Limitierungen, auf die ich hinweise. Durch die einfache Anwendung und Ermittlung von Größen kann Größendiversität eine simplere Alternative zu Biodiversität darstellen.

Des Weiteren erörtere ich die Umstände einer Phytoplanktonblüte im Winter 2011 in Bezug auf das Nahrungsnetz, insbesondere Zooplankton und Fischlarven, in der Nordsee und weiteren gemäßigt-kühlen Ökosystemen. Die Seltenheit von Größendaten von Zooplankton, noch dazu im Winter, stellt eine Schwierigkeit für die Bereitstellung von Initialisierungsdaten für Ökosystemmodellierung dar. Ökosystemmodelle beginnen normalerweise im Winter, obwohl entsprechende Zooplanktonkenntnisse fehlen. Gleiches gilt für Nahrungsnetzinteraktionen und Energieflüsse an der Basis des Nahrungsnetzes. Deshalb ist es auf langfristiger Sicht unumgänglich, dass weitere Probennahmen und Anwendungspotential von Zooplankton in Bezug auf die Analyse von Fischrekrutierungserfolgen ermöglicht werden.

3. Outline of publications

Dudeck, T., Möllmann, C., Rohlf, N. and Hufnagl, M. (2017) Zooplankton size as indicator for zooplankton biodiversity. *Marine Ecology Progress Series*: *submitted*

Dudeck, T., Rohlf, N., Möllmann, C. and Hufnagl, M. (2017) Winter zooplankton dynamics in the English Channel and Southern Bight: trends from 1991 to 2013. *Journal of Plankton Research*: *submitted*

Dudeck, T., Rohlf, N., Möllmann, C. and Hufnagl, M. (2017) Winter prey: Survival of North Sea herring larvae in relation to zooplankton size and abundance. *Marine Ecology Progress Series*: *in preparation*

4. General introduction

4.1 Climate change and bottom-up controls of ecosystems

All oceans of our planet are very dynamic and have a major influence on the earth's climate. The entire system can be regarded as a gigantic solution. With no external perturbations suspended particles sink and dissolved chemicals strive for equal concentrations just like they do in test tubes. But our planet has a constant exchange between atmosphere, hydrosphere, cryosphere, lithosphere and biosphere. Hence external perturbations are the norm. Currents, created by wind and different densities of water, induce an eternal mixing of the fluid environment. In boreal seas, these external forces are additionally affected by seasons. Increasing winds and decreasing water temperatures are characteristic of autumn and winter. The water column becomes well mixed, low light intensity and low temperatures reduce primary production and biological growth in general. In spring, stronger solar radiation and replenished nutrient supplies give rise to new growth of plankton and other organisms. This season of growth comes to a halt when warm temperatures and low wind speeds stratify the water column and nutrients become depleted in the photic layer (see also the critical depth model by Sverdrup, 1953). A temporal succession of environmental conditions and biological growth thus occurs. It has been a focus of marine research, because the succession not only occurs on a temporal scale, but also on a trophic scale. It is referred to as the trophic cascade.

Beginning at the abiotic level of physical forces such as temperature, it chains through primary producers and their immediate producers until it reaches organisms, which have a multi-annual life span. Consequently, the food chain starts from the "bottom", which is why scientists refer to this chain of effects as "bottom-up" controlled food chains (or resource-driven; e.g. Ware and Thomson, 2005; Frederiksen et al., 2006). If the multi-annual or top predators have a larger influence, these food chains are dubbed "top-down" controlled (or consumer-driven; e.g. Möllmann and Köster, 1999; Worm and Myers, 2003; Casini et al., 2006). There is also evidence for multi-level cascades with both controls (Casini et al., 2008). It is still debated, which ecosystems are bottom-up or top-down controlled and there is no universal mechanism (Frank et al., 2007). Independent of this debate, as the cascade is initiated by bottom-up controlled processes, scientists have focussed on spring and summer time for surveys and models (Hannon and Joiris, 1989) and winter surveys for comparison have only occasionally been carried out (e.g. Atkinson and Peck, 1988).

Especially in regard to climate change and the Intergovernmental Panel on Climate Change reports (IPCC, 2014) ecosystem analyses tried to estimate the transport of energy through the annual succession (Walters et al., 1997; Möllmann et al., 2008; Gilbert et al., 2014). However, there has to be a base stock of organisms, which will grow and reproduce and ultimately initiate the flow of energy. In fisheries ecology, this standing stock is regarded as spawning stock biomass (SSB), which includes all mature fish of a single species. The lower ends of the food chain, though, have much shorter life spans, often with multiple generations within a year (Allan, 1976). Nevertheless, as growth is impeded during winter, there is usually a single generation or cohort of cells (primary producers and eggs) or organisms (adults or larvae stages) that survives winter and thus forms the standing stock biomass for the next succession in spring (Sommer et al, 2006). The importance of their survival has been recognised, but poor coverage of winter surveys indicates that the importance of the plankton standing stock in winter has not been acknowledged for management purposes.

If we want to be prepared for the consequences of climate change, we need to understand the effects that rising water temperatures have on the plankton standing stock (Möllmann et al., 2003). Changes in biomass and individual condition (such as size) can have effects on the trophic cascade and life stages of economically important fish species (Beaugrand, 2003). In that respect, the North Sea provides an ideal test bed to analyse the change in winter zooplankton standing stock as it combines the necessary geographic location, good data coverage, previous knowledge of food web dynamics and continuing effects of climate change (Beaugrand, 2004).

4.2 English Channel and the southern North Sea

The North Sea is a European shelf sea that is one of the most extensively exploited ecosystems of the world. From oil and natural gas extraction to multispecies fisheries (http://www.bsh.de) the North Sea has experienced considerable change through anthropogenic effects. Its location between Scandinavia in the north, Great Britain in the west and central Europe in the south and east makes it a central trade route, but also one of the best studied marine ecosystems in the world. The shallow mean depth of 30 m in the south and the gradual decline of the seafloor to 100 m mean depth in the north, before dropping to over 500 m in the Norwegian trench, allow easy sampling and fishing routines (Fig. 1). The current system in the North Sea is mainly driven by tides and wind force resulting in an anti-clockwise gyre (Otto et al., 1990). This gyre transports Atlantic water entering the North Sea in the north and in the southwest through the North Sea. Due to the strong inflow of saline Atlantic water and the major freshwater systems in the south there is a salinity gradient from approximately 35 in the central north and 33 and less in the German Bight and close to the southern shorelines (Schott, 1966).

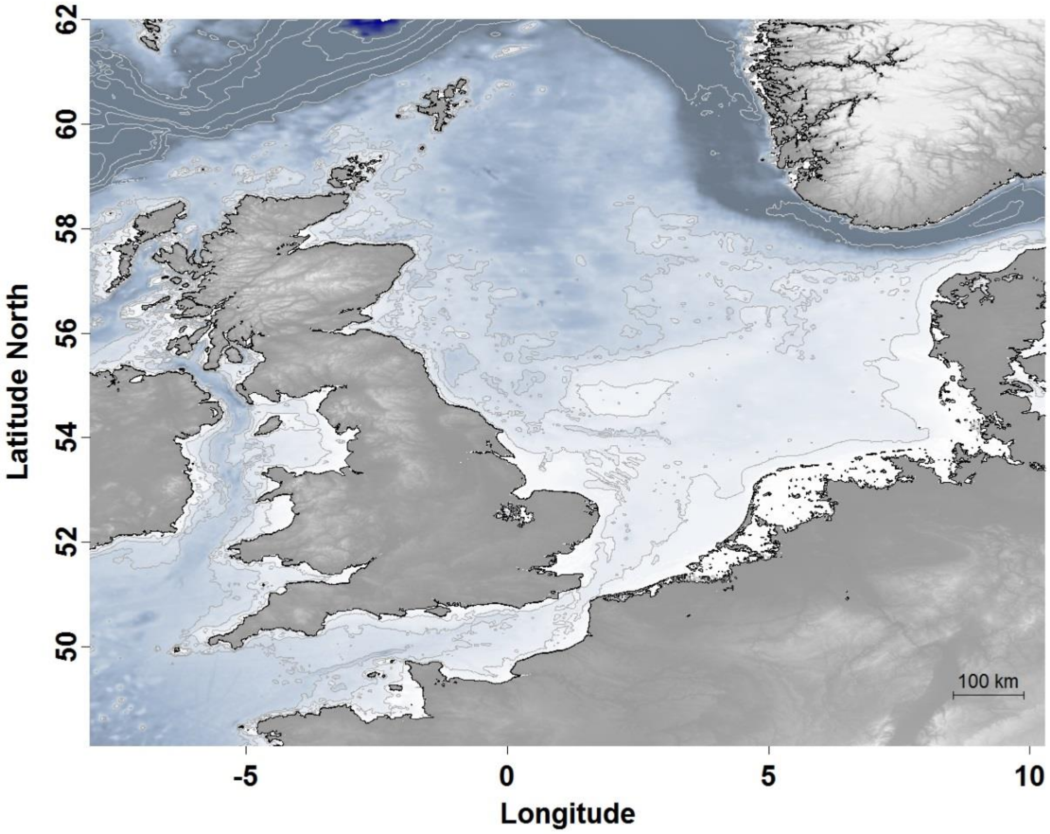

Fig. 1. Map of the North Sea and English Channel in the south with depth contours. Lighter shades of steelblue show shallower depths (data from www.noaa.gov).

The English Channel is the southern connection of the North Sea to the North Atlantic Ocean. It is bordered by the French and Belgian continental shores in the south and by the British coast in the North. Considering the width of the strait it is much narrower than the northern entrance of the North Sea, reaching a smallest width of only 27 km. As a consequence, Atlantic water inflows are also smaller compared to the northern entrance to the North Sea. Yet, due to its funnel shape, the current system here is very dynamic and of considerable importance for the southern North Sea in that it facilitates the addition of Atlantic water into the southern North Sea (Bailly du Bois et al., 1995). In the wider western entrance of the Channel the water depth can reach over 150 m while in the Strait of Dover, the narrow eastern entrance, water depth reaches a maximum of 40 m. Water exchange in this area is facilitated by two mechanisms: The first is a predominantly western wind, which pushes saline Atlantic water north- and eastwards into the North Sea. The second is tidal movement, which causes the water to change its flow direction twice a day in and out of the North Sea.

Following the currents, the English Channel connects to the North Sea via the Strait of Dover and opens into southern North Sea in an area, which is called the Southern Bight. Being part of the North Sea it is much shallower with a mean depth of approximately 40 m. It is also the site of two main European river deltas: the Thames and the Rhine-Meuse. The latter is the largest river outlet in northern Europe. Atlantic water masses flow south into the Bight, where they meet English Channel water and continue flowing in an anti-clockwise direction along the Dutch and German coasts. These saline waters thus mix with nutrient-rich freshwater and transport them further. This alongshore current carries several ichthyoplankton species with them (Daan et al., 1990). The hatched larvae are then transported with the currents in an anti-clockwise direction towards the German Bight, where the nursery areas are located. The lack of data and being the origin of important North Sea water masses and fish larvae, the English Channel and Southern Bight are the focal regions of this study.

4.3 Herring in the southern North Sea

The shallow, less saline south of the North Sea is an important spawning and nursery area for fish such as plaice (*Pleuronectes platessa*, Linnaeus 1758), common dab (*Limanda limanda*, Linnaeus 1758) and herring (*Clupea harengus*, Linnaeus 1758)(Daan et al., 1990). Here, especially the Southern Bight, where the Atlantic water enters the North Sea in the southwest, is the spawning area of two of the most commercially important fish species: plaice and herring. Both fish stocks have experienced a decline during the early 1990s and a recovery towards the new millennium. However, the recruitment of plaice has been at an average level since the mid-1990's with an increasing trend since 2000 (ICES, 2017), whereas recruitment of herring has been at low levels during the same period (ICES, 2014). Considering the increase in both spawning stock biomasses, there has been a negative spawner-recruit relationship. Studying the early life stages of these fish and their possible bottom-up controls in the surroundings of their spawning area is thus of peculiar research interest to disentangle the reasons behind the variable recruitment. In the case of plaice, Nash et al. (2012) and Hufnagl et al. (2013) looked at the increased mortality of the larval life history stage. The latter found that connectivity and thus survival of eggs and larvae to the nursery grounds is limited and successful drifts of larvae were close to the spawning area. Nash et al. focused instead on top-down control and explained that predation on plaice larvae during the drift is density-independent, whereas predation on the nursery grounds is density-dependent. This might explain the ecological reason behind the short drifting routes and some of the variability in plaice recruitment. North Sea herring has been investigated extensively as it is one of the commercially most important fish stocks in Europe, suffers high recruitment variability and has a complex life history (ICES, 2014; Nash and Dickey-Collas, 2005; Simmonds, 2009; Gröger et al., 2010; Payne, 2010; Hufnagl et al., 2014). As in plaice, herring larval survival has been a major research target and found to be a major factor affecting recruitment strength (Fässler et al., 2011).

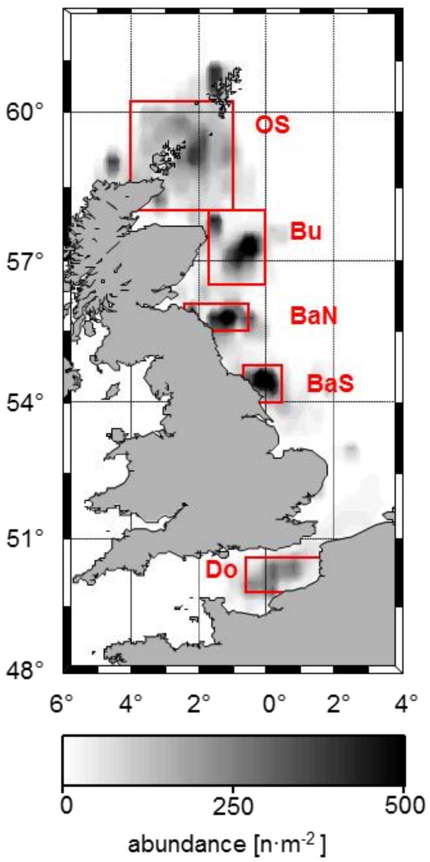

Fig. 2. Locations of North Sea autumn spawning herring spawning grounds and abundances of larvae (Hufnagl et al., 2014).

The North Sea autumn spawning herring has four major spawning areas: Orkney-Shetlands, Buchan, Banks and Downs (Fig. 2). The most southern spawning ground, the Downs compartment, has increased its supply of herring larvae compared to the other spawning compartments (Payne, 2010). It seems decoupled from the other three spawning grounds, possibly providing a recruitment buffer in case of recruitment failure. Unfortunately, the Downs spawning component is the most unpredictable and dependencies, such as prey availability and successful drift, could not be accurately determined using combined field data and modelling approaches (Hufnagl et al., 2014).

Due to the fact that the herring larvae hatch during early winter sampling has been rare due to the dynamic currents and rough seas. The International Herring Larvae Survey (IHLS) has provided ichthyoplankton samples for monitoring abundances and sizes of herring larvae from the Downs spawning ground, but the zooplankton information contained in these samples has not received any attention so far. In this borderland between the North Sea and the Atlantic data are rare concerning the abiotic and biotic environment, despite its immense value as a transient ecosystem. As a result, bottom-up controlled processes have not been investigated in conjunction with the herring larvae from the Downs region despite the major research effort in the past decade. To resolve the complexity of bottom-up processes the area between the United Kingdom and the continental shores we need to look at the dynamics of lower trophic levels.

4.3 Plankton as lower trophic levels

Plankton is defined as those organisms in the hydrosphere, which main mode of transport is the passive drift in currents. They are capable of movement within the general water masses, but do not possess enough forward propulsion to determine their final destination. Phytoplankton form the base for all aquatic life. With their ability of transforming light energy into biological growth they form the lowest trophic level of the aquatic ecosystems. It is commonly referred to as primary production. Depending on light, nutrient and temperature conditions phytoplankton forms blooms in spring, with diatoms dominating at first under nutrient-rich conditions, followed by dinoflagellates (Sarthou et al., 2005). These blooms are crucial in most ecosystems and start a succession of energy transfer between trophic levels. Zooplankton forms the second level in the marine food web and in the mentioned succession. Similar to phytoplankton, it can be divided by its size into micro- (< 200 µm), meso- (200 µm < x < 2000 µm), macrozooplankton (> 2000 µm) and even larger classes ("megazooplankton"). It is the mesozooplankton, however, that is regarded as the integral part of zooplankton. Microzooplankton is usually dominated by large herbivore dinoflagellates, which, as mixotrophs, can also be, and often are, classified as phytoplankton. Macrozooplankton are often planktonic stages of larger organisms ("meroplankton") or very large zooplankters such as jellyfish, which do not show the same life histories as other plankton. Important taxonomic groups of zooplankton include copepods, chaetognaths, cladocerans, appendicularians, but also euphausids and pteropods. Being mostly the herbivores of the sea, zooplankton functions as the central link between primary production and higher trophic levels. In fact, it is so abundant in the world's oceans that even some top-predators are feeding on zooplankton (e.g. basking shark, *Cetorhinus maximus*). It has even been proposed that humanity will increasingly eat large zooplankton if fisheries management fails ("fishing down the food web", Pauly et al., 1998). All in all, the importance of zooplankton for marine ecosystems has long been recognised.

Early explorers like Sir Wyville Thompson and marine ecologists such as Haeckel already noticed the immense diversity of forms and life history traits of zooplankton in the 19th century (Johnson and Allen, 2005). Most zooplankton species have a specific life cycle involving multiple larval stages and a relatively short life span between a few weeks and one year. Their growth is tightly linked to temperature and food supply (McLaren, 1963; Huntley and Boyd, 1984). Consequently, the peak of zooplankton abundance occurs usually just after the peak of phytoplankton bloom in spring in temperate regions, sometimes followed by a second peak of phytoplankton and afterwards zooplankton (e.g. Wiltshire et al., 2008). During these bloom periods secondary production, which is the growth of organisms feeding on primary producers, is high. Normally, it is regarded as the equivalent expression for zooplankton production (Williams, 1984). Especially more short-lived species such as cladocera and small copepod species thrive and consume large proportions of the primary production.

Yet short-lived and long-lived species need to survive until the next suitable conditions arise after the bloom season ceases. There are different strategies to cope with this problem. Producing eggs that are capable of resting until more favourable conditions arise is one option (Marcus, 1996). *Temora longicornis* is one European representative of the resting egg strategy. The resting eggs can be divided into quiescent, diapause and delayed-hatching eggs (Chen and Marcus, 1997). Quiescent eggs can be directly awakened by preferential environmental cues, while diapause eggs have a fixed resting period during which they do not awaken. Delayed-hatching eggs have a shorter resting time than diapause eggs, but are also not triggered by favourable environmental conditions during resting time (Tietjen, 2013). The second option is to invest the available energy for somatic growth and energy storages to increase the chance of individual survival. Båmstedt and Ervik (1984) showed that *Calanus finmarchicus* can overwinter as copepodite V stage in diapause. Growth and stage development is halted until the end of winter. Final development and egg production is thus postponed to the more productive spring and summer season. Ji *et al.* (2009) showed in a combined observation/modelled approach how spatial distribution and seasonality of abundance can be explained by different reproductive strategies. Copepod's reproductive mode, their thermal tolerance and their predation strategy are the main life history traits defining the species niche within their order. Broadcast spawners such as *Calanus finmarchicus* freely spawn their eggs while egg-carrying copepods like *Oithona similis* transport their eggs in sacs until hatching and some, as mentioned before, can produce resting eggs.

Just as environmental conditions differ depending on temperature, salinity, predation and available food so do the strategies of zooplankton species to survive the harsh conditions of winter in temperate regions. Considering the increasing water temperature in northern European waters (Wiltshire and Manly, 2004; Hawkins et al., 2003; Edwards et al., 2002) there is concern that the capability of surviving the winter could change. Increased winter temperatures raise the metabolic rate, and thus energy demand, of ectotherm zooplankters, reducing their capability to survive low food conditions. Furthermore, earlier onset of spring water temperature rise could trigger egg hatching too early for optimal phytoplankton (prey) conditions. Phytoplankton growth in winter is light-limited and may not be initiated simultaneously with largely temperature-triggered hatching of overwintering eggs of copepods. A predator-prey mismatch can be the result and diminish the copepod offspring that would dominate the late spring bloom. Such a mismatch scenario is usually associated with fish larvae. Larvae of many fish, e.g. herring, cannot readily adapt to environmentally triggered conditions, which would provide suitable prey concentrations. This is because they have a longer life cycle and a greatly fixed location and timing of spawning (Iles, 1964). Thus, a mismatch scenario would arise (Cushing, 1975; Sinclair and Tremblay, 1984). A mismatch scenario occurs, when the time of first feeding of fish larvae (or larvae of other predatory organisms) does not coincide with a time of high prey abundance (such as bloom conditions). The main reason for this effect is the bottom-up controlled nature of the fish larvae food web (Peck et al., 2012). Rising water temperatures in spring shift the onset of phytoplankton blooms further to the beginning of the year. Additionally, warmer winter temperatures can also trigger early plankton blooms. The spawning of fish eggs and their time of hatching is less plastic and not or not only linked directly to environmental cues. Thus, a lag can occur between highest prey abundance and the occurrence of large numbers of fish larvae, thereby increasing their vulnerability to starvation (Cushing, 1990). While the mismatch scenario has been studied for spring conditions, there is a lack of evidence for this effect arising from bottom-up processes in winter. It is hence of great importance to study the trends in winter conditions and the simultaneous trends in phyto- and especially zooplankton during winter. This is the principal aspect of this thesis.

As mentioned above, one of the major taxonomic groups of zooplankton and especially mesozooplankton, is the subclass copepoda. It currently contains over 14000 species (Walter and Boxshall, 2017). The continuing success story of copepods is based on a variety of life history traits. Copepods can be found in all lakes (Boxshall and Defaye, 2008) and oceans (Fig. 3), from the neritic to the bathypelagic zones. Individual species have adapted to a wide variety of salinity and temperature to survive (Hirche, 1987; Bhattacharya, 1986). Despite their specific thermal and salinity tolerances, laboratory experiments have shown that these tolerances can sometimes be broader under otherwise ideal conditions (e.g. no food limitation) or for short periods of time (Cervetto et al., 1999). This environmental plasticity, the adaptation of feeding strategies (Kiørboe, 2011) and the diversity of egg production (Kiørboe and Sabatini, 1994) have significantly contributed to the high survival rates of copepods in marine and freshwater systems. Studying their dynamics was thus of high priority during recent decades. Yet, sampling of zooplankton is difficult.

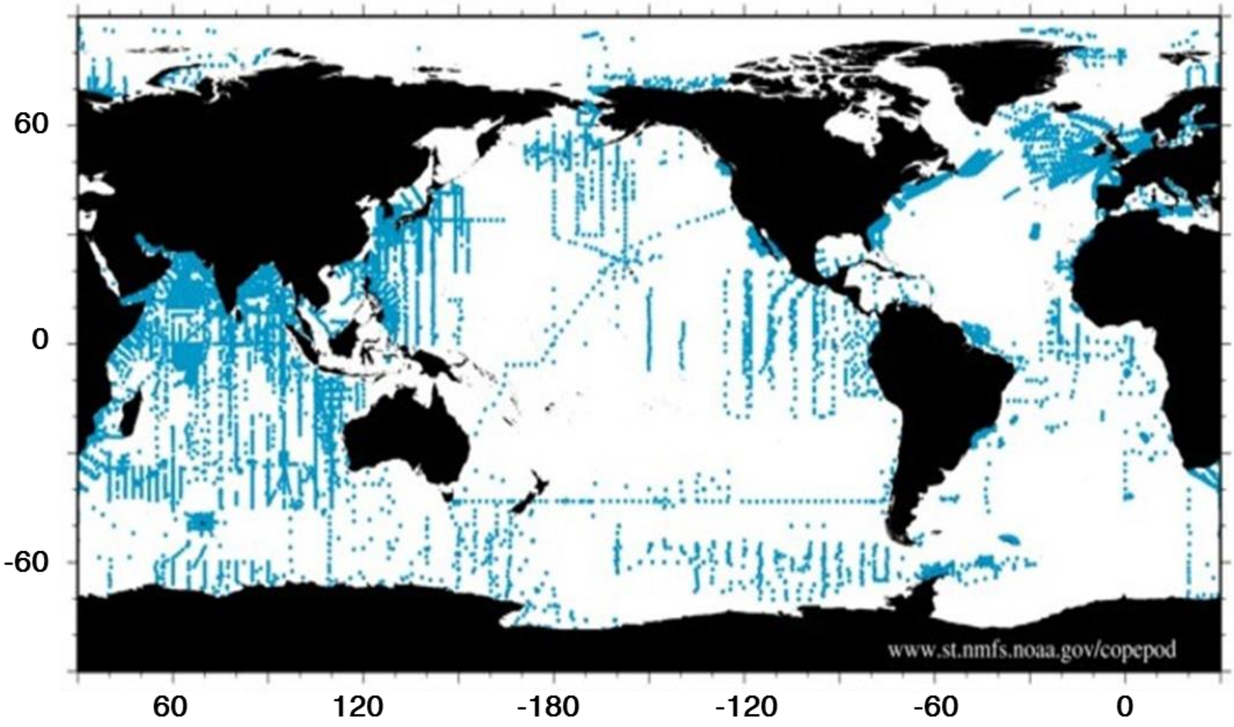

Fig. 3. Records of individuals of the subclass copepod. Taken from the COPEPOD database (www.st.nmfs.noaa.gov/copepod).

4.4 Sampling strategies and Zooplankton time series

Various plankton nets have been established since the beginning of the 20th century, all with varying catch efficiencies and applications (Colton Jr. et al., 1980; Gjøsæter et al., 2000; Stehle et al., 2007). But sampling with and comparability of plankton nets are not the only difficulties. Being so small and delicate, the plankton samples need to be carefully collected, conserved and analysed using specific techniques. Motoda subsampling (Motoda, 1959) and Utermöhl's method (Utermöhl, 1958) are just two prominent examples. The additional complexities of higher diversity and microscopic size in comparison to fish samples or samples of other larger marine organisms led to the development of technologies with the aim of simplifying the sampling and expanding survey areas and times. One of the main achievements of this era is the Continuous Plankton Recorder (CPR). The Sir Allister Hardy Foundation established the Continuous Plankton Recorder in 1946 (Reid et al., 2003) to sample zooplankton on a large scale with minimal effort. Ships of opportunity tow this small, sturdy device, which collects plankton with a 270 µm mesh at around 10 m and stores it internally. Although being the longest running, spatially resolved plankton dataset in the world, it also shows the misery of collecting plankton. Researchers have to choose between high frequency sampling, spatial resolution and detail of data. The CPR, for example, has a high frequency of sampling, larger spatial coverage (although in narrow transects) and high taxonomic detail. Yet, all the plankton has been collected at a fixed depth and due to the small opening of the device, CPR data has largely been used for presence/absence analysis (Richardson et al., 2006). Other time series of zooplankton available in the northeast Atlantic are the monitoring stations of the ICES Working Group on Zooplankton Ecology (WGZE; ICES, 2013). WGZE's members collect plankton samples frequently throughout the year at a specific location. Apart from the long-term monitoring, the focus of these time series lies on seasonal patterns and species composition. The stationary character of the three sites available in the southern North Sea and English Channel (L4, John et al., 2001; Gravelines, Le Fevre-Lehoerff et al., 1995; Helgoland Roads, Boersma et al., 2015) make them difficult to compare. But no matter the spatial extent or time scale, all of the available time series lack an important ecological characteristic: size. In addition to taxonomic identification of plankton, size measurements are time consuming and the various shapes of zooplankton require careful calibration. Size was therefore often regarded as secondary to taxonomic identification and, taking known growth curves of various planktonic species into account, not considered further. Scanners (i.e. ZooScan; Grosjean et al., 2004; Gorsky et al., 2010), cameras (FlowCam, Sieracki et al., 1998; Blaschko et al., 2005) and machine-learning algorithms (i.e. in Plankton Identifier, Gasparini and Antajan, 2013) helped path a way to automatically recognise species and measure size simultaneously. Nowadays optical sensors take photographs of the plankton *in situ* (Video Plankton Recorder, (VPR; Davis et al., 1996) and *in vitro* (e.g. ZooScan, Fig. 4 a-d). It has thus become much easier to sample plankton data and to store it digitally. Small scale phenomena like vertical migration, feeding mechanisms and reproduction can be measured on surveys rather than in the laboratory, which opened new doors for plankton research. The new methods can also provide data to verify ecosystem models with its ability to measure size and detailed trophic interactions (Möller et al., 2012). Yet, extensive zooplankton time series of individual size, which span over more than a decade, do not exist in the North Sea region. With the many links of body size to physiological and ecological processes in mind a new zooplankton time series can provide valuable information on intra- and interspecific changes that otherwise go unnoticed.

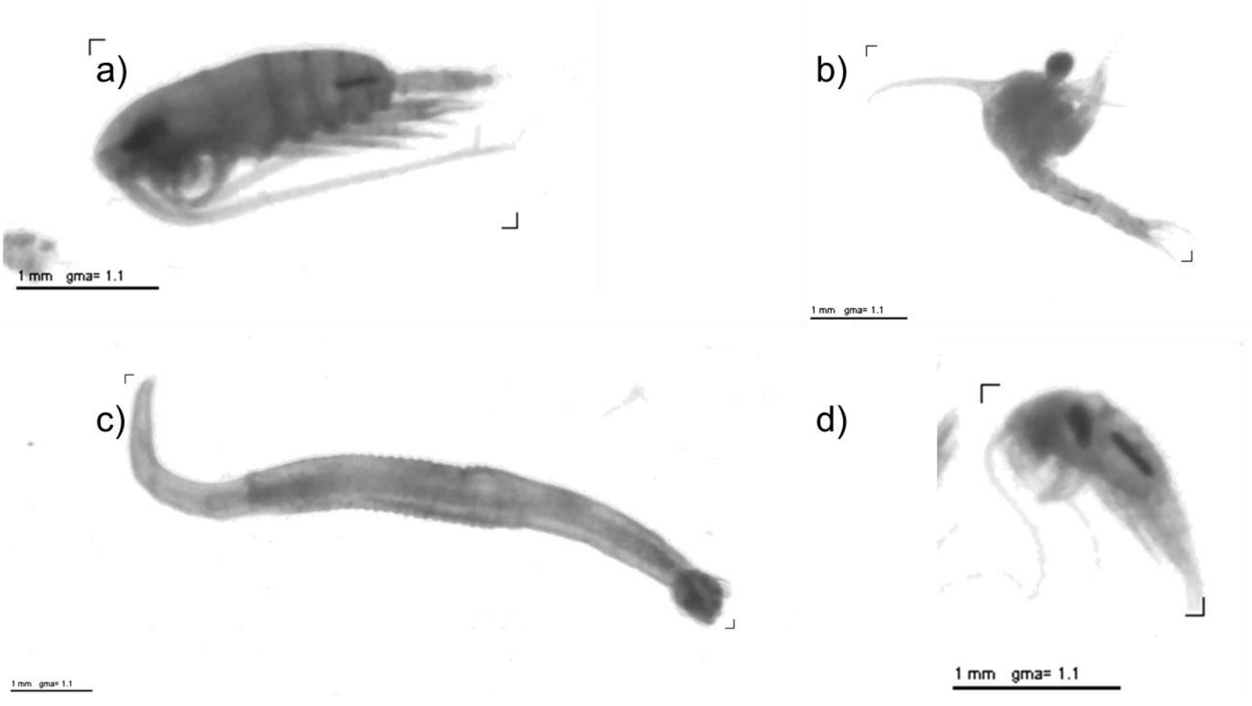

Fig. 4 a-d. ZooScan images of four different taxonomic groups: a) Calanoid copepod, b) Zoea larvae, c) Chaetognath and d) *Temora sp.* Note the 1 mm scale bar.

4.5 Biodiversity, Biomass and Size

The North Sea, amongst other European seas, has undergone fundamental changes as an ecosystem in recent decades (Beaugrand, 2004; Alheit et al., 2005). Considering that these changes occurred at all trophic levels (Alvarez-Fernandez, 2012; Beaugrand et al., 2003) it has been a management goal to apply the ecosystem-based approach to fisheries management (Folke et al., 2004). Yet, the monitoring of all trophic levels is complex and time consuming. It has thus become a major research goal to find suitable environmental indicators for "good environmental state", which are easy to monitor and respond well to changes in the ecosystem (Millennium Ecosystem Assessment, 2005). One of these indicators is biodiversity. Biodiversity can be measured in many ways, but one of the most common ones is the Shannon-Wiener Index (Shannon and Weaver 1949, in Pielou 1969). It represents not only the species richness, but also the evenness in abundance. It can thus detect changes that lead to the dominance of single or group of species and the loss of important, previously dominant species. Biodiversity has been accredited to stabilise the ecosystem and increase resilience against external forces (Hooper et al., 2005). However, counting species and their abundances is challenging. When considering biodiversity of organisms that are not visible to the naked eye it becomes a major problem. That is why plankton biodiversity has only been calculated for a handful of local stations and for the Continuous Plankton Recorder dataset (ICES, 2013). Nevertheless, biomass is especially suitable due to the ability to be modelled. The need for assessments of ecosystem states and their projections into the future under different scenarios has become a major necessity for ecosystem management (Jørgensen et al., 2010). Biomass, for instance as grams of carbon, can be easily applied and used in ecosystem models as shown by Zhou et al. (2010). But for adequate biomass calculations size measurements are needed. Usually, mean values of size or biomass of species are taken from the literature, temporal surveys or growth functions in hypothetical models (Huntley et al., 2006; Baird and Suthers, 2007), because size measurements under the microscope are very slow and imprecise. Yet, actual size of organisms may have changed for plankton under warmer temperature scenarios or during different seasons. In that case using literature mean sizes could not be appropriate anymore. That is why size is a critical component of zooplankton dynamics, but has been largely disregarded until now.

Going further, Everett et al. (2017) summarised the discrepancy between zooplankton model results and field samples. They highlighted the necessity of continuous data for modelling and the immense datasets, which are already available. But also, they underlined the differences in what is needed and what is available regarding zooplankton size and biomass data. Yet, with the rise of optical sensors like VPR and ZooScan measuring size has become much easier and more applicable. It provides new opportunities to look at size distributions of plankton at wider temporal and spatial scales. Due to the links to physiological functions (Peters, 1983; Moore and Folt, 1993), growth and predator-prey relations (Woodward et al., 2005), size has also been used in ecosystem modelling and state analysis. Using normalised biomass size spectrum theory (NBSS; Sheldon, 1972; Platt and Denman, 1977) Zhou et al. (2010) have modelled all trophic levels with simple size (as biomass) and abundance inputs. Mean sizes and mean trophic levels have also been used in fisheries management research (Jennings et al., 2002). It shows the importance of size in an ecosystem, yet the relationship between size and biodiversity as an ecosystem state measurement has not been assessed. Considering the importance of zooplankton as the central trophic link in temperate marine ecosystems, improving the knowledge of zooplankton biodiversity can greatly inform managers about changes in the environmental status. It is therefore one of the questions of this thesis, whether the biodiversity of zooplankton can be improved by size structure measurements to extract new ideas about potential indicators of good environmental status.

4.6 Objectives and scope of the thesis

The objectives of this thesis were to (I) establish a new zooplankton time series based on samples of the International Herring Larvae Survey, (II) find potential zooplankton trends and their drivers as well as ecological shifts associated to these and (III) find a relation between zooplankton size and abundance and Downs herring larvae survival. In addition to the first three objectives I also aimed at (IV) finding a biodiversity indicator based on size, which could identify shifts in ecosystem status. Using modelled and *in situ* data of environmental drivers, spatially explicit abundance data and new methodological approaches the bottom-up relations of the lower trophic levels in the southern North Sea and east English Channel during winter were hypothesised.

In chapter I the goal was to find trends in zooplankton size, abundance and diversity and link these trends to environmental conditions present in this dynamic region. To accomplish that I examined zooplankton in winter when the Downs herring larvae have hatched and are transported through the study region. For this study zooplankton samples from 1987 to 2014 were scanned and analysed. Due to the previous research articles, which found changes in the North Sea ecosystem linked to climate change, it was expected to see them in winter zooplankton dynamics as well. As most zooplankton research has been focussed on zooplankton abundance, an additional focus in this study was the size-based approach as the size of organisms has been linked to changes in environmental conditions such as temperature.

The aim of chapter II was to relate the herring larvae survival of the Downs compartment of the North Sea autumn spawning herring to the zooplankton dynamics found in chapter I. The hypothesis was that zooplankton abundance, but also size, had an influence on the survival of herring larvae. A prey-size to predator feeding range mismatch could lower the chance of survival despite an increase in prey abundance. Abundances and sizes of zooplankton and herring larvae were thus examined and evaluated based on the IHLS and IBTS0 survey data.

To apply the complex interrelations between abiotic factors, zooplankton and fish larvae in ecosystem management there is a need for effective indicators. In chapter III size diversity of zooplankton was used as a possible substitute for zooplankton biodiversity. Recent advances in optical technology made it easier to measure size instead of taxonomic detail. The use of size also has several advantages over taxonomic detail, for example in that it can be related to size-based ecosystem models, and can be used in an automatized fashion to permanently monitor zooplankton dynamics. It was hypothesised that size diversity during winter related well to taxonomic diversity and would show the same trends in space and time as taxonomic diversity. Therefore size diversity could be used as an alternative or additional component of biodiversity as a principal indicator of good environmental status.

5. Chapter I

Winter zooplankton dynamics in the English Channel: trends and drivers from 1991 to 2013

5.1 Abstract

Due to low light intensities and decreased temperatures winter has long been regarded as a period of minor importance in marine zooplankton ecology with static, low concentrations and growth rates of organisms. However, rising water temperatures and the importance of fish larvae survival during winter make zooplankton ecology in this period more relevant nowadays and there is growing evidence that winter conditions influence spring bloom strength. We therefore established a new winter zooplankton time series based on the International Herring Larvae Survey, which has sampled the east English Channel since 1988. Four separate areas of the study region were identified with different congregations of zooplankton. In all areas zooplankton size decreased whilst total zooplankton abundance increased, reaching its maximum in 2011. Zooplankton abundance dynamics were mainly related to temperature, chlorophyll *a* concentration and North Atlantic Oscillation index. Depth and Atlantic water inflow strongly influenced zooplankton size. Increased chlorophyll *a* concentration and high abundances of smaller copepods indicated bottom-up controlled secondary production since 2010 and a possible winter bloom in 2011 in the North East of the study area. Although early herring larvae abundance was independent of zooplankton and environmental drivers our findings can help parameterise ecosystem models for larval survival.

5.2 Introduction

European marine ecosystems have experienced several changes and shifts in the past decades (Alheit et al., 2005; Weijerman et al., 2005; Conversi et al., 2010). Owing to high fishing efforts and increasing water temperatures the North Sea has seen an increase in environmental pressures from both ends of the food chain (Baudron et al., 2014). This led to further research investigating the reasons and impacts of the changes in North Sea ecology (Beaugrand, 2003) indicating that zooplankton composition and abundance were main bottom-up drivers of ecosystem dynamics (Reid et al., 2003). In the North Sea, trends in zooplankton dynamics could mainly be attributed to increased Atlantic water inflow and temperature change (Heath et al., 1991; Becker and Pauly, 1996). One of the two gateways for Atlantic water into the North Sea is the English Channel. The warmer, more saline Atlantic water is, depending on wind conditions and residual tidal currents, pushed northwards through the English Channel into the Southern Bight of the North Sea at varying degrees. Especially during winter, when the temperature difference between the cold North Sea and warm Atlantic water is largest, the influence of the water exchange may have the largest ecological impact on the transition area. Yet, the effects of the winter conditions on the most likely biological respondents, the phyto- and zooplankton, have not been investigated.

The zooplankton community in this area consists of generalists, warm-water adapted, lusitanian species from the Bay of Biscay, where the English Channel forms the Northern distribution margin, and cold-water adapted boreal species from the North Sea, where this region forms the southern distribution margin. As a transitional zone between the North Atlantic and the North Sea with its hourglass shape and strong tidal mixing, the hydrographic conditions in this area are very dynamic. Local processes may furthermore be masked by strong, wind-induced inflow events. Using Continuous Plankton Recorder (CPR) data Alvarez-Fernandez et al. (2012) threw some light into this dynamic region and showed the occurrence of ecological shifts in the 1980s and 1990s. The obtained results were consistent with the only two other time series in this region, Plymouth (L4; United Kingdom; John et al., 2001) and Gravelines (France; Le Fevre-Lehoerff et al., 1995). Coinciding changes in zooplankton dynamics can also be found in the time series of Stonehaven (United Kingdom; Valdés et al., 2005), Dove (United Kingdom; Clark et al., 2001c) and Helgoland (Germany; Boersma et al., 2015) in the North Sea. Yet, these time series serve either the purpose of local monitoring (fixed station) or spatial coverage (CPR). It is, however, the only available data set on zooplankton dynamics during winter conditions. That is why the data itself is often used to tune and evaluate ecosystem models with a zooplankton component (Broekhuizen et al., 1995; Lewis et al., 2006). These models usually start in winter and need the data as start estimates. While the data provides insights into zooplankton composition, abundance and seasonal trends it can be assumed that the use of fixed point data or fixed depth data for ecosystem modelling is limited due to the amplification of sampling bias effects (as discussed in de Mora et al., 2013). Only permanent larger scale surveys can overcome this problem. Unfortunately, these usually exist only for a short time span due to a lack of permanent funding and are therefore embedded in different projects (e.g. GLOBEC, Kühn et al., 2008). It is hence most desirable to make the best use of existing surveys or to reanalyse existing data and to use stored samples from long established surveys to get a better and holistic picture of zooplankton dynamics.

Most ecosystem models use existing datasets of zooplankton to validate and tune their parameters and functions. Quite often winter conditions are not considered and modelled zooplankton starts each year in January with the same low concentration and only evolves – bottom up driven - from the phytoplankton dynamics in the respective year. However, the zooplankton data on which the models rely on are mainly collected in spring and summer or represent fixed point data. Hence the starting bulk of zooplankton is estimated so that the model predictions fit with the field data collected in summer. In the case of the North Sea ecosystem models the eastern English Channel is a boundary region where parameterisation is difficult and deviance is high (Girardin et al., 2016). Like the rest of the North Sea, temperature has risen in this area over the past decade (ICES, 2013). Experimental and field studies suggested that temperature affects growth and size of zooplankton (Leandro et al., 2006), but ecosystem models - with few exceptions (Baird and Suthers, 2007; Stock et al., 2008) - estimate total zooplankton biomass while size of zooplankton has rarely been implemented. This is not only a shortcoming of the models, but mainly based in the fact that field surveys also neglect zooplankton size. Hence individual zooplankton sizes from surveys in relation to environmental pressures have not been investigated so far.

In this study, we supply a spatially resolved time series of winter zooplankton abundance and size in the eastern English Channel and Southern Bight from 1991 to 2013. The aim of our analysis was to investigate whether zooplankton abundance and size have changed over time and whether this change was different between regions. We further wanted to identify if environmental pressures such as temperature, caused these changes. It was possible to investigate the zooplankton dynamics in this region with respect to location, environmental drivers and herring larvae abundance. We analysed trends in zooplankton size and abundance in relation to temperature, salinity, phytoplankton concentration, depth, Atlantic water inflow and North Atlantic Oscillation index using stored, but so far unanalysed samples and the ZooScan optical device. We identified four spatial zones in all of which general size and biodiversity were decreasing while abundance of zooplankton, especially of small copepods, increased. A maximum in zooplankton abundance and a minimum in zooplankton size was determined for winter 2010/2011, in which the data suggested conditions that resembled a winter plankton bloom. Our statistical models found both large and small scale environmental drivers to be affecting zooplankton dynamics. Herring larvae abundance seemed to be unrelated to any variables used in this analysis. The analysis will help parameterise starting conditions for North Sea ecosystem models and help accounting for winter bloom conditions if certain thresholds are surpassed.

5.3 Material and Methods

5.3.1 International Herring Larvae Survey

Zooplankton was sampled contemporaneously with the International Herring Larvae Survey (IHLS), which started under the administration of the International Council for the Exploration of the Seas (ICES) in 1967. The four areas covering the spawning areas of North Sea autumn spawning herring, Orkney-Shetlands, Buchan, Banks and Downs, were sampled on a regular grid between September and January. Only the German samples collected each January from 1991 onwards in the Downs part of the region (ICES areas IVc and VIId between latitudes 49.5°N and 53.5°N and longitudes 2°W and 5°E) were analysed. In contrast to samples from some of the other spawning areas these were stored for further analysis. As displayed in Fig. 5 zooplankton was sampled on stations roughly 10 nautical miles apart using a modified Gulf III sampler (“Nackthai”) with 280 - 330 µm mesh size (Bridger, 1958; 280 µm were only used until 1995). The device was towed in an oblique fashion at 5 knots for approximately three to ten minutes depending on water depth. Samples were preserved in 4% formaldehyde – fresh water solution. A summary of the survey’s history and application is described in Gröger and Schnack (1999). The number of stations covered by the surveys varied from 20 to over 100 depending on weather conditions.

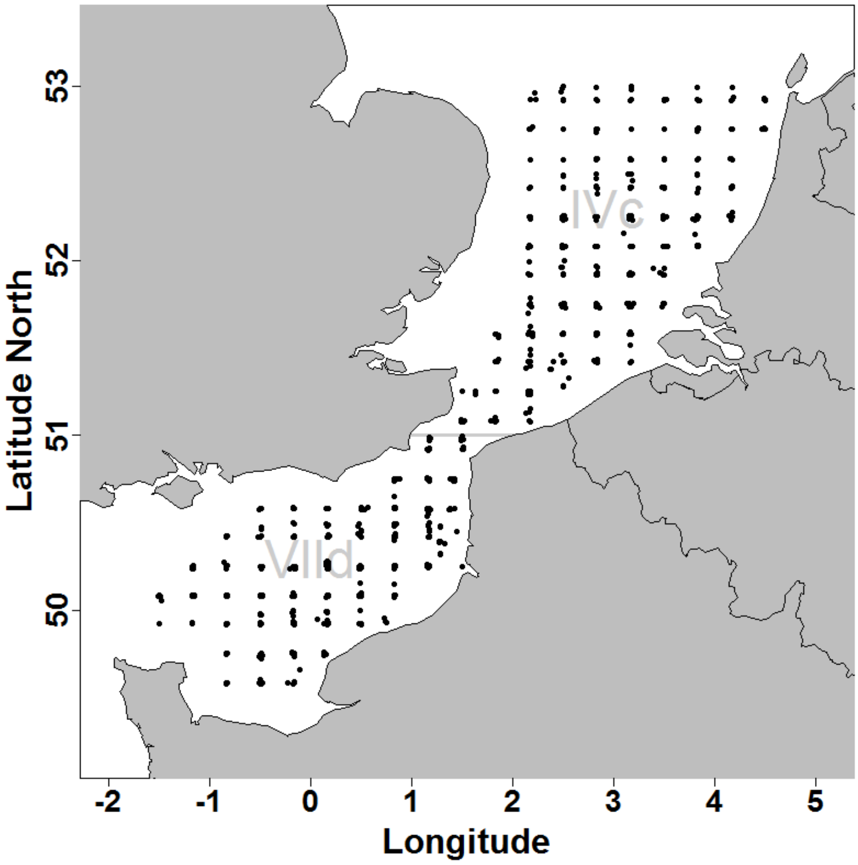

Fig. 5. Map of the English Channel showing the location of all 968 stations used for the time series analysis.

Sampling took place throughout the day roughly every hour. The oblique hauls filtered the entire water column and thus vertical zooplankton migration and the time of sampling should not have an effect on the net contents. Except for 2009 (20 stations) 50 stations were randomly selected each year for our analysis. Unfortunately, samples for the years 1993, 1996 and 2008 were missing altogether making it a 20 year time series between 1991 and 2013 with a total of 968 stations.

5.3.2 Sample processing and ZooScan Analysis

In order to remove part of the error by different net mesh sizes, samples were filtered with a 330 µm gaze, formaldehyde was flushed off with fresh water and the sample content split into analysable fractions using the Motoda method (Motoda, 1959). To reach a number of particles suitable for scanning (Gorsky et al., 2010) usually less than five splits were necessary (1/32). We used a ZooScan device (Gorsky *et al.*, 2010; version 2) with a 2400 dpi resolution to take images of the whole subsample. Scanning and automatic plankton identification was done by ImageJ software (version 1.41o) with ZooProcess (version 7.19) and Plankton Identifier software (Gasparini and Antajan, 2013; version 1.3.4). Yet, automatic classification of plankton had its limits. As summarised by Vandromme et al. (2012), automatic classification may be biased due to contamination, i.e. copepod-shaped debris classified as a copepod. Because of the turbulent waters in the English Channel during winter, removing debris and contamination was one focus of our method development. Prior to deciding which stations to analyse we excluded all stations with a debris fraction higher than 20% as these may have clogged the net and influenced its catchability. Further, three steps were applied to reduce the occurrence of contamination: 1.) particles on the scanning tray were separated by hand, 2.) digital separation was carried out with the B/W mask function of the ZooProcess software to divide all touching objects and 3.) after classification, all particles were rechecked by eye for correct classification as the large diversity of debris shapes caused a poor performance of automatic classification (77.7 % mean success rate).

5.3.3 Environmental Data

During most cruises the “Nackthai” sampler carried a CTD sensor recording temperature and salinity. Unfortunately, a full range of CTD data were not available for 240 stations. Zooplankton displacement is often driven by hydrodynamic conditions and less by active movement. Therefore, we also wanted to include data from the months before the survey, as earlier conditions could have affected the dynamics and distribution more significantly than the instantaneously measured hydrographic conditions. In the end, to investigate possible links between zooplankton dynamics and bottom-up drivers, we decided to use reanalysed and modelled data from the Operational Ecology (OPEC) database as these were available for all areas and dates and fit the *in situ* conditions best. Plymouth Marine Laboratories’ POLCOMS-ERSEM system was used to backward-model and extract sea surface temperature, salinity and chlorophyll *a* data (Allen et al., 2001; Holt and James, 2001) for this database. The OPEC data are a rather conservative estimate with a high degree of confidence as it *in situ* data and observations are linked via a Kalman filter. The high correlation of the field data and the modelled data regarding temperature and salinity justified the use of the OPEC database as input for the abiotic variables. Further we used

Atlantic water inflow into the North Sea from the Hamburg Shelf Ocean Model (HAMSOM; Backhaus, 1985) as annual variable for water exchange.

5.3.4 General trend analyses

Due to the hour glass shape of the Channel region and as a different behaviour of estuarine and more offshore located deeper areas can be expected we divided the study area into different compartments depending on a similarity index of the samples. Every station was assigned to a grid cell using a 28 by 14 raster defined with the R package “raster” by Hijmans and van Etten (2013). Using all environmental and biological variables a cluster analysis based on Euclidean distances was applied to cluster the stations into areas. Each grid cell was assigned to the four main areas depending on the largest proportion of samples in the cell belonging to that one area. An analysis of variance (ANOVA) with Bonferroni adjustment was carried out to test for differences between areas. For the following analyses we used data within each compartment separately in case that trends and signals in the data were masked due to local processes and dynamics. To prepare for the visualisation of trends, we rescaled the data by subtracting the variable means from the annual means and divided them by the standard deviation. This standardisation procedure was used so that all variables could be used for equal scaling of anomalies in a trafficlight plot. In an effort to have a higher taxonomic resolution we further used a subset of 638 stations for the calculation of taxon specific data. These samples were separated into 14 taxa: unidentified copepods and copepodites, *Temora sp.*, *Candacia armata*, calanoid copepods, chaetognaths, malacostraca, zoea larvae, cumacea, amphipods, euphausids/mysids, cladocera, appendicularians, echinoderms and polychaets in contrast to the remaining samples where all copepods and remaining crustacean were only identified as copepods or malacostraca. Size diversity and taxonomic diversity were calculated using the Shannon-Wiener Index. For the calculation of size diversity we used size bins starting at 300 µm ESD and increasing the bin width by a ratio of 1.14 between lower and upper border of the size bin. Herring larvae abundance data were directly derived from the IHLS samples.

5.3.5 Generalised Additive Mixed Models

Before applying generalised additive models we did a pre-analysis on which ecological variables to include in the prediction. Temperature, salinity and chlorophyll *a* concentration were extracted for the months November, December and January and average values for those months were calculated. Pearson correlation index was then used to determine if a certain monthly value or the overall mean was more related to the biotic variables. By applying this procedure we avoided inflating the models explanatory power while keeping only the variables of the most relevant time period for modelling. The biotic response variables were zooplankton abundance and size. Atlantic water inflow and North Atlantic Oscillation Index (NAO) were used as annual variables.

We applied generalised additive mixed models (GAMM; Lin and Zhang, 1999) to investigate the significance of environmental variables on zooplankton abundance and size and how they were driving these. To compensate for unknown annual disturbances of unaccounted natural variation we added “year” as a random mixed effect to the model. Using the gam function provided by the “mgcv” package in R (Wood, 2006) we selected the best model by selecting only the significant variables of the model in a stepwise method. The smoothing functions were restricted to five knots to avoid overfitting and get more mechanistic relations that could be used for numerical modelling. All GAMMs were based on a Gaussian error distribution.

5.4 Results

5.4.1 The winter zooplankton time series

1.28 million particles were scanned and digitalised in total. Roughly 45% of these particles were identified as organisms and used for creating and analysing the zooplankton time series. The size spectra of 12 taxa from roughly two thirds of the samples is given in Fig. 6. Overall mean size of zooplankton caught was 699.75 µm ESD. The time series is currently available via the corresponding author and will be made available after publication.

5.4.2 Spatial clustering

Based on the composition of the clusters in a particular spatial grid cell, we could identify four spatial compartments corresponding to the cluster analysis. The resulting spatial segregation is represented in Fig. 7. It comprises of an area resembling British North Sea coast (Area 1), an area around the Belgian-Dutch coast (Area 2), which is influenced by the

Rhine-Meuse delta waters, a centre region from the French coast spreading northeast into the North Sea (Area 3) and an area of Atlantic waters at the western boundary (Area 4). Analyses of variances revealed significant differences between the areas concerning average temperature, chlorophyll *a* concentration and zooplankton size (table 1). Areas 2 and 4 were also different from the other areas regarding zooplankton abundance. The low herring larvae abundance found in area 2 was

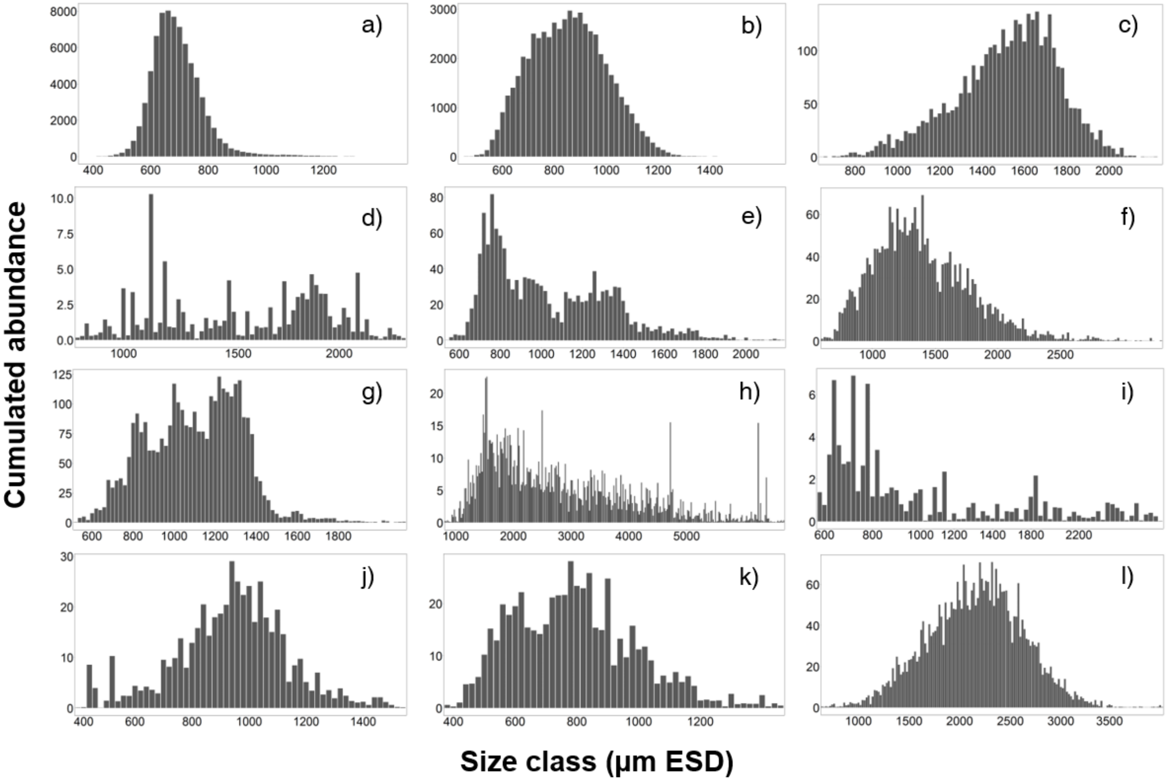

Fig. 6. Size spectrum of 12 zooplankton taxa. Cumulated abundance for each 20 µm size class for a) unidentified copepods and copepodites, b) *Temora sp.*, c) calanoid copepods, d) *Candacia armata*, e) zoea larvae, f) amphipods, g) cumaceas, h) shrimp-like zooplankton (e.g. euphausids), i) unidentified malacostracans, j) appendicularians, k) echinoderm larvae and l) chaetognaths.

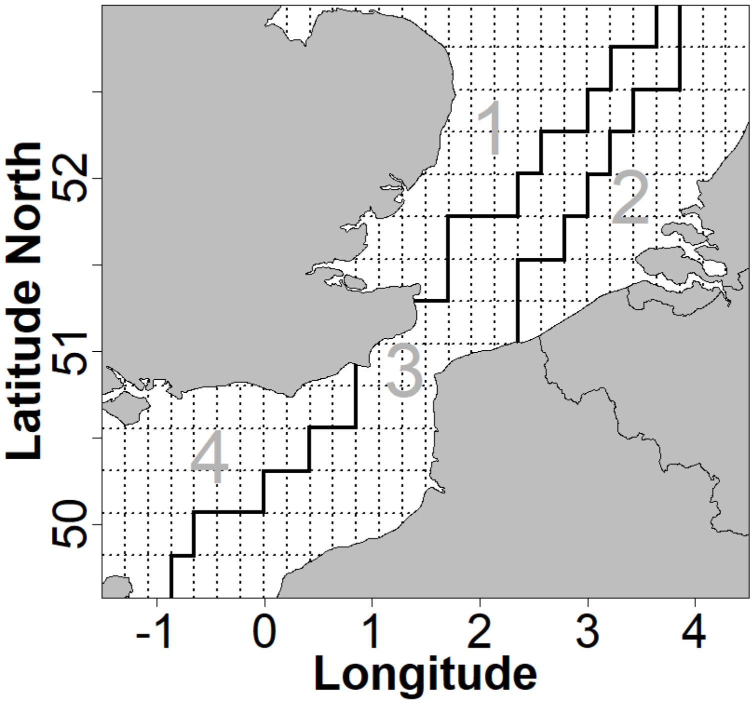

Fig. 7. Map of spatially segregated compartments as revealed by cluster analysis. Underlying raster grid and area identification number shown in grey.

significantly different from the higher abundances in area 4 ($p < 0.001$) and 3 ($p < 0.05$) while the herring larvae abundance in area 4 was significantly higher than those found in areas 1 ($p < 0.001$) and 2 ($p < 0.001$).

Area 2 (close to the Rhine-Meuse estuary) was the coldest and most chlorophyll-rich while area 4 (the most western one) was the warmest and least chlorophyll rich. These areas were also the most and least saline, respectively, but the difference was only significant between these two areas and not significant regarding areas 3 and 1. The data were split according to the regions and analysed separately to account for spatial differences in zooplankton dynamics.

5.4.3 General trends in zooplankton dynamics

We found a generally decreasing size trend as seen in Fig. 8. The reduction in size was mainly driven by a decrease in copepod size and an increase in their abundance, which made up over 90% of the zooplankton taxa found. 2010 to 2013 showed exceptionally low mean zooplankton sizes. Most other taxa, like non-copepod crustaceans, also decreased in mean

Table I. Regional ecosystem characteristics. Total means, standard deviations (SD), slopes of the temporal trends (Trend) and significance of the difference between clusters as revealed by Analysis of Variance (ANOVA) with level of confidence (* p < 0.05, ** p < 0.01, *** p < 0.001).

		Area 1	Area 2	Area 3	Area 4
Temperature	Mean	6.88	6.40	7.85	8.96
°C	SD	0.94	0.98	0.82	0.72
	Trend	0.03	0.02	0.03	0.01
	ANOVA	***	***	***	***
Salinity	Mean	33.97	32.86	34.15	34.60
psu	SD	0.41	0.77	0.33	0.20
	Trend	-0.01	-0.01	0.01	0.00
	ANOVA		***		***
Chlorophyll *a*	Mean	0.43	0.81	0.61	0.32
mg C m^{-3}	SD	0.14	0.28	0.19	0.11
	Trend	0.01	0.01	0.01	0.01
	ANOVA	***	***	***	***
Zooplankton	Mean	165.02	676.57	181.78	43.17
N m^{-3}	SD	176.51	637.09	137.16	29.89
	Trend	16.28 **	48.54 *	9.16 *	1.81
	ANOVA		***		***
Zooplankton					
Size	Mean	1012.32	829.01	956.91	1150.09
µm ESD	SD	155.82	82.65	100.73	131.92
	Trend	-16.70 ***	-7.65 **	-9.16 **	-8.17
	ANOVA	***	***	***	***
Herring Larvae	Mean	48.35	41.42	249.36	391.33
N m^{-2}	SD	122.19	62.72	342.43	694.36
	Trend	8.63 *	3.44	30.60 **	63.57 **
	ANOVA	*, not with area 2	*, not with area 1	*, not with area 4	*, not with area 3

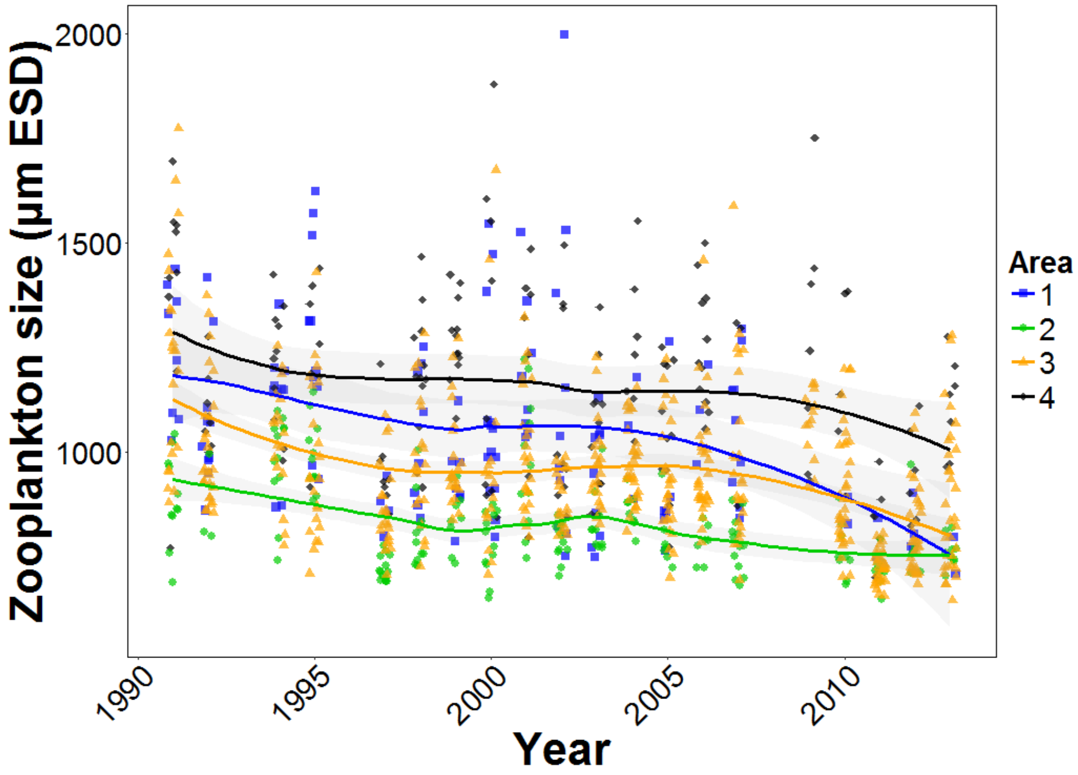

Fig. 8. Mean size of zooplankton per station as equivalent spherical diameter (ESD). Solid lines are based on Loess smoothing function with the shaded area representing the standard error.

size, which implies that it was not only a composition effect. The higher standard deviations in size for areas 1 and 4 indicate higher zooplankton diversity, which rendered the negative size trend in area 4 not significant. Yet, in both areas the mean size decreased visibly. In conjunction with the reduced size zooplankton abundance was elevated from 2010 to 2013 (Fig. 9). Before that period a comparatively lower mean abundance was observed. This decreasing size trend was correlated to the increased abundance of smaller copepods and copepodites that could not be further distinguished ($p < 0.05$).

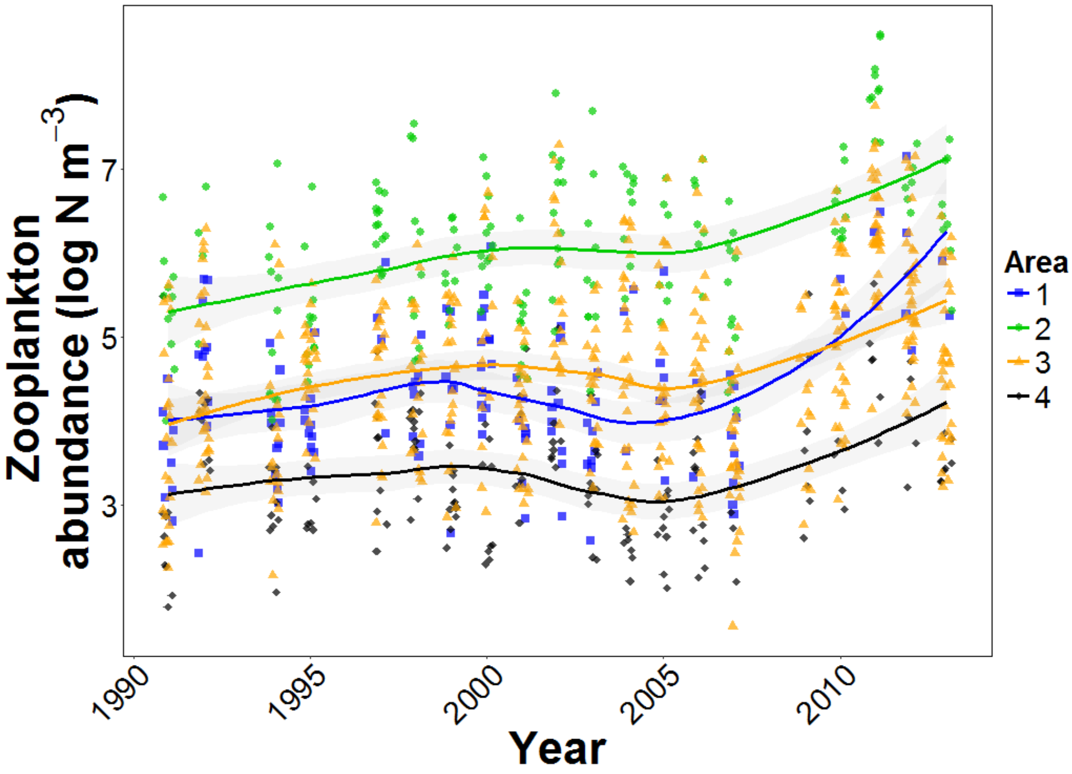

Fig. 9. Zooplankton abundance as mean number per cubic metre per station. Solid lines are based on Loess smoothing function with the shaded area representing the standard error.

We could see no spatial differences in the zooplankton dynamics other than general differences in mean size and mean abundance. In area 2 (most eastern one) zooplankton abundance was the highest while size was the lowest. Area 4, to the west, on the other hand showed the lowest abundance and largest size of zooplankton. Abundance and size in the central and northern part of the study area, areas 3 and 1 respectively, was of intermediate level, but showing the same temporal trends as the other areas. Most taxonomic groups showed a negative size vs. abundance relation with fewer, but larger individuals at the beginning of the 1990s, followed by a period of variable sizes and abundances in the 2000s and very abundant, but small zooplankton since 2011 (Fig. 10). Both size and taxonomic diversity indices also showed a declining trend. Most of the size related and environmental data declined in this area. Abundance indicators, however, have increased over time.

Considerable variability was evident for all variables. For example, temperature increased, but very cold winters like 1996/1997 deemed the trend insignificant over the considered period. Chlorophyll *a* concentration was only very high since 2010. Mean salinity varied only slightly and remained on a comparatively high level between 1994 and 2010.

5.4.4 Drivers of change

Despite unusually high chlorophyll *a* concentrations in the entire study area since 2011 and a slow warming of the water there was no significant linear trend in winter chlorophyll *a* concentration, temperature and salinity over the 20 year time period. The correlation analysis revealed that the mean value between November, December and January had a higher explanatory power than any specific month. Hence, these were used for the GAMM analysis. The very cold winter of 1997 and high interannual variance asked for non-linear methods such as GAMMs to be used for the identification of potential environmental drivers. The addition of year as a random effect factor improved the overall performance and the residual structure of the generalised additive models. All models resulted in including large and small-scale influences as well as depth as a spatial indicator.

The North Atlantic Oscillation Index (NAO) was included as a significant variable of abundance models in all four areas and in areas 2 and 3 of the size models. It indicates the big influence of large scale mechanisms in this region. For zooplankton size the large scale influence seemed to be better represented by Atlantic water inflow (inflow) as it appeared in every model except for area 3. Temperature and chlorophyll *a* concentration resembled the most important environmental drivers for zooplankton abundance. Especially for the regions influenced by North Sea waters, areas 1 and 2, chlorophyll *a* concentration explained most of the deviance in the data. In contrast to our expectations size was not related to temperature. Variations in chlorophyll *a* concentration significantly explained zooplankton size in the Atlantic water influenced waters, areas 3 and 4, whereas size was mainly explained by depth and inflow or NAO in areas 1 and 2.

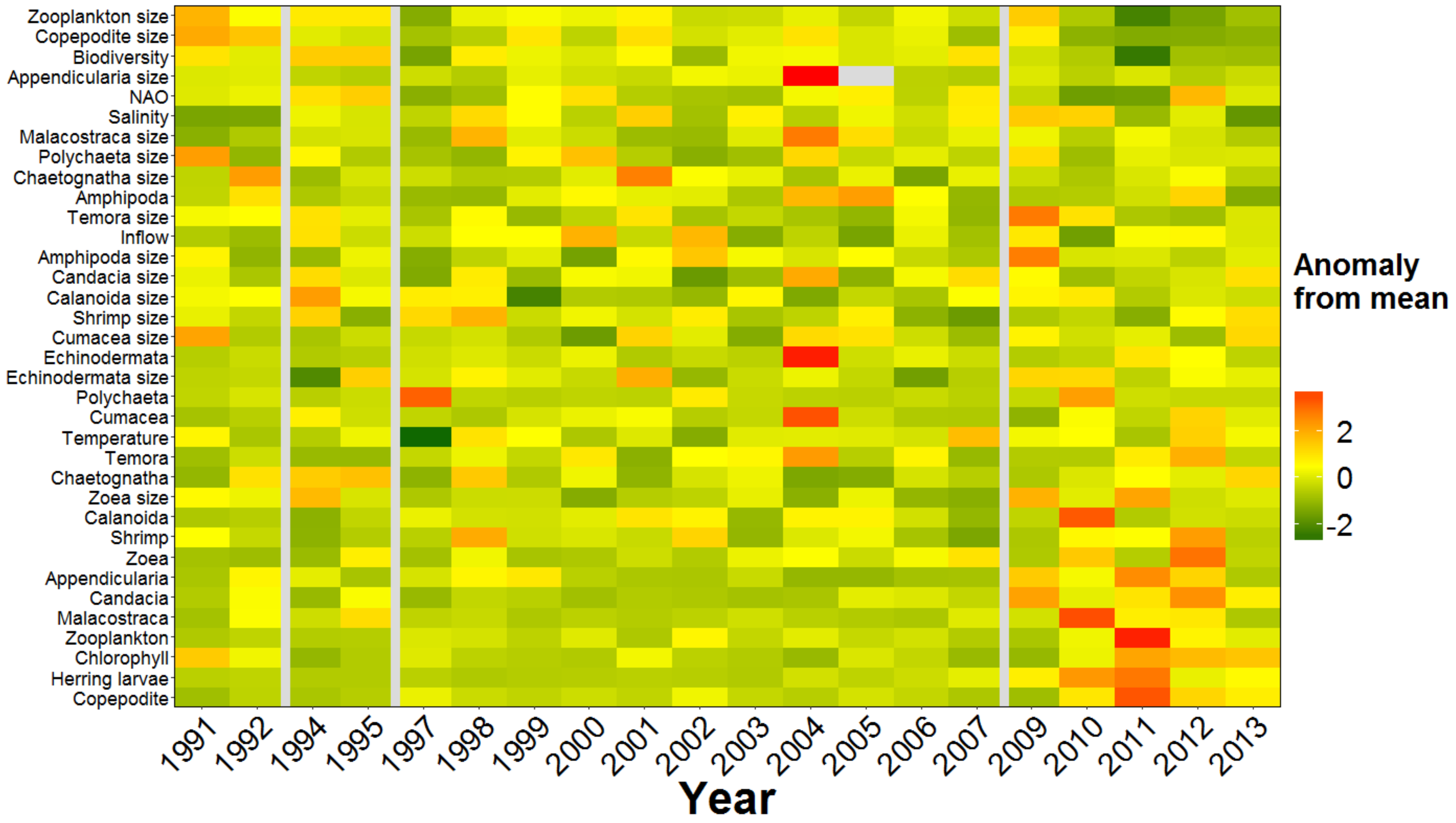

Fig. 10. Trafficlight plot with all environmental and biological variables considered in the analysis. Missing years 1993, 1996 and 2008 are marked as grey vertical lines. Especially the period 2010-2013 stands out of the overall variability. Grey tiles represent missing data.

Salinity was only a significant predictor variable in area 1, where the influence of the Thames delta was visible. All in all, zooplankton abundance was influenced by local as well as large scale mechanisms. These mechanisms explained between 0.414 and 0.615 of the deviance. The GAMMs for zooplankton reached an explained deviance between 0.24 and 0.54. Temperature showed a negative influence over most of the temperature range with an almost linear decreasing effect between 6.5°C and 9°C. A positive effect was recorded at 8-9°C and below. Each area exhibited similarly shaped smoothing functions for the environmental drivers as shown in Fig. 11 a-d. Chlorophyll *a* concentration showed an increasing positive effect on zooplankton abundance after a certain threshold. This was 0.8 µg C m^{-3} in cluster 2 and 0.45 mg C m^{-3} in cluster 1. We also found this threshold-like influence of chlorophyll *a* concentration in area 4 (0.3 µg C m^{-3}) and area 3 (0.45 µg C m^{-3}), but the small number of datapoints at the positive end of the curve deemed these insignificant.The above-threshold concentrations of chlorophyll *a* occurred both at the same time and in the same area, area 2, as the elevated abundances of small copepods. It therefore suggests a bottom-up relationship resulting in a winter plankton bloom in 2011. Increasing depth was generally negatively associated with zooplankton abundance and positively with zooplankton size. The NAO index affected zooplankton abundance negatively between -1 and 2. Extreme anomalies beyond these NAO index values had a very positive effect. This was mainly due to the fact that the NAO index between 2010 and 2012 was extreme (-1.88; -1.80 and 2.25 respectively) which correlated well with the highest abundances and smallest zooplankton sizes during these years. It confirms the potentially combining effects of large and small scale influences on local zooplankton dynamics.

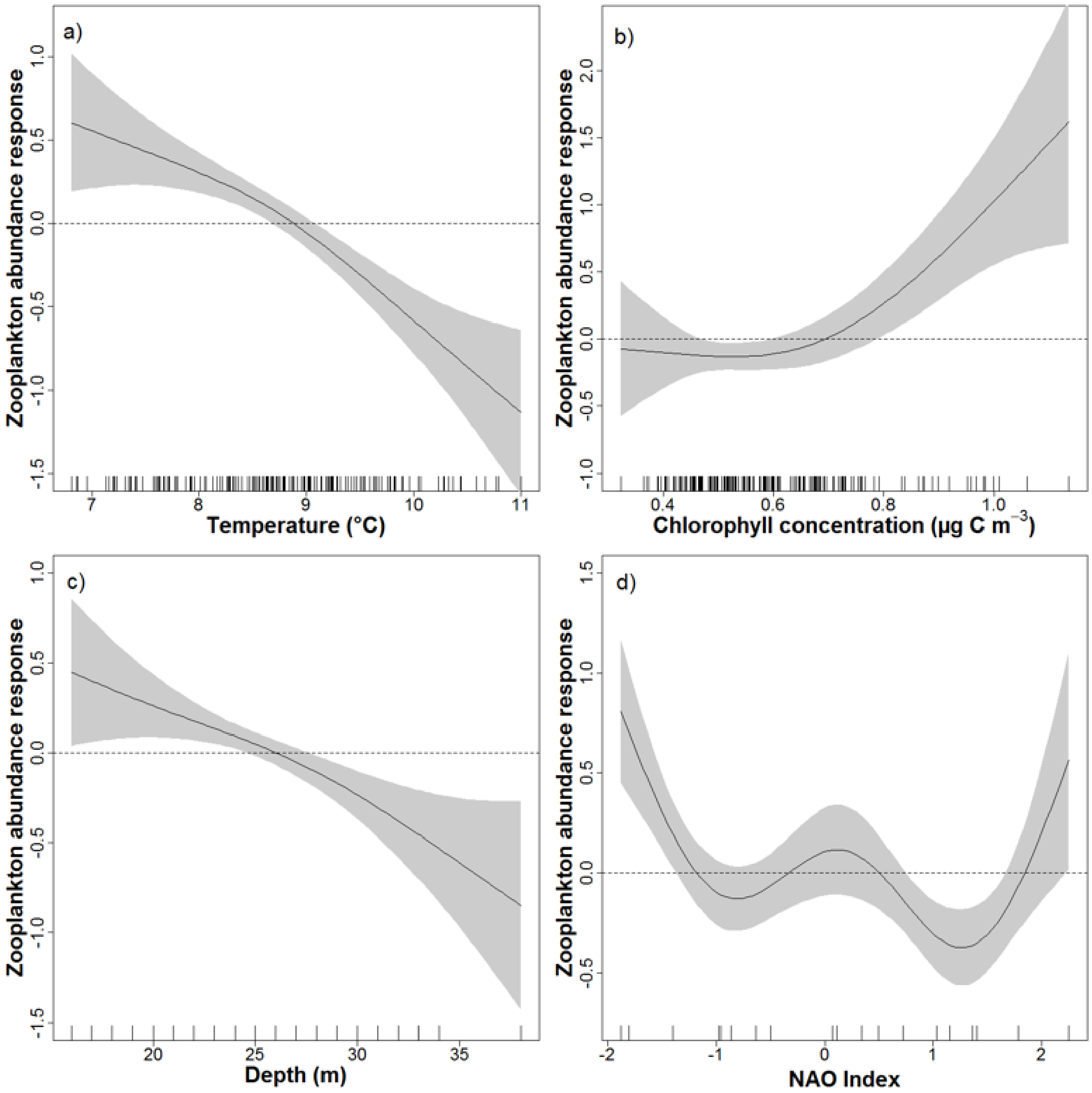

Fig. 11 a-d. Individual functions of the Generalised Additive Mixed Models representing temperature (a), chlorophyll *a* concentration (b), depth (c) and North Atlantic Oscillation Index (d) as explanatory variable for zooplankton abundance in area 2.

5.5 Discussion

In our analysis we could show that also during winter interannual variability in zooplankton dynamics occurs, although zooplankton abundance was, of course, generally low compared to annual averages reported elsewhere (3064.31 N m^{-3} at L4 station, Eloire et al., 2010;

3308.33 N m^{-3} at Gravelines 2016, Antajan et al., 2017; ICES, 2013). Zooplankton size decreased over time while zooplankton abundance increased during the study period. These trends were evident in all of the four identified areas, which enabled us to reject the hypothesis that local differences exist, e.g. through aggregation by currents, riverine inflow or through the influence of Atlantic or North Sea water. The North Atlantic Oscillation Index (NAO) and Atlantic water inflow could be identified as signals of these large scale effects. They showed a strong influence on zooplankton size. Years with a high NAO and strong inflow, such as in the year 2000, coincided with the higher abundance of larger zooplankton, whereas in 2011 higher abundances of small zooplankton coincided with low NAO and reduced inflow. This is most likely due to the shift in zooplankton composition that showed a gradient from west to east (Pitois and Fox, 2006) and varied during recent decades (Alvarez et al., 2012). High NAO and a strong inflow from the Atlantic into the North Sea will drive more of the larger western individuals into the English Channel and southern North Sea, raising the average size of zooplankton. This is reflected in our study by the zooplankton size in the different spatial clusters. Area 2 off the Dutch and Belgian coasts contained most of the small-to-medium sized copepods while area 4, the most western part of the study region, contained comparatively more quantities of larger calanoid copepods as well as individuals of *Candacia armata*. The difference in copepod regimes was also reflected by the size diversity and taxonomic diversity, which were highest in area 4 and lowest in area 2. Nevertheless, the generally decreasing size trend could be attributed to rising water temperatures. Halsband and Hirche (2001) found a negative correlation between temperature and size of individuals of *Temora longicornis* in the North Sea. These cold-water-adapted species made up a majority of the copepods in the samples and our results support the findings that a rise in temperature negatively effects copepod size, although these signals may be masked by composition changes.

In contrast to zooplankton size, the increasing trend in zooplankton abundance was mainly a response to slightly rising water temperatures and higher concentrations of chlorophyll *a*. Food limitation is a common reason for the delay of secondary production in many zooplankters (Durbin et al., 2003). An increase in temperature with a simultaneous increase in food supply may thus trigger the hatch and survival of copepod nauplii and copepodites, starting an early food chain in winter and leading to higher abundances of zooplankton. While this causality holds true for much of the time series chlorophyll *a* levels were comparatively high in 2011 despite low water temperatures, leading to an even greater abundance of zooplankton. This has already been documented in the Gulf of Maine, where a winter plankton bloom occurred in 1999 that lead to an increase of zooplankton (Durbin et al., 2003). In fact, the elevated chlorophyll *a* concentration and very high abundance of small copepods in area 2 of our study region indicate that these conditions also lead to a winter bloom in early 2011. Phytoplankton and zooplankton data at Gravelines station in the same area support these findings (ICES, 2013). Durbin et al. argued that the cold, less saline shelf waters helped stratify the water column, enabling phytoplankton to stay above critical depth. The occurrence of the plankton bloom mainly in area 2 near the Rhine-Oosterschelde estuary, with about 2200 m^3 s^{-1} of discharge the greatest riverine freshwater source of the North Sea (Berendsen, 2005), could suggest a similar cause in this area. McQuatters-Gollop (et al., 2007) also suggested that North Sea primary production is limited by light and low temperatures during winter. Yet, there is no documentation that the strong mixing in the eastern English Channel has been overcome by freshwater input to form a stratified water column and better light conditions for phytoplankton. Although the salinity was significantly lower in area 2 than in the other areas, the salinity had no significant impact on the explanatory power of the generalised additive model in this area. So despite other studies where colder conditions had beneficial effects on phytoplankton biomass (Keller et al., 1999) more *in situ* data is needed to identify the drivers of the phytoplankton bloom during winter. Considering the abundance of zooplankton it is possible that the combination of lower energy demand due to lower temperatures and higher energy supply in form of phytoplankton could have resulted in enhanced zooplankton growth in area 2 compared to higher temperature conditions. In warmer area 4, zooplankton growth may be food limited while in the other areas it was not. The generally larger zooplankton in the warmer areas 3 and 4 would also require even more energy to survive, further increasing the need for food under warmer conditions (Gillooly et al., 2001). Higher food concentrations in the other areas may thus support a rise in temperature and lead to enhanced zooplankton growth and development during future winters.

Although we observed general trends occurring in all areas we also found local differences in scale in hydrographical conditions, which justified the separation of the study region into four areas. Waters from the English Channel are well mixed during winter and pushed back and forth by tidal currents, which explained the lower explanatory power of the models in areas 3 and 4. The northernmost study area, area 1, is almost exclusively influenced by waters from inside the North Sea and zooplankton is transported counter-clockwise through area 2 and then back into the North Sea. Environmental conditions in these regions are more stable compared to the western ones. The higher explanatory power of the models for these areas supports this. It also explains why the high abundances of area 2 did not spill over to area 1 as the direction of advection is opposite way. Depending on inflow and wind conditions the four areas can be connected to varying degrees, which needs to be taken into account for zooplankton modelling purposes.

The numbers of herring larvae caught on the survey were independent of both environmental and biological variables. Our study suggests that the missing correlation may be rooted in the spatially separated congregations of herring larvae and zooplankton. Highest abundances of zooplankton were recorded in area 2 whilst herring larvae were largely located in area 4 and the western part of area 3. The majority of herring larvae caught was less than 16 mm in size and mostly fed on plankton smaller than 500 µm ESD (Hufnagl and Peck, 2011), which is the effective size the modified Gulf III net catches. Hence, it can be excluded that herring larvae had a direct predatory effect on the analysed zooplankton in areas 3 and 4. What the effect of the grown herring larvae will be when they have been transported by the currents to area 2 where large quantities of small prey are located cannot be examined here and will require more studies on samples taken later in the season. The identified chlorophyll *a* - zooplankton relation suggested potential secondary production if certain thresholds are overcome as shown by the generalised additive mixed models (Fig. 11b). When the growing herring larvae reach area 2 and the zooplankton standing stock found there the predator - prey connection could provide more details on herring larvae survival. In this case it would be necessary to sample zooplankton and herring larvae between after the IBTS0 survey (International Bottom Trawl Survey for 0-ringer herring). The IBTS0 collects herring larvae in February and is used to estimate the survival of the larger herring larvae from the northern spawning components of the North Sea autumn spawning herring, but the smaller Downs larvae are usually excluded from the analyses. Sampling of Downs herring larvae in March or April is thus needed to estimate the Downs larvae survival and compare the dynamics in respect to zooplankton abundance and size. Recent analyses conclude that the Downs proportion of herring larvae increased and a coherent analysis of the reasons behind the shift in larvae stock composition is needed

(Fässler et al., 2011). Providing confirmation on whether the secondary production goes on and thus supplies the local zooplankton stock despite zooplankton having been carried away by currents may thus explain the enhanced survival of the Downs herring larvae.

6. Chapter II

Changes in herring recruitment related to bottom-up forces in winter: Evidence from 1991 to 2013

6.1 Abstract

The autumn spawning stock of North Sea herring has suffered poor recruitment during the 2000s. Despite relatively high spawning stock biomass recruitment has only recently shown signs of improvement. In contrast to other spawning components the Downs part of this stock has gained in importance since 2002. We investigated the reason behind this increase, especially at the end of the 2000s, from a bottom-up perspective of the food web. Larval indices showed a strong correlation with chlorophyll, zooplankton size and abundance as well as the initial number of herring larvae in the English Channel and Southern Bight region of the North Sea. High abundances of small zooplankton and phytoplankton were available off the Rhine-Meuse delta and coincided temporally with larger numbers of herring larvae in the late larvae surveys. Principal component analysis revealed that temperature and North Atlantic Oscillation exhibited minor influences on herring larvae abundances compared to lower trophic level factors. Our findings suggest bottom-up controlled processes affect the survival of Downs herring larvae and small-scale processes are more important than previously assumed.

6.2 Introduction

The North Sea autumn spawning herring stock (NSAS) is one of the most important and well-known fish stocks in the world. It consists of four spawning components along the British coastline: the Orkney-Shetland, the Buchan, the Banks and the Downs spawning components. The spawning window starts in August around Orkney-Shetland and is shifted later in time the further south the spawning ground is located (Fig. 12). The latest of the NSAS herring spawn between November to January in the Downs region in the English Channel. Considering these different spawning locations and times, field surveys have been carried out on the different spawning grounds since 1972 (Gröger et al., 2001) with the aim of monitoring stock development and recruitment strength. For a more accurate assessment and prediction of the NSAS, the International Council for the Exploration of the Seas (ICES) has adopted an approach by Payne (2010), in which the recruitment composition, based on the four spawning areas, is estimated. Including the level, composition and origin of recruitment has shown to improve the detail of the assessment of the NSAS (ICES, 2014). Furthermore, it has illustrated that the early life history of fish is a variable, but important component of fish stock assessment.

Over the past two decades the NSAS has undergone considerable change. The stock declined in the early 1990s to 0.9 x 10^6 tonnes, but recovered back to over 1x 10^6 tonnes in 1997 and to over 2.5x 10^6 tonnes in 2002 (ICES Advice on North Sea herring, 2015). In 2002, a strong recruitment year was evident, but despite a growing stock biomass, recruitment declined and remained at a low level after that (Payne et al., 2009). Only recently, in 2013, recruitment increased, but declined again in 2015. Several studies focused on the reasons for the poor recruitment during the 2000s (ICES, 2007) and a link between the North Atlantic Oscillation Index (NAO) and Atlantic Multidecadal Oscillation (AMO) was found (Gröger et al., 2010). Yet, it is the Downs component that has increased rather steadily during the 2000s and even more so since 2010 (ICES, 2014). Gröger et al. (2010) decisively used the large scale NAO and AMO to avoid local collinearities and intrinsic noise. But the reasons for the distinct increase in importance of the Downs component may be found in these local phenomena, which would explain the different trends of the other components, despite the same influence of both NAO and AMO. A change in phytoplankton abundance or zooplankton composition could be one of the ecological reasons for the increased survival and new dominance of the Downs component (Alvarez-Fernandez et al., 2012). However, there is considerable lack of data in this region in winter, making it difficult to integrate local phenomena and larger scale conditions and link them to multiple trophic levels (Girardin et al., 2016). This has so far hindered a detailed analysis of bottom-up factors and their influence on herring recruitment.

In this study, we investigate the abundance of herring larvae from the Downs component in relation to environmental conditions in the English Channel and the southern North Sea. We combined data from the International Herring Larvae Survey in January and from the International Bottom Trawl Survey in February and March with modelled abiotic data and *in* *situ* plankton samples taken in the same area and during the same season. We related the survival of the Downs herring larvae to bottom-up controls of the ecosystem and compare the potential difference to the other spawning components.

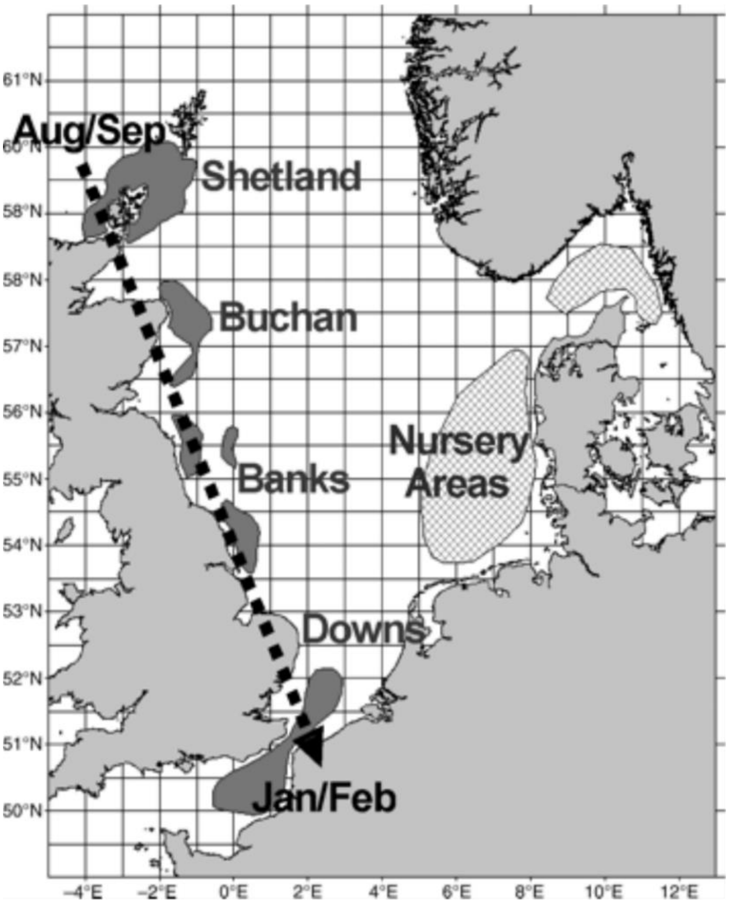

Fig. 12. Spawning areas and timing of North Sea autumn spawning herring stock (Gröger et al., 2010).

6.3 Material and Methods

6.3.1 International Herring Larvae Survey

Herring larvae were sampled on the International Herring Larvae Survey (IHLS). The survey covers the four NSAS spawning grounds Orkney-Shetlands, Buchan, Banks and Downs, between September and January. Only the German samples collected during the first half of each January from 1991 onwards in the Downs part of the region (ICES areas IVc and VIId between latitudes 49.5°N and 53.5°N and longitudes 2°W and 5°E) were available for analysis. Survey stations were approximately 10 nautical miles apart. A modified Gulf III sampler (“Nackthai”) with 280 - 330 µm mesh size (Bridger, 1958; 280 µm were only used until 1995) was towed in an oblique fashion at five knots for approximately three to ten minutes depending on water depth. Samples were preserved in 4% formaldehyde - fresh water solution. A summary of the survey's history and application is described in Gröger and Schnack (1999).

6.3.2 IBTS0 survey

Starting in February each year the International Bottom Trawl Survey (IBTS) has been carried out across the North Sea, including the NSAS herring nursery grounds. After sunset, herring larvae are caught using a Methot Isaacs-Kidd trawl net (MIK) with 2 m diameter and 1000 µm mesh size. The MIK is towed in the same way as the "Nackthai". The so-called IBTS0 survey has so far mainly been used to estimate the surviving herring larvae from the three more northern spawning grounds and to calculate the spawning component abundance index (SCAI), which is used to assess recruitment and spawning stock biomass. For the assessment, herring larvae are binned in 1 mm length intervals and counted. For the recruitment assessment, the Downs component is left out by assuming that all larvae less than 20 mm in length originated from that spawning ground. These smaller larvae are excluded from the recruitment-stock assessment despite ongoing debates about its usefulness (ICES, 2014). For the analyses we derived the Downs herring component by taking the abundance of all larvae below 20 mm length. All others were assumed to belong to the Orkney-Shetland, Buchan and Banks components (OSBB). Furthermore, we derived overall recruitment and the spawning component abundance index (SCAI) from the ICES herring assessment working group (ICES, 2014).

6.3.3 Zooplankton Analysis

Zooplankton data were derived from the same samples as for the collection of herring larvae. The samples were flushed with freshwater over a 330 µm sieve and then split until the number of organisms was suitable for scanning using the Motoda method (Gorsky et al., 2010; Motoda, 1959). The smallest fraction was 1/32. We used a ZooScan device (Gorsky et al., 2010; version 2) with a 2400 dpi resolution to analyse the zooplankton samples. Generally, we followed the same protocol as described by Schultes and Lopes (2009). Due to time constraints and debris contamination 50 samples with less than 20% debris were randomly chosen each year. Automatic classification of individual organisms was checked manually for highest possible accuracy. Apart from total zooplankton abundance and size, copepod and chaetognath abundance and size was also calculated.

6.3.4 *Environmental Data*

The source of environmental data was carefully evaluated. As the focus of the analysis was based on the Downs spawning component and the influence and importance of their survival, we restricted the focus area of environmental influence to the eastern English Channel and the Southern Bight. Merged satellite (e.g. SeaWiFS) and *in situ* datasets were selected from the GlobColour project (Fanton d'Andon et al., 2009; Maritorena et al., 2010), but lastly found unfit, because there were surprisingly large gaps in the spatial coverage (i.e. due to cloud cover). Temperature and salinity could be directly derived from the IHLS, but showed considerable temporal lack of data. In the end, the integrated dataset from Operational Ecology (OPEC) was used (OPEC, 2014). It applies a re-analysis of all available data using the POLCOMS-ERSEM (Allen et al., 2001; Holt and James, 2001) in combination with a Kalman filter. This integrative approach provided the most consistent temporal (1991 – 2013) and spatial data coverage for the corresponding larvae data. Sea surface temperature, salinity and chlorophyll *a* concentration (mg m^{-3}) were finally used as environmental variables.

6.3.5 *Statistical analyses*

We used a trafficlight plot to investigate general trends in all variables. For that we normalised data so that the means were 0 with a standard deviation of 1. This procedure made the different variables graphically comparable. To detect breakpoints and different ecosystem states we also applied a regime shit analysis using the changepoint package in R, using the PELT algorithm and a minimum segment length of 4 years (Killick et al., 2016). For zooplankton and IHLS larvae data, we needed to leave out the missing years and link the year before and after the gap to apply the algorithm. Therefore the breakpoints for these variables can be regarded as having a possible deviation of one year. We calculated a correlation matrix to investigate possible direct and indirect interactions between trophic levels and environmental conditions. These matrices were based on Pearson correlation coefficients. Further, we applied a principal component analysis (PCA) to all abiotic and lower trophic level variables (zooplankton abundance, zooplankton size, chaetognath abundance and chlorophyll *a* concentration) to combine the components of bottom-up control. Resulting principal components were then compared to larval herring indicators.

6.4 Results

6.4.1 Biotic and abiotic trends and points of change

The reanalysed OPEC data and IHLS temperature and salinity data were significantly correlated (ρ = 0.78, $p < 0.01$). This indicated that the OPEC dataset represents the hydrographic conditions in this region well. A summary of all analysed variables is displayed in Fig. 13. It shows the small number of herring larvae present during the 2000s and a successive increase towards the end of the last decade. Since 2008 the larval abundance of all components was higher than before 2008 while herring larvae size followed the opposite trend. The SCAI displayed a remarkably steady increase while the IBTS0 index and overall recruitment marked high anomalies at the beginning of the 1990s and between 1999 and

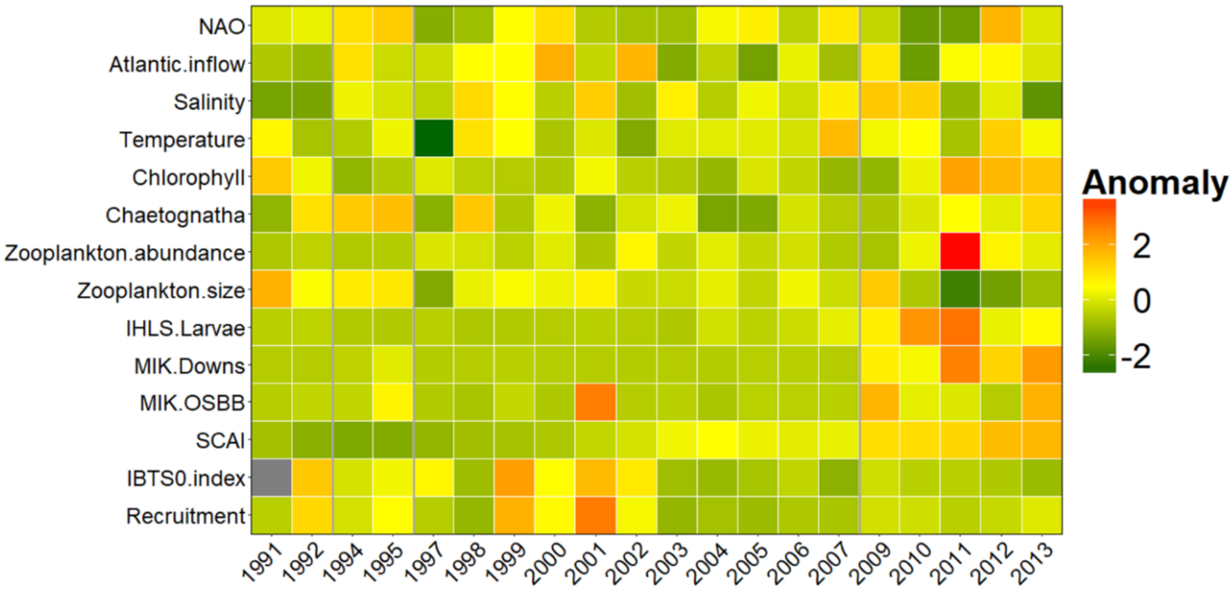

Fig. 13. Trafficlight Plot of the available variables. Colours represent the anomaly from the overall mean (normalised to 0 with a standard deviation of 1). Grey vertical lines indicate missing years of data.

2002. It is clearly visible that herring larvae were abundant again since 2008, but these did not transfer to the SCAI nor the recruitment index. Abiotic factors did not reveal such clear patterns. Temperature increased slightly over time while NAO and salinity varied from year to year. Chlorophyll *a* concentration and zooplankton abundance were elevated between 2010 and 2013, as were chaetognaths. Zooplankton size showed the opposite trend. In the end, biological parameters displayed more periodicity than abiotic parameters.

Regime shift analyses identified multiple breakpoints in herring larvae and zooplankton data. Abiotic factors such as sea surface temperature and sea surface salinity were very variable and no breakpoint could be identified. No breakpoint could also be determined for chlorophyll *a* concentration, despite relatively low variance. The upward shift in chlorophyll *a* concentration occurred in 2010 and the set minimum segment length masked a possible shift. A single breakpoint was detected for North Atlantic Oscillation and three for atlantic water inflow. Both variables varied largely over the course of the time series, but the fluctuation of the NAO remained around a lower mean level after 1995. Breakpoints in mean Atlantic inflow levels occurred in 1996, 2002 and 2007, thus roughly every 5 years. Zooplankton breakpoints were synchronised: Both abundance and size changed contrarily to each other in 1995, 2000, 2004 and 2009. Though not in parallel to Atlantic inflow, it nevertheless also resembled a 5 year cycle of change. Chaetognath abundance, however, was uncorrelated to zooplankton and showed a lower mean level between 1998 and 2009 in respect to the periods before and after. Herring recruitment and the MIK larval index (IBTS0 index) had similar breakpoints, four in total, which can be summarised as a period of medium recruitment before 1999, three years of high recruitment and a drastic decline after 2002 followed by a slight increase in 2008. The SCAI, despite three detected breakpoints, showed a constant increase with only a time of stagnation between 2002 and 2009. 2008/2009 was also the major changepoint of the larval abundances and sizes. OSBB (Orkney-Shetland-Buchan-Banks spawning component larvae) mean abundance was elevated from 2008. For the Downs larvae, this occurred a year later, both for the early and late larvae (Fig. 14, IHLS.larvae and MIK.Downs). Sizes of the late larvae, showed the opposite behaviour, a decreased level, but with the same changepoints.

6.4.2 Herring larvae and trophic relations

In Fig. 14 we could see that the recruitment indices changed after 2002. IBTS0 index and recruitment remained low while the SCAI continued increasing. Yet, the larvae abundance did not show the transition in 2002, but rather in 2008. Here, larval abundance suddenly rose and larval size dropped sharply. A similar trend was visible in the next lower trophic level: zooplankton. It also increased in abundance while shrinking in size after 2008. Going even further in the food web, chlorophyll *a* concentration peaked between 2010 and 2013. We could not see such distinctive patterns in the abiotic conditions, which fluctuated more and seemed relatively unconnected to the trends of the biotic variables. Despite rising mean water temperatures and an increase in primary production (as indicated by chlorophyll *a* concentration) they were not significantly correlated ($\rho = 0.2$, $p > 0.05$). Chlorophyll *a* did not increase steadily over the years as did temperature, but was instead only elevated between 2010 and 2013 with a peak in 2011. Both salinity and temperature showed no significant correlation with any of the examined biological variables. Atlantic water inflow did not show significant relationships with any investigated variables (zooplankton, chaetognaths, number of herring larvae, SCAI). A low, but significant negative correlation was present between the NAO and the number of herring larvae collected by the IHLS in the English Channel ($\rho = -0.46$, $p < 0.05$).

In contrast to the abiotic influences on herring larvae, we saw evidence for bottom-up controlled processes in the larvae's food chain during winter (Fig. 15). Primary production had a significant positive influence on zooplankton abundance ($\rho = 0.58$, $p < 0.01$) and the proportion of Downs larvae in the MIK surveys ($\rho = 0.69$, $p < 0.001$). The latter was also positively correlated with the abundance of herring larvae found in the English Channel in early January ($\rho = 0.75$, $p < 0.001$). Yet, chlorophyll *a* did only weakly significantly correlate with zooplankton size ($\rho = -0.48$, $p < 0.05$), but not with herring larvae size (both Downs and OSBB: $\rho < 0.3$, $p > 0.05$). Nevertheless, a positive influence of phytoplankton on higher trophic levels was observed.

Zooplankton abundance not only correlated significantly with chlorophyll *a* concentration, but also with the number of Downs herring larvae in the MIK surveys ($\rho = 0.67$, $p < 0.001$). It did not correlate with OSBB larvae however ($\rho < 0.2$, $p > 0.05$). Zooplankton abundance increased and a corresponding decrease in zooplankton size thus indicated a higher proportion of small zooplankton, especially smaller copepods and copepodite stages.

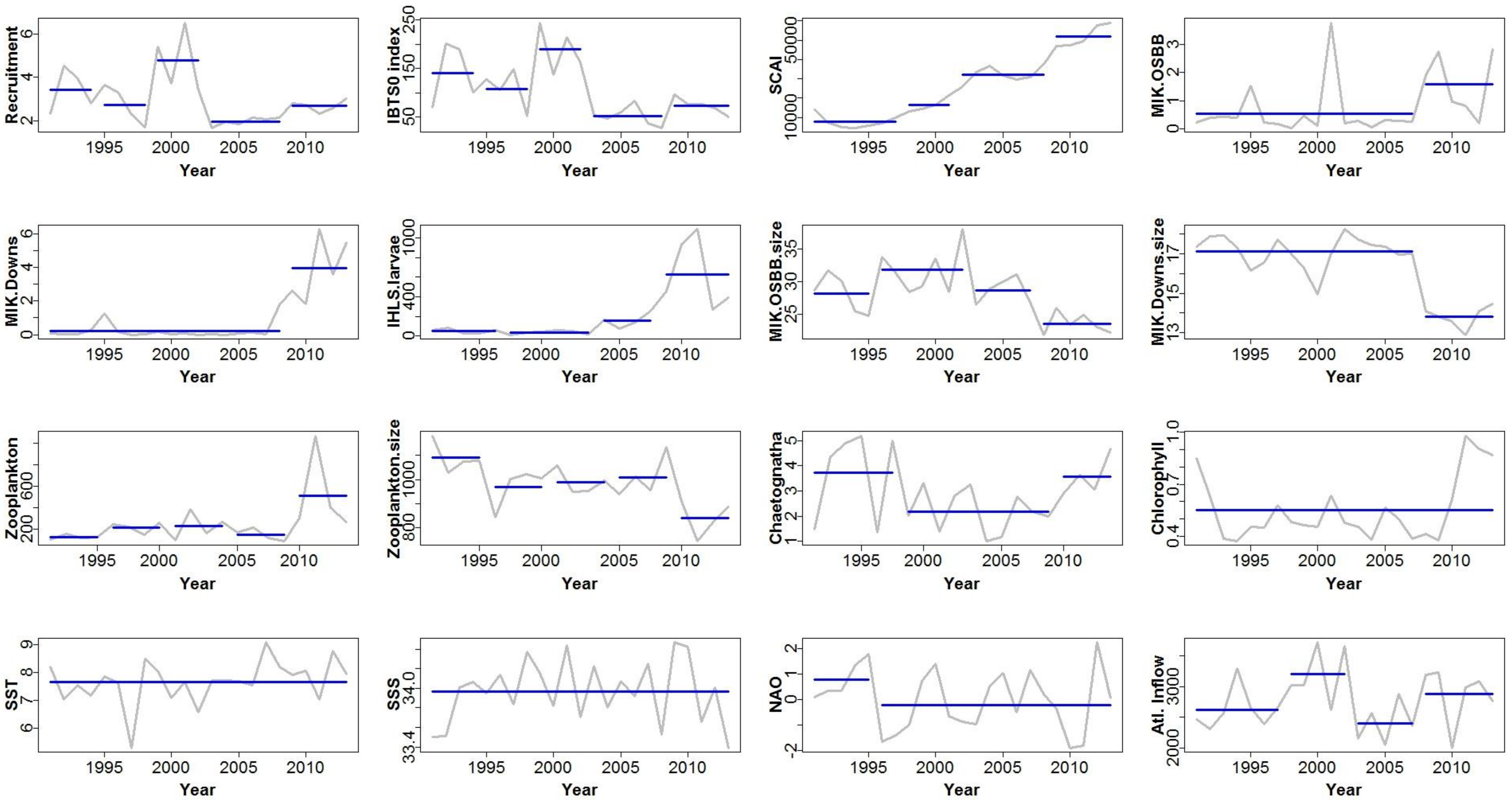

Fig. 14. Time series plots with detected breakpoints using the changepoint package in R. Note unequal x-axes for zooplankton, chaetognath and IHLS.larvae plots due to missing data (years 1993, 1996 and 2008). Recruitment, IBTS0 index, SCAI, sea surface salinity (SSS); NAO and Atlantic.inflow were dimensionless. MIK.OSBB, MIK.Downs and IHLS.larvae in larvae m^{-2}; MIK.OSBB.size and MIK.Downs.size in length in mm; Zooplankton and chaetognatha in number of organisms m^{-3}; °C Zooplankton.size in µm; Chlorophyll *a* concentration was recorded as mg m^{-3} and sea surface temperature (SST) in °C.

The smaller, abundant zooplankton in addition to increased phytoplankton abundances and greater numbers of herring larvae from the Downs establish a set of correlations that can be displayed in a network plot (Fig. 16). This network of significant correlations highlights the connections that resemble a food web starting from the primary producers. It also justifies zooplankton size as a possible connective trait that facilitates the links between nodes.

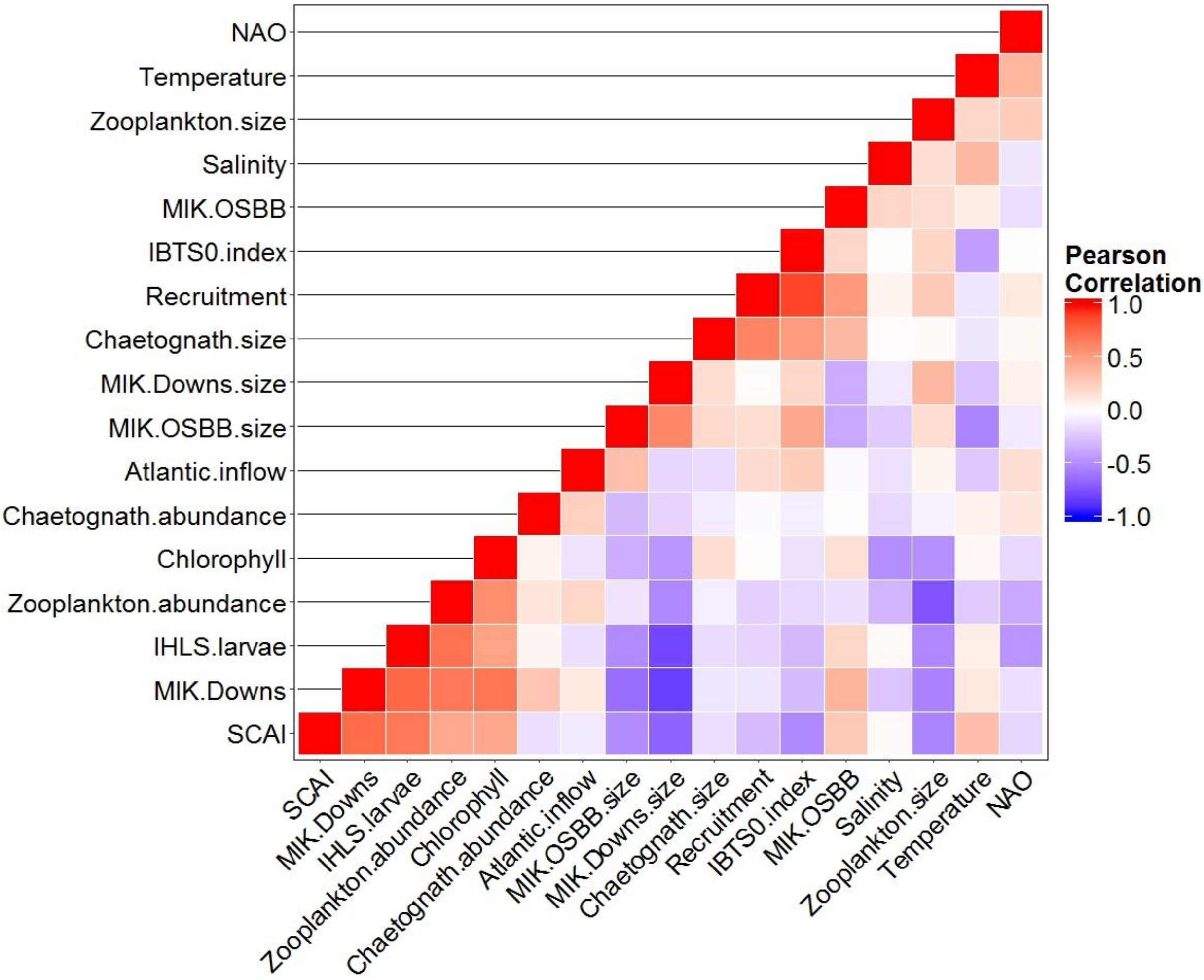

Fig. 15. Correlation matrix of abiotic and biotic variables. Negative correlations are indicated by shades of blue and positive correlations are coloured in red.

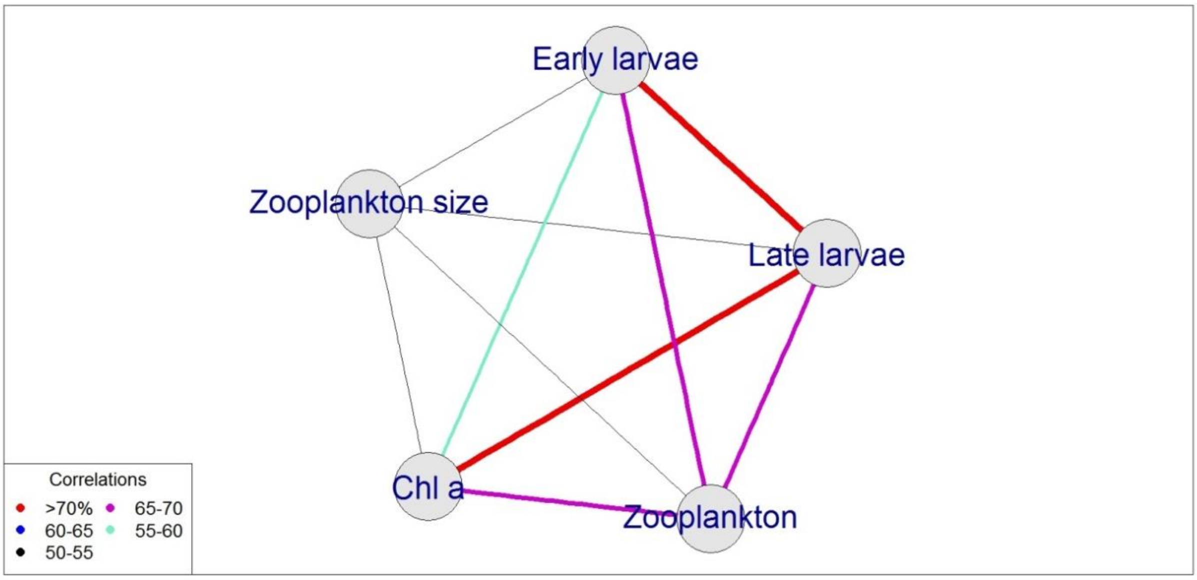

Fig. 16. Map of correlations between different levels of the winter food web. IHLS larvae are depicted as Early larvae and MIK larvae as Late larvae. Correlations with Pearson coefficients of less than 0.5 were left out.

6.4.3 Principal components

The principal component analysis (PCA) resulted in six principal components with the first three representing 88% of the cumulative variance (Table 2). Indicated by the high loadings of chlorophyll *a* concentration, zooplankton abundance and size, PC1 mainly represents the lower trophic levels (phyto- and zooplankton). PC1 accounted for 42 % of the variance of the data and did not show a trend throughout most of the time series. However, three distinct positive spikes could be detected in 1997, 2002 and 2011. Especially for 2011 there is a prominent peak caused by the high abundance of small zooplankton and primary producers. Temperature and NAO mainly determined PC2. The strong negative loadings accounted for 20 % of the variance of the data. In the early 1990's and since 2012 PC2 was positive while for the rest of the time series it remained around zero or below. Higher salinities and the NAO mainly made up PC3, which showed a steady increase over time. It contributed 17 % to the variance of the data. Principal component 4 explained the next 11 %, but showed no clear pattern and was thus disregarded.

Table 2. First three principal components and their loadings. The cumulative variance explained by the components are displayed underneath.

	PC 1	PC 2	PC 3
Zooplankton	0.51	-0.1	0.15
Zooplankton size	-0.51	0.2	-0.12
Chlorophyll *a*	0.48	-0.36	0.04
Temperature	-0.23	-0.75	0.28
Salinity	-0.35	-0.09	0.7
NAO	-0.25	-0.5	-0.63
Cum. Variance	0.49	0.69	0.88

When comparing the larval indicators to the principal components we could see a clear positive relation between PC1 and Downs MIK larvae as well as with the SCAI. However, other relationships varied and indicated more complex dependencies that could not be justified with our data. Principal component 1, based largely on zooplankton abundance, zooplankton size and phytoplankton concentration, remained the best indicator for herring larval survival for the negative peaks that occurred in 1997, 2002 as well as for increased abundances and survival since 2008 (Fig. 18). Yet, it is visible that the trends of the PCs departed in 2007 (Fig. 17). The positive survival of Downs herring larvae may well be founded in the rise and separation of the three PCs, but the detailed interdependencies between these could not be examined with the provided data.

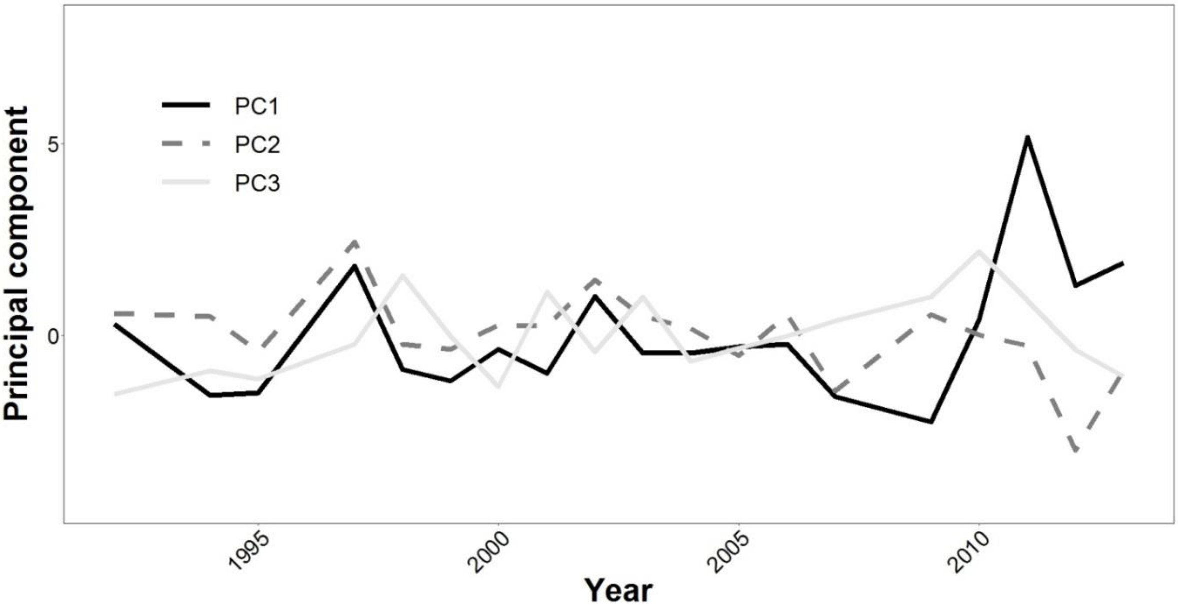

Fig. 17. Principal components over time. Notice that years 1993, 1996 and 2008 do not have datapoints.

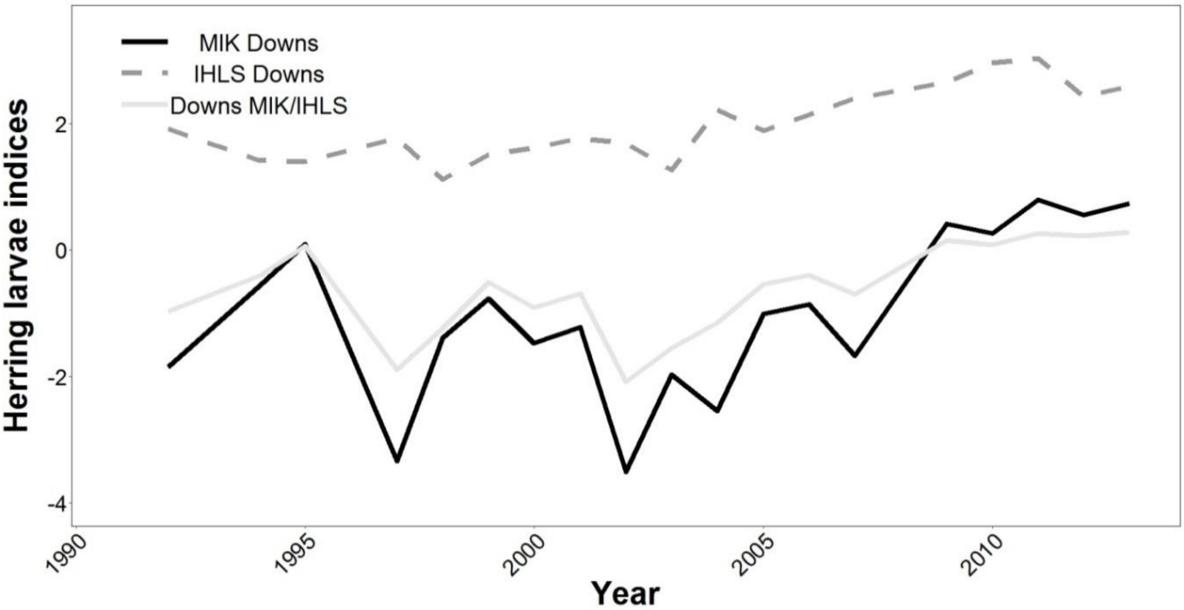

Fig. 18. Downs herring larvae over time. MIK and IHLS larvae are in number m^{-2}.

Overall, we saw that the abundance of herring larvae was influenced by the North Atlantic Oscillation index, but the survival and resulting higher abundance of later stage herring larvae from the Downs spawning component was significantly related to prey abundance in the forms of primary producers and zooplankton in the Southern Bight. Overall recruitment did not reflect this correlation due to the fact the Downs spawning component has still an inferior importance compared to the Orkney-Shetland spawning component.

6.5 Discussion

We found that herring larvae benefited directly and indirectly from increased primary production. Zooplankton, as well as phytoplankton, was positively correlated with the Downs larvae and their abundance. While the early larvae may directly feed on the algae present, which results in a food limitation in winter, an increase in algal concentration improves the survival of food limited early larvae. When the larvae grow, they benefit from increased zooplankton abundance as food. Smaller zooplankton size, which was also found to be correlated with Downs larvae, adds to the positive effect of increased prey abundance. It indicates increased zooplankton reproduction, which means that more nauplii, the preferred food of small herring larvae, and copepodites were present and fitted the prey size spectrum of herring larvae. But prey consumption is not on its own affecting larval growth. When food limitation is a possible explanation for trophic relations, it is also necessary to understand the factors indirectly affecting growth.

Water temperature may have a two-fold influence on the larval survival in this aspect: A direct effect is the increase in energy demand caused by higher temperatures and physiological dependencies connected to it (Houde et al., 1997). Temperature-dependent growth models for fish larvae have consequently been the main method of modelling larval development (Heath et al., 1997). Higher temperatures may result in faster growth, which can increase survival of larvae by developing faster through a period of small size and high mortality (Werner and Blaxter, 1980). Yet, higher temperatures also require more energy, which rapidly decreases chances of survival by increasing food demands during the critical period (Blaxter and Hempel, 1963). In consequence, higher temperatures can be beneficial for larval survival, but only in combination with abundant food resources. A second effect of temperature is the increase in probability of early primary production. It has been argued that phytoplankton growth is neither temperature nor nutrient limited during winter and early spring, but instead it is solar radiation, which determines the onset of primary production (Hitchcock and Smayda, 1977). Nevertheless, in mesocosm experiments phytoplankton and copepod nauplii appeared earlier during the winter-spring succession under elevated temperature conditions (Sommer et al., 2006). As a result, increased temperature can provide the potential for faster phytoplankton growth in case of extended periods of cloudless weather. In our data, this may be reflected by the fact that despite increasing water surface temperatures over time we did not observe a simultaneous increase of chlorophyll *a* concentrations.

The assumption that during winter larvae are generally food limited has been investigated multiple times (Hufnagl et al., 2014; Leggett and Deblois, 1994). It has also been argued that successful transport of the larvae to their nursery areas in the German Bight are of major importance to the stock recruitment (Dickey-Collas et al., 2009). Here, we could show that in case of early onset of primary production the influence of prey abundance is superior. High prey abundances coincided with an increase of herring larvae. In the case of herring larvae from the Downs component this has not been documented before as samples on winter zooplankton abundance and especially zooplankton size are scarce. Until the concise analysis of the separate spawning components by Payne (2010), it had been assumed that the importance of the Downs component to the overall recruitment of North Sea autumn spawning herring (NSAS) is low. Separating the herring larvae by spawning location in the IBTS surveys is difficult and the Downs larvae are characterised as the smallest (length < 20 mm, ICES, 2014). The other larvae hatch earlier and are therefore likely to be larger. Because of uncertainty concerning the catch efficiency of the MIK net, the Downs larvae are commonly removed from the assessment. It is still possible, though, to compare the Downs component itself against bottom-up processes, which is the subject of this study. Due to the low recruitment and an increasing proportion of the Downs component to the SCAI in recent years it has gained new attention. Nevertheless, the most recent spike in NSAS recruitment in 2014 was caused by the larvae of the other components (ICES, 2014). This domination of the Orkney-Shetland-Buchan-Banks larvae (OSBB) was also the reason why the spawning stock biomass (SSB) was excluded from the analysis. In principle, the SSB would be positively correlated to larvae abundance. However, we assumed that the Downs larvae caught in the IHLS are early larvae and thus indirectly relate to SSB. The direct abundance of early larvae, though, connects only to the SSB spawning in that area whereas total SSB may have masked possible bottom-up signals by its correlation to the dominating presence of the OSBB larvae.

Unfortunately, lower trophic level data were not available after 2013. However, we saw in our investigation that the overall recruitment did not relate to primary and secondary production. This is based on the low proportion of the Downs larvae in years of high recruitment. It shows, though, a masking effect by the other components. When relating abiotic and trophic relationships for herring larvae we recommend to investigate the individual components separately. Local phenomenon may pose threats or advantages for larval survival that remain overlooked when comparing standard recruitment indicators. In this aspect it is necessary to put the different large-scale and small-scale factors influencing herring larval survival together. Gröger et al. (2010) presented evidence for the connection between the NAO as well as the Atlantic Multidecadal Oscillation index (AMO) with NSAS larvae. We also found a relation between NAO and herring larvae at the spawning site. These larvae, however, have barely started feeding, which is why their relation is more connected to large scale processes responsible for wind speeds, water movements and successful egg dispersal and development. In turn, the survival of these larvae might be more closely related to prey abundance and factors influencing physiological conditions (Hufnagl et al., 2014).

In the POLCOM-ERSEM model phytoplankton growth is also limited by solar radiation. Yet, in 2011 and from then on, phytoplankton concentrations were elevated. This elevation occurred mainly near the Rhine-Meuse river delta. The decreased salinities in the area together with calm winds and higher temperatures can cause a temporary stratification, which prevents phytoplankton from sinking below the critical depth. This effect would reduce light availability and could give rise to early phytoplankton blooms as observed in 2011. Breton et al. (2000) also showed a larger phytoplankton biomass at stations in coastal areas compared to stations in the offshore current system. Despite this difference, they also provided evidence that phytoplankton biomass is variable, but can be relatively high near the bottom in winter months. This could account for some of the variance in larval survival due to undetected prey available to the larvae near the bottom. For herring larvae, these prey fields would be highly beneficial concerning their survival. Overall, it highlights the need for combined analyses of effects on the separate spawning components of NSAS. Our study identifies even more aspects of the Gordian knot, which is formed by environmental conditions, growth, mortality and prey availability (Hufnagl et al., 2014). In addition to the large scale effects of NAO and AMO, there are more local dependencies that act on the individual spawning sites and the larvae in that region. Hence, our results may only apply to the Downs component, but the bottom-up effects of winter chlorophyll and zooplankton may also explain the sudden bursts of surviving larvae from the more northern spawning components, especially the Orkney-Shetland spawning stock. More factors like zooplankton composition (Alvarez-Fernandez et al., 2012) and top-down controls are also potential threats to herring larval survival, but chlorophyll *a* concentration, zooplankton abundance and size should be more closely monitored as the principal drivers of Downs larval survival.

7. Chapter III

Zooplankton size as an indicator for zooplankton biodiversity

7.1 Abstract

The role of zooplankton as mediators of energy transfer in marine ecosystems has been widely acknowledged. However, this knowledge has not been used sufficiently in ecosystem-based management. One main reason for this is the lacking application of zooplankton biodiversity, for example as an indicator of good environmental status. Based on a long-term time series collected during winter in the southern North Sea we could show that a simpler trait-based approach can be applied to study long-term trends in biodiversity. We found a significant correlation ($\rho = 0.90$, $p < 0.001$) between size diversity and zooplankton taxonomic diversity (both calculated as Shannon Wiener Index). While this correlation was independent from sampling time and location its stability was sensitive towards the minimum size class included in the analysis. While still having a robust, significant correlation throughout the sensitivity analysis we recommend the use of small minimum size classes and a size bin width scaling ratio of 1.14, between upper and lower size class limits, for best indicator performance. Our results demonstrate that the easier and faster determinable size diversity of zooplankton can be a suitable indicator for zooplankton biodiversity in the tested region and season. It may thus constitute a cost-efficient indicator in ecosystem-based monitoring programs.

7.2 Introduction

In a changing marine environment the need for indicators that rapidly and reliably detect these changes is, and has been, a major research issue (Hooper et al., 2012; Carpenter et al., 2014). Ecosystems around the world have been, and still are, experiencing natural or man-made changes in species compositions, trophic interactions and food web functioning (Drinkwater et al., 2009; Folke, 2004), entailing significant economic and social consequences (Millennium Ecosystem Assessment, 2005). The classification, monitoring and prediction of ecosystem states has thus moved more and more into the focus of interest of scientists and managers. As a result, finding suitable ecological indicators to describe ecosystem states has become a primary goal of biological research. Under the European Marine Strategy Framework Directive (MSFD, 2008/56/EC European Commission, 2008) biodiversity is listed as the first descriptor of good environmental status (GES). For a long time, it has been argued that biologically diverse communities are more resistant to external perturbations (MacArthur, 1955; Hooper et al., 2005; Tilman et al., 2006) or promote a higher stability of productivity (Isbell et al., 2009). Ensuing investigations raised concern about ecosystem functioning in regard to decreasing biodiversity (Donohue et al., 2013). This threshold-like behaviour of effects is why biodiversity has been considered a good indicator for GES. But as with any indicator, biodiversity can be a matter of scale. Depending on available information biodiversity is based on abundance and richness of defined species or species groups/classes. Increasingly complex resolution of biodiversity has emerged, with the possibility of detecting early, subtle changes in species composition at the cost of expensive, more complex methods. For management purposes, large-scale surveys and long-term monitoring using these methods are unhandy. The method of choice would be as detailed as possible, but at the same time standardised, cost efficient and rapid, allowing wider spatial and temporal analyses and immediate results. Therefore, high-throughput, cheap and “easy-to-apply” indices are desired.

Following the line of argumentation that a higher diversity stabilises productivity it is even more important to study biodiversity at the basis of the food-web than at higher trophic levels. Under the MSFD the basic trophic levels to monitor are phyto - and zooplankton. Yet studying the biodiversity at the base of food web becomes increasingly difficult due to the often miniscule differences between species and the larger handling time due to the small sizes. During the past decade the rise of non-invasive, optical sensors for zooplankton sampling, like the Video Plankton Recorder (Davis et al., 1996) has helped solving this problem, but the method has been restricted by optical resolution, visibility of taxonomically relevant details on the images and image recognition algorithms. To a large extent, previous methods overlook a simple measurement that is now available due to the optical sensors: size.

Size can be measured objectively and automatically without the need of complex algorithms or high quality imaging. Additionally, size is an essential biological trait that is tightly linked to physiological processes (Peters, 1983; Moore & Folt, 1993) and trophic interactions (Woodward et al., 2005). In the aquatic environment, the different trophic levels and functional groups are usually dominated by a particular species or genus, each with a particular size range occupying its species-specific niches (Beaugrand, 2003). Considering those species-specific size distributions, it is possible to determine a size diversity, which has so far mainly been used for particle analysis in physics or material science (e.g. sediment characteristics, Vandenberghe, 2013). Considering size-based automatic classification to determine size diversity it might be a highly valuable “easy-to-use” indicator for zooplankton biodiversity.

In this study we compared taxonomic diversity and size diversity based on 23 years of zooplankton samples collected in the southern North Sea and the Eastern English Channel. We investigated the correlation between the two types of zooplankton biodiversity dependent on varying the lowest size class and differing overall size class scales. In general, we found the correlation between taxonomic and size diversity to be robust. Our study suggests that at least in low diversity systems taxonomic groups occupy mostly a restricted number of size niches, which may be used for trait-based analysis. In conclusion, for ecosystem monitoring, the easily measurable size diversity can be a useful proxy for zooplankton biodiversity.

7.3 Materials and Methods

7.3.1 Data collection

All zooplankton samples analysed for this study were obtained during the International Herring Larvae Survey (IHLS). Sampling was performed annually in January from 1988 onwards. Samples collected at stations between latitudes 49.5°N and 53.5°N and longitudes 2°W and 5°E (ICES areas IVc and VIId, see Fig. 16), covering the southern North Sea (Southern Bight) and the east English Channel, were used. Sampling was conducted using a “Nackthai”, a modified Gulf III sampler (Bridger, 1958), equipped with nets of a mesh size of 280 – 330 µm and towed in an oblique fashion at 5 knots (280 µm mesh sizes were only used until 1995). Samples were preserved in 4% formaldehyde. For the analyses 30 stations were randomly selected from each year, except for 2009 where only 20 stations in total were available. Samples collected during the years 1990, 1993, 1996 and 2008 were missing for logistic reasons altogether making it a 23 year time-series. Between 1988 and 2014 a total of 674 stations were included (Fig. 19).

7.3.2 *Sample processing*

Samples were flushed off formaldehyde in a 300 µm sieve and split according to the Motoda method (Motoda, 1959) until the number of particles was suitable for scanning (Gorsky et al., 2010). In most cases the number of fractionations was less than five (1/32), thus samples were not segregated into two coarse size fractions as advised in the ZooScan (see below) manual for dense spring or summer samples (Antajan and Vandromme, 2013, pers. comm.).

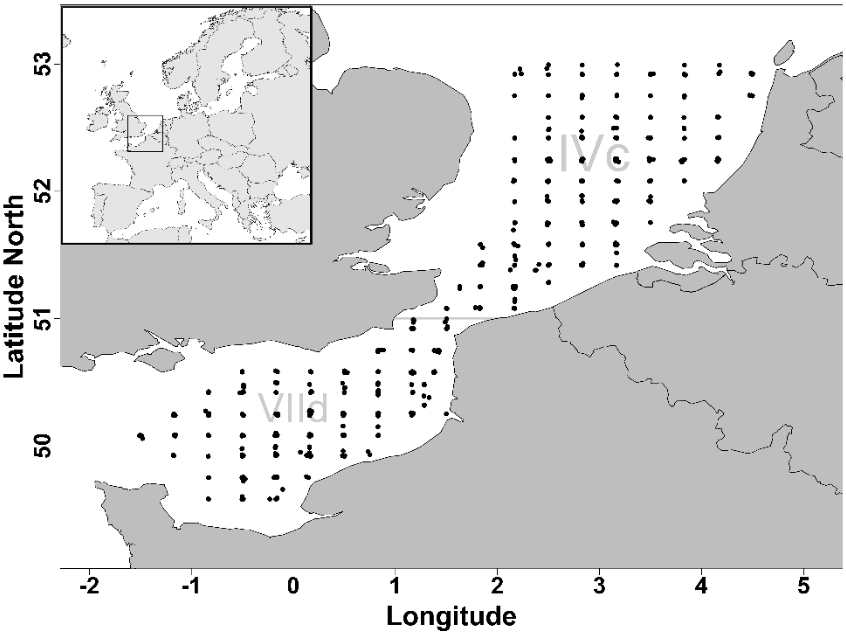

Fig. 19. Map of the study area in the English Channel covering ICES areas IVc and VIId and showing the location of all 674 stations used in the analysis.

Higher particle numbers and subsequent higher split factors would lead to biased results of rare species and rare size classes (here especially large zooplankton).

A ZooScan device (Gorsky et al., 2010; version 2) with a 2400 dpi resolution was used for species classification and size determination (Grosjean et al., 2004). Similar to a common flatbed scanner the ZooScan produces a digital image of a sample put on glass surface. The particle threshold was set to 300 µm equivalent spherical diameter (ESD) related to the mesh size of the modified Gulf III sampler. Scanning and automatic plankton identification was done using the ImageJ software (version 1.41o) with ZooProcess (version 7.19) and Plankton Identifier software (Gasparini and Antajan, 2013; version 1.3.4). All analysed particles included in later analysis were checked by eye for correct classification allowing for highest classification accuracy.

7.3.3 Zooplankton diversity analysis

The aim here was to develop methods that allow for an analysis of biodiversity without any a priori expert knowledge and the statistical design was selected accordingly. For this purpose 14 coarse taxa were classified: chaetognatha, cladocera, appendicularia, echinodermata, polychaeta, *Temora spp.*, calanoida, *Candacia armata*, unidentified copepods, amphipoda, cumacea, shrimp-like, zoea larvae and unidentified malacostraca. Size was standardised as equivalent spherical diameter and calculated from the particles' area on the ZooScan as described by Schultes and Lopes (2009). We calculated diversity using the Shannon Index (*S*, based on natural logarithm; Shannon and Weaver, 1949, in Pielou, 1969), provided by the R package "vegan" (Oksanen et al., 2008), both for taxonomic data, forthwith termed taxonomic diversity, and size data, in the following termed size diversity, from abundance per taxonomic or size class, respectively.

To compensate for the decreasing number of individuals with increasing size we increased each following size class' width by applying a ratio of 1.14 between lower and upper size bin limit (306, 312.12, 318.36, … , 13200 µm ESD). The ratio of 1.14 has been widely used in size spectrum applications for Laser Optical Plankton Counters (Checkley et al., 2008). Abundance of all zooplankter per size class was then determined and a Shannon Index calculated. All size-diversity indices, determined for each sample, were then correlated with the taxonomic diversity index of the corresponding sample using a Pearson correlation index. We further tested the sensitivity of the index in relation to the smallest size class applied. This test should simulate the sensitivity of the size diversity index to differences in mesh sizes or optical resolution of the sampling devices. Minimum size classes for the test ranged from 300 µm ESD to 800 µm ESD. All particles smaller than the minimum size class were excluded.

In a hydrographically dynamic region like the English Channel annual means can be driven by local extreme events. We exploited the spatial resolution of the data and divided the study region into a grid consisting of 28 equally spaced grid cells to investigate spatial differences in diversity. Due to missing geographical data before 1991 and in 2014 the spatial analysis was restricted to the time period from 1991 to 2013. Means of taxonomic and size diversity per grid cell were calculated and averaged for four time periods with roughly equal amount of data (1991 – 1997, 1998 – 2002, 2003 – 2008 and 2009 – 2013).

7.4 Results

7.4.1 Zooplankton composition and annual biodiversity

Zooplankton groups showed typical bell-shaped size distributions for each year, reassuring that the sample sizes were large enough. Up to sizes of 1800 µm equivalent spherical diameter zooplankton composition was dominated by copepod groups (Fig. 20), whereas chaetognaths dominated the size fraction between 1800 and 3200 µm ESD. Larger zooplankton above 3200 µm ESD were almost exclusively shrimp-like crustaceans, i.e. euphausids, except for a few rare catches of large polychaetes and amphipods. As can be expected from previous studies (e.g. Record et al., 2010) that analysed winter samples in terms of species richness the taxonomic diversity was low (*S* = 0.05 – 2.1). However, the annual variation was considerable and indicated an overall decline in taxonomic diversity

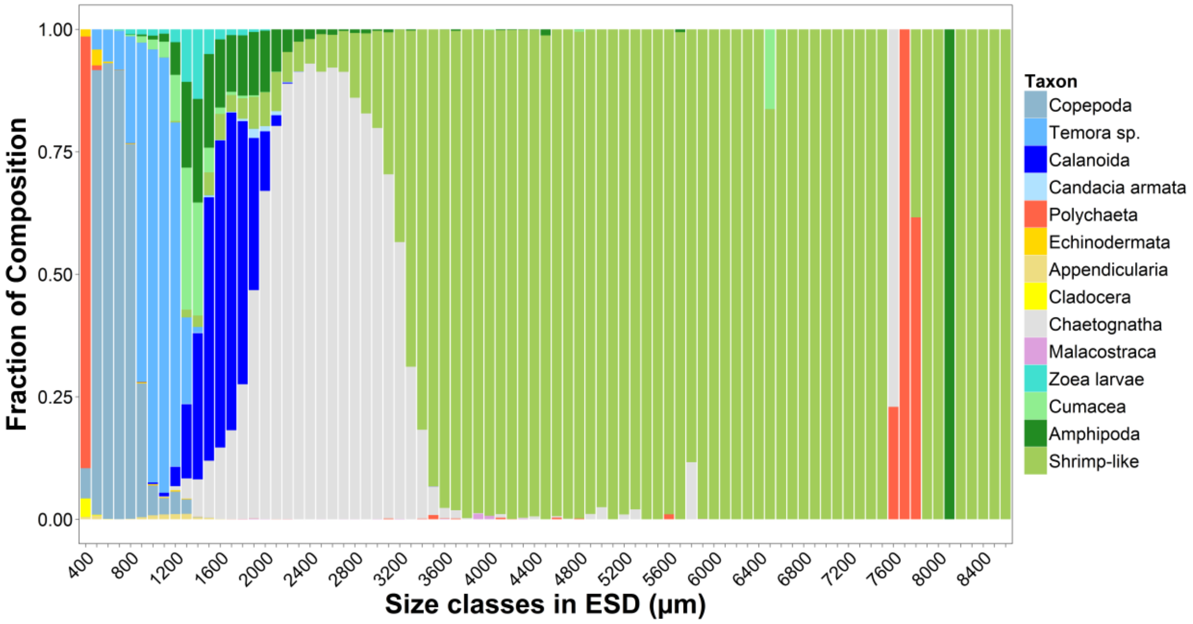

Fig. 20. Taxonomic mean composition of all pooled samples. Note that the size classes are on a linear scale (100 µm classes) and are incomplete for display purposes (< 8600 µm).

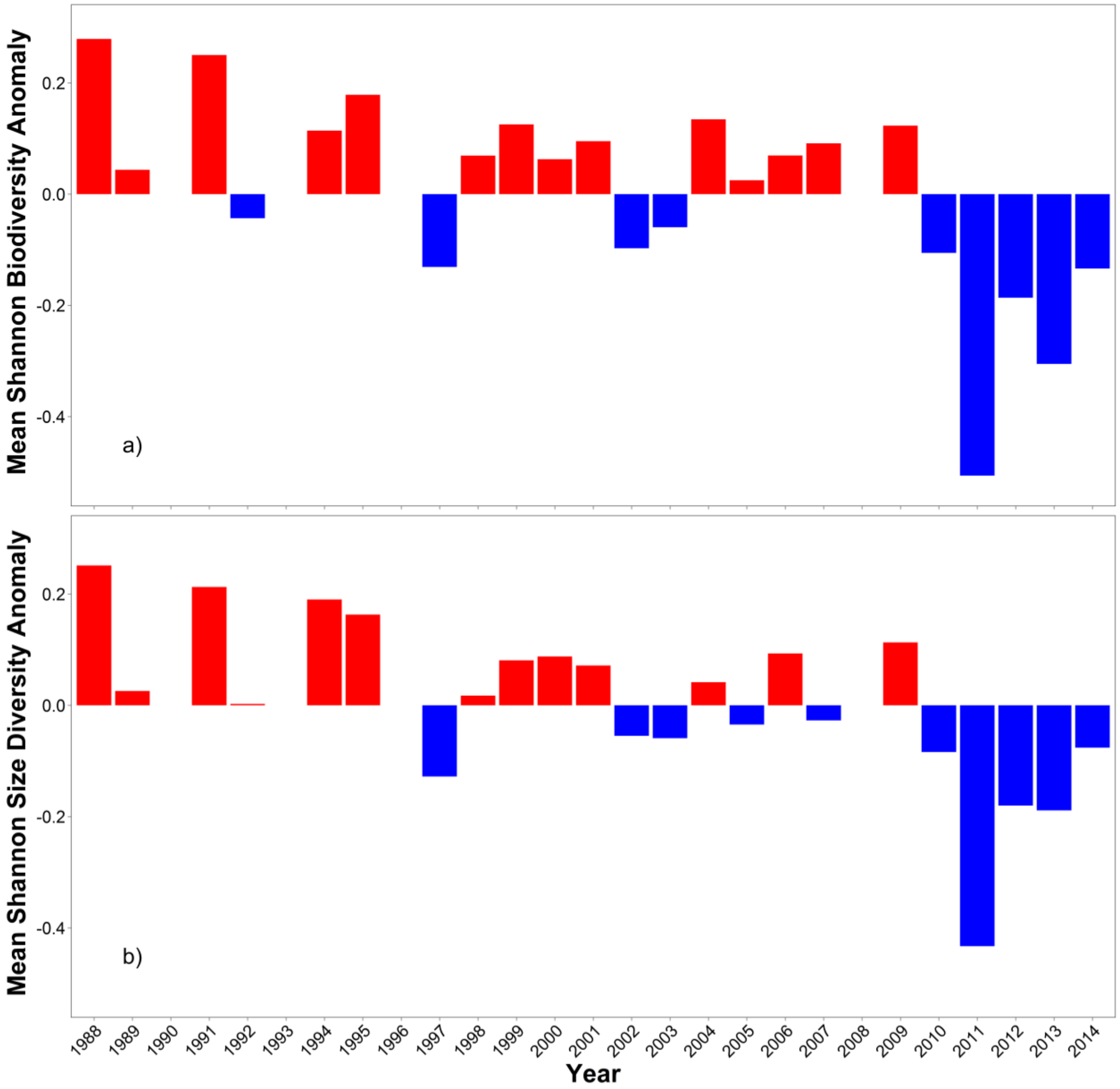

Fig. 21 a-b. Taxonomic diversity (a) and size diversity (b) as annual anomalies from an overall mean Shannon diversity index S.

(Fig. 21 a). After a period of relatively high diversity (0.65) it decreased after 1996 and fluctuated around the long-term average level of 0.52. After 2009/2010 a sudden drop in diversity from 0.47 to 0.33 occurred and especially in 2011 a very low taxonomic diversity was observed (0.19). Simultaneously, size diversity displayed a similar amount of variation and decline, though on a slightly larger scale (Fig. 21 b; 1.24 – 2.7). The anomaly difference was never higher than 0.1 and depicted the same periodic changes as taxonomic diversity.

7.4.2 Correlation analysis

We tested the relationship between taxonomic and size diversity and found highly significant Pearson correlations coefficients ($p < 0.001$) of up to 0.90 (Fig. 22 a - f). The mentioned maximum correlation was determined for a starting size class of 500 µm and a scaling ratio for upper and lower size class limits of 1.14 (i.e. 500, 570, 649.8, 740.772, … µm size class borders). While a significant relationship ($p < 0.05$) was always present using this ratio shifting the minimum size class had an effect on the correlation. The correlation between size diversity and taxonomic diversity was the strongest if the starting size class was close to the minimum of the size spectrum (300 µm in this case). However, using 500 µm ESD as starting size class performed best, while the two lower classes revealed slightly lower, but still very high correlation coefficients ($\rho = 0.87$ and 0.88, Fig. 22 a - c). When larger starting size classes were chosen the variance increased and the correlation hence decreased. The fact that the Shannon size diversity index was mostly higher than the corresponding

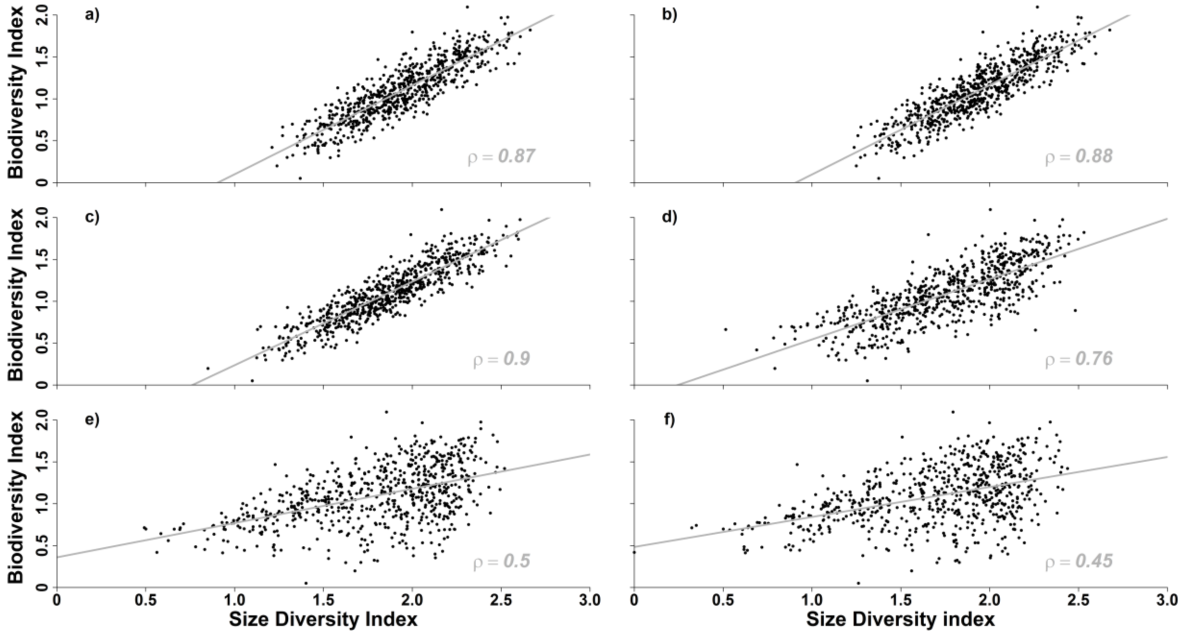

Fig. 22 a-f. Size diversity correlated well with biodiversity based on a size scale exponent of 1.14. Initial size classes were varied from a) 300 µm to f) 800 µm in 100 µm increments. 500µm as initial size class (c)) revealed the highest correlation of $\rho = 0.90$.

taxonomic diversity index was due to the higher number of size classes compared to the number of taxonomic groups.

7.4.3 Spatially explicit diversity analysis

To determine whether the diversity differences were driven by local phenomena we investigated if the decline in diversity occurred across the entire study area. Multi-annual means for an 8 x 8 cell grid were calculated. These gridded means showed that the declining diversity trend was present in all parts of the study area (Fig. 23 a - h) and for every grid cell. Yet, whereas the drastic decline in diversity can be seen most dominantly in the northeastern region after 2000, the areas close to the British shores only saw a drastic decrease in diversity since 2009. The spatial analysis also verified that size diversity correlated significantly with taxonomic diversity ($p < 0.05$) even on these smaller spatial scales and time ranges. Variance between the two diversity indicators was larger due to the smaller sample size per grid cell, but the correlation was still high ($\rho = 0.48 - 0.86$). Using size diversity it was possible to identify the low biodiversity in the grid cells near the Dutch shore and the greater declines of biodiversity near the English coast since 2009.

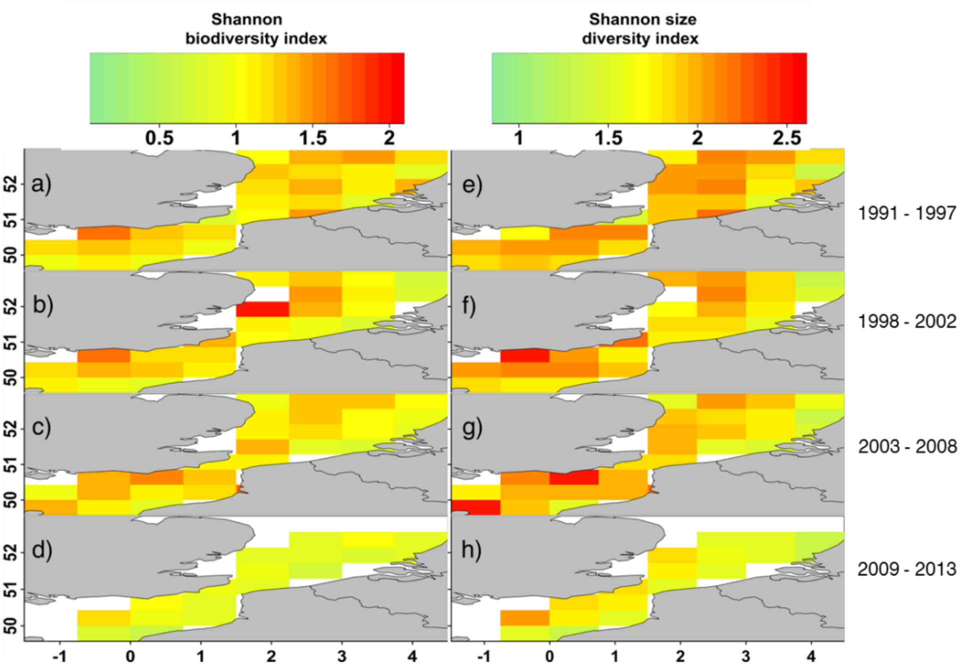

Fig. 23 a-h. Shannon diversity indices for taxonomic diversity (a - d) and size diversity (e - h) based on means per grid cell for four time periods since 1991. Note the difference in scale. Time periods included five years of data each.

7.5 Discussion

7.5.1 Size diversity as potential biodiversity indicator

In our study we investigated the potential of zooplankton size diversity as a complementary indicator for zooplankton biodiversity. We found that the significant and high correlation between the size diversity and taxonomic diversity supported our hypothesis of a tight relationship between the two indicators. Size diversity in this case turned out to be a suitable indicator for biodiversity of zooplankton if size data of sufficient resolution are available. Most importantly, the correlation between both indicators of biodiversity was highest if the lowest size class had also the highest abundance of particles. This seems similar to normalised abundance size spectrum theory (Kerr and Dickie, 2001) and size spectra calculated from *in situ* data (Marcolin et al., 2013). We also tested normalized biomass size spectrum as an indicator, but it did not show a significant correlation with taxonomic diversity (results not shown). When using size diversity as an indicator, it is advisable to take the minimum size class as a starting point and increase the size class width by a factor of 1.14 for each consecutive size class. Excluding most of the smallest organisms increases the variance and thus size diversity may not represent biodiversity anymore. For example, using only 5 size bins when starting at 800 µm ESD with a scaling ratio of 2 (800, 1600, 3200, … µm ESD size class borders) the correlation was less than $\rho = 0.2$ in our study and hence not applicable for indication. The choice of the required size resolution should be made *a priori* for a quick and automatic detection. It can already easily be examined on board of a ship by determining the biomass after using e.g. 300 µm, 500 µm and 1000 µm meshes or previous expert knowledge. We recommend the use of size bins starting at the nets' effective catching size. That way it can be quickly integrated into established ecosystem monitoring.

7.5.2 Reasons for the effectiveness of size diversity

Similar to taxonomic diversity size diversity could be used to monitor ecosystem stability and good environmental status according to the MSFD. The link to ecosystem stability - that is associated with taxonomic diversity - should also be noticeable with size diversity as indicator and hence widen the spectrum of indicators available for ecosystem management.

Supposing that a lost species had a key trait that impacted the food web, the loss could be detected in the lower or higher size classes as cascading trophic effects even if the species is replaced with a species with a comparable size distribution. Most species occupy a specific size range with restricted plasticity, which is the reason for a link between size diversity and taxonomic diversity. The individual size range is picked up by the size diversity index and a loss of that size range will be reflected in a decreasing abundance in it. This is predominantly true in ecosystems with low taxonomic diversity like the open ocean in which the trophic levels or certain size ranges are dominated by a single species. Here, size diversity can show some advantageous traits. If, for example due to increased temperature or selective predation pressure, a species has a decreased size range this will be reflected in decreased size diversity whereas taxonomic diversity would not show the signal. It may thus also reflect the prey availability for predators since predators are reliant on prey size ranges. Similarly, changes in food chain length and increased predator abundance will be reflected in increased size diversity. Their species-specific functional traits and behaviour, however, cannot be accounted for, which may limit the use of size diversity to lower trophic levels in which individual behaviour is not as complex as in long-lived species. A certain species response to ecological or environmental drivers, which adds to the stability of the ecosystem, cannot be resolved. If, however, extensive knowledge cannot be accumulated, size diversity has proven to describe the state of the ecosystem very well. Dolan et al. (2002) showed that differences in phytoplankton and microzooplankton communities along a transect through the south-east Mediterranean Sea could also be described by their size diversity, even though they used only three coarse size classes. Taxonomic diversity revealed no additional information on the state of the ecosystem compared to size diversity. Taking a step further with even lower taxonomic diversity, but greater implications, one can consider the wide application of size diversity in boreal forest management (Lexerød and Eid, 2006). Here, size diversity monitoring of tree size parameters ensures the economic viability of forest management. By controlling diversity of tree sizes forest managers are able to maintain a constant supply of different types of wood and are more flexible towards future demands. A more diverse forest provides also a wider habitat range and thus a higher biodiversity of animals. In conclusion, size diversity estimates allow for a comparatively easy monitoring of different biological and economic aspects that are desired for management. It shows the ability of the index to be more detailed, or sensitive, regarding life stages of species. Given the size classes have been adequately scaled it is possible to resolve both life history stages of zooplankton as well as fish, which would be advantageous regarding ecosystem management. Size diversity could be an early indicator for environmental, anthropogenic and ecosystem related changes.

7.5.3 Future relevance

There are indications that species respond to temperature changes by migration or distribution shifts (Beaugrand et al., 2002) and it is likely that there will be somatic responses too (Atkinson, 1994; Leandro et al., 2006). Most physiological mechanisms are highly affected by temperature (Moore and Folt, 1993) and as pointed out earlier, size is strongly correlated to physiological processes (Peters, 1983). Hence, ecosystem responses to climate change occur to a large extent on the individual level, but are only noticed on the population and community level, which has been largely disregarded in management and research (Perry et al., 2010). Size diversity changes may indicate possible changes before they occur on the population level. Such indications would be hugely beneficial and advantageous over taxonomic diversity as a single indicator.

7.5.4 Potential application

To determine their applicability indicators are often tested for their sensitivity to ecosystem changes. Spatial patchiness of certain plankton groups will influence the size diversity index, which is beneficial concerning change detection. On the other hand, this also means that a single sampling effort may not be enough to allow for generalisations and spatially explicit surveys are needed for the implementation of the MSFD. Seasonal plankton bloom formation will likely affect size diversity too, but both requirements, spatial and seasonal coverage of the survey, are also true for taxonomic diversity monitoring. Yet, the calculation of size diversity can be done much faster than taxonomic diversity and thus would improve the integration in established surveys as demanded by the MSFD. Using optical sensors like Laser Optical Particle Counters (LOPC; Herman et al., 2004), Video Plankton Recorders (VPR; Davis et al., 1996) and Underwater Vision Profiler (UVP; Picheral et al., 2010) instruments, which basically run in an automated fashion, it should not consume additional survey time on board. In that respect, the LOPC can even be placed on a buoy-like or stationary platform (Checkley et al., 2008), which enables a constant monitoring of zooplankton size diversity over the course of a year. Laboratory based optical instruments like the Flowcam or ZooScan can help digitise already gathered samples and help standardise the different monitoring options. A sophisticated and standardised international effort to establish a constant zooplankton size monitoring scheme for a better estimation of zooplankton diversity on a large scale is needed for the ecosystem-based management approach for fisheries under the MSFD. Besides the multitude and ease of field applications, the simplicity of size diversity allows for an approximation of the status of zooplankton in ecosystem models. In many of these models nutrient cycling and primary production is the main focus and often only traits like herbivory and carnivory are implemented for zooplankton as these are important for equalising biomass calculations. The mean size of a trophic level though has effects both on lower and higher trophic levels. It distils the information to a single variable with a few, but well documented assumptions about ecological importance and its relation to underlying physiological processes (Peters, 1983). The fast and easy monitoring of zooplankton size diversity may give early indications of possible changes in prey availability and the option to model the consequences of biodiversity loss for fisheries management.

8. General Discussion

8.1 Time series and methods evolved

In the course of this thesis I established a new time series of zooplankton in the English Channel and the Southern Bight of the North Sea. There are several aspects that make this time series unique and important for further research. First, the time series is for the month of January, a month rarely sampled for plankton due to the assumption of low primary and secondary production. Yet, winter zooplankton is important for the plankton succession in spring. Considering overwintering stages of zooplankton, e.g. copepods, and species-specific strategies, like the production of dormant eggs, the winter period is critical for ecosystem dynamics in that it determines the standing stock for the secondary production. Unfortunately, the winter dynamics are poorly understood, which is especially due to a lack of detailed spatial and temporal data. The few permanent sampling stations have been combined by the ICES working group on zooplankton ecology (WGZE; ICES, 2013). Other data originate from occasional cruises for certain projects (e.g. Durbin et al., 2003). In combination with the lack of satellite data due to increased cloud cover in winter (Reed et al., 1994) and poor model estimates in the face of non-existent reanalysis data there is a need for winter surveys and plankton data. It is even more important for understanding winter zooplankton dynamics in regard to climate change and its impact on winter conditions and for quantifying crucial ecological processes during this time (Bromirski et al., 2003; IPCC, 2001).

The second aspect why this time series is of importance is its location. In the eastern English Channel and the Southern Bight of the North Sea, commercially important fish species, among them herring, plaice and sole, spawn and have their offspring drift through this area to their nursery grounds in winter (Cushing, 1969; Houghton and Harding, 1976). Surveys exist for the individual larvae assessments (e.g. IHLS). But although plankton nets have commonly been used and plankton has also been caught, they have not been analysed due to time restrictions, labour restrictions or missing standardisation. Only the German and Dutch conductors of the survey store their samples for longer time spans, while samples collected during the Dutch surveys are disposed of after 5 years. As our analyses showed, there is still important ecological information in these samples.

The only additional information on lower trophic levels in my study areas (ICES areas VIId and IVc) were collected at the Gravelines station next to a power plant at the French coast or with the Continuous Plankton Recorder data (CPR; Warner and Hays, 1994). The CPR dataset is extensive and has been used for several related studies before (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2002). For abundance estimates, however, the data can only be restrictively used due to the small opening of the device, the shallow, constant depth and low spatial coverage, especially in the eastern English Channel. Our dataset is the only available zooplankton abundance estimate for this area in winter.

The third aspect, which makes this time series unique, is zooplankton size. Zooplankton size has rarely been accounted for and especially for the North Sea size data are scarce (Mauchline, 1998). Size measurements are not included in standard protocols of zooplankton time series and available data come from experiments or studies about a single season or event (e.g. Halsband and Hirche, 2001). Being a fundamental trait in ecosystem dynamics it is astonishing how regularly size has been disregarded. In case of inclusion of size in, for example, ecosystem models, these are often taken as mean sizes of particular species or taxonomic group. But the short life span results in intra-annual generations developing at different conditions. Their ectotherm physiology likely corresponds to different growth and final sizes of the adult stages in all plankton groups between these conditions (Angilletta et al., 2004). It is therefore crucial not to generalise zooplankton size. Instead, I could document that sizes of most zooplankton groups in our study had decreased in size (Chapter I). Predator-prey relationships are often closely connected via size (Scharf et al., 2000; Costa, 2009) and consequently, changes in the size spectra of prey need to be investigated more thoroughly.

The final methodological aspect of this time series is the use and application of pre-existing samples and the further establishment of optical semi-automatised methods in the analysis of large numbers of plankton samples. I used samples that have rested on shelves for decades in part, the oldest originating from 1987. Other institutes such as the GEOMAR Helmholtz Centre for Ocean Research and Wageningen Marine Research have verified that there are thousands of unused plankton samples in their storages waiting to be discarded

(Svend Mees and Cindy van Damme, pers. comm.). Analysing and digitising plankton samples remains a time consuming and labour-intensive work. But, as in this case, a common interest in the data exists and cooperation is much appreciated. Sampling and analysis of valuable, additional data is therefore only a matter of effort and automatization. With modern, optical sensors this has become easier and more affordable. Video Plankton Recorder (VPR; Davis et al., 1996), Laser Optical Plankton Counter (LOPC; Herman et al., 2004) and ZooScan (Gorsky et al., 2010) are only a few possible instruments, which can be used for this purpose. Especially the LOPC is comparably small and can be made to fit plankton nets. A LOPC/plankton net tow would provide additional size spectrum, phytoplankton and zooplankton data at no additional labour costs except for digital analysis. Considering the ecosystem approach to fisheries and analysis of a good environmental status of the ecosystem these already existing sampling procedures would provide valuable data on multiple trophic levels.

8.2 Climate change and its indirect effects on the trophic cascade

The idea of good environmental status has gained in momentum in recent years (Borja et al., 2013). As a response to ecosystem-based management of fisheries it is necessary to monitor changes in the ecosystem that go beyond single species or single trophic level assessment. Especially since Beaugrand's (2004) and Alheit et al.'s publication (2005) on regime shifts in the North Sea and Baltic Sea the focused of marine ecology and fisheries research involved not only the top-down control of fisheries, but also the upwards cascading effects, seasonal and interannual variation as well as climate change and other derived effects.

I saw a small, but relatively constant rise in water temperatures in both the reanalysis data of the POLCOM-ERSEM model as well as the *in situ* data from the IHLS CTD signals, the latter of course with a higher variance. In winter, temperature effects can be more pronounced. As explained in Chapter I and II, rising temperatures increases the resting metabolism of ectotherm organisms, thereby raising their energetic needs (McLaren, 1963; Newell and Branch, 1980). In combination with food scarcity and vulnerability of early life stages these higher energy requirements can negatively influence the probability of an organism's survival. If there was no food limitation higher temperatures could actually accelerate growth and therefore increase chances of survival and reproduction (Hirche et al., 1987). Food limitation is perhaps the main restriction of secondary production. Next to temperature it is the main bottom-up--driver in this ecosystem. Starting from the most basic energy source, light, carbon dioxide and nutrients, phytoplankton growth is the key player concerning food limitation. But phytoplankton growth is contained by low light levels during winter (Hitchcock and Smayda, 1977). Temperature and predation have been found to only indirectly affect primary production in winter (Oviatt et al., 2002). Instead, high cloud cover, short daylength and constant turbulence prevent phytoplankton cells from extended periods of sufficient light intensity and thus energy supply. Yet, there are documentations of elevated primary production during winter months. Behrenfeld (2010) described the potential of increased phytoplankton growth rates already occurring in mid-winter. The increased mixing of water leads to a negative change in phytoplankton-zooplankton encounter rates, thereby allowing phytoplankton to grow, despite of an absence of stratification. Durbin et al. (2003) showed the effects of a local winter phytoplankton bloom, which had positive effects on higher trophic levels. It provided evidence of the importance of such early production events.

While these examples demonstrated the potential for increased growth, they also show that these occasions are not the norm, but rather occur on a local scale under irregular circumstances. At Georges Bank in 1999, likely reasons for the event were increased freshwater inputs that led to stratification and thus increased exposure of phytoplankton cells to light. A comparable mechanism might have caused the increased phytoplankton biomass in 2011 of the Dutch coast as documented in Chapter I. River runoff from the Rhine-Meuse system could have caused stratification. Unfortunately, I could not verify this hypothesis with river run-off data. Climate change, however, is thought to increase river runoff through increased rainfall and higher temperatures during winter (IPCC, 2013). Both factors promote stratification. Hence, climate change may foster occasional winter plankton blooms and a continuous shift towards an earlier onset of the spring bloom. This in turn can have major implications on fish recruitment, such as mismatch scenarios between fish larvae and their prey (Cushing, 1990). Fish are less flexible in their spawning behaviour, especially when they have fixed spawning grounds and times. They rely on the synchronous timing of plankton blooms and the beginning of feeding of their larvae, although this reliance may extend well beyond the critical period (Bollens et al., 1992). A shift in timing of ecological processes at the beginning of the year can therefore have consequences on many different nodes of the food web (Casini et al., 2008).

Besides prey abundance also prey size is a key variable here and determines prey availability and predator-prey match or mismatch. For phytoplankton, it is probably less relevant. Diatoms, for instance, put their energy into reproduction instead of somatic growth when favourable conditions arise. Size is therefore less variable. In contrast, zooplankton such as copepods grow through several larval and copepodite stages (Mauchline, 1998). Predators such as fish larvae feed on specific life stages due to their size matching their prey size spectrum (Turner, 1984). Earlier phytoplankton growth means that larval stages of zooplankton can also be reached sooner. Two consequences could arise from the shift: Later and larger life stages of zooplankton appear at the time of critical feeding of fish larvae and (I) do not fit into the prey size spectrum anymore as well as (II) compete with fish larvae about similar prey. Both effects show how size can reduce prey availability despite high abundances of prey per se. In our analysis, we could see that zooplankton size actually decreased since 1991. Even within taxonomic groups such as *Temora sp.* mean size decreased. The reduction in size may be facilitated through rising water temperatures and the temperature-size rule, which then favours smaller volumes of ectotherms (Angilletta and Dunham, 2003). Concerning the feeding strategy of herring larvae (detection, S-shape like formation and striking) it means less energy per prey item. Yet, it also means that more prey items may fit into the size range available to the predator (e.g. due to mouth gape limitations).

Size at different life stages naturally depends on species and species composition. Copepodites of several species in the North Sea have different size ranges and thus prey size spectra available to fish larvae rely on their occurrence and size. It has been documented before that species geographical ranges shift in the wake of climate change (Richardson, 2008; Perry et al., 2005). For zooplankton, the most prominent example was the displacement of *Calanus finmarchicus* by *Calanus helgolandicus*, which corresponded to the NAO and related factors (Fromentin and Planque, 1996). In the face of warmer water temperatures both species have shifted their distribution to the North. Similar tendencies also exist for the English Channel, where Lusitanian species are abundant in the Atlantic waters and more boreal species are located to the east in the Southern Bight (ICES, 2013).

Increasing water temperatures, and further increasing wind speeds, can redistribute the Lusitanian species such as *Candacia armata* further east, potentially displacing other species in the Southern Bight and rearranging the size spectrum and timing of reproduction. Alvarez-Fernandez et al. (2012) have shown similar shifts in zooplankton composition in the area of the English Channel. The CPR data showed clear signs of regime shifts at the end of the 1990s. Our data suggests another shift that occurred more recently, between 2008 and 2010. Regime shift analysis using the changepoint package in R suggested that the change in zooplankton size, diversity and abundance was enough to be termed a regime shift. A weaker change was detected for 1998 and 2002. Though it remains to be seen whether the new regime continues or whether it was a temporal extreme. Nevertheless, the timings of these events coincide with changes in herring recruitment (Chapter II). The dependencies of herring recruitment are manifold and subject to cascading effects.

8.3 Herring recruitment and its relation to trophic cascades

Recruitment is the number of offspring that reach a certain life stage so that they can be counted as part of the fish stock. For example, we speak of recruitment to fishery if that life stage finally appears in catch statistics. It depends largely on the survival success of larvae during three critical periods: egg hatching and first feeding, larval drift and survival and finally growth and survival on the nursery grounds. Hjort famously declared the time of first feeding as the “critical period” (1914). The importance of the critical period has been highlighted by several studies as summarised by Houde (2008). Aberrant drift and member-vagrant hypothesis have also been confirmed to have potential effects on elevated recruitment of herring (Fortier and Gagné, 1990). Yet, these have mainly been tested against the start and endpoints of transport models (e.g. Christensen et al., 2007). Apart from physical transport and behaviour, the food web also acts on the survival of larvae during the drift. Predation and the growth out of the predator pit are crucial processes during the drift period (Bailey and Houde, 1989). Natural mortality is assumed to be very high (Peterson and Wroblewski, 1984; Pepin, 1993). Unfortunately, data is lacking and quantification is impossible. To estimate top-down control in herring larvae is thus difficult. In other areas like the Benguela upwelling system, end-to-end models were used to overcome this lack of data, but the modelling approaches vary in accuracy and performance (Travers et al., 2009).

That is the reason for the research focus on bottom-up controls for herring larval survival during the transportation phase between hatching and nursery grounds and the need for field data.

Unfortunately, lower trophic level data are scarce too. I sought after phytoplankton, temperature, salinity and zooplankton measurements collected during the transport phase of herring larvae. *In situ* measurements were rare and largely punctual (i.e. permanent monitoring stations of WGZE, ICES 2013). Satellite data were barely available due to cloud cover (i.e. HERMES). Winter data were largely unavailable because of these circumstances. In this study, I provide one of few comprehensive datasets and analysis on winter lower trophic level ecology in the southwestern North Sea. It was possible to relate larval survival to bottom-up controls. While initial abundances and survival of herring larvae could be related to large-scale indices like North Atlantic Oscillation index (NAO) and Atlantic Multidecadal Oscillation (AMO; Gröger et al., 2006) I could show that growth and ultimately survival is also linked to small-scale processes like primary and secondary production. In the Southern Bight, phytoplankton and zooplankton blooms were initiated near river outlets. In other parts of the study area, for example further offshore, an increase in primary production was visible as well, but not to a similar extent. This leads to the idea that certain prey fields for herring larvae exist. If the larvae are not transported through these prey fields they will have a diminished chance of survival (Hinrichsen et al., 2003).

Conclusively, local prey fields, induced by small-scale processes, support the survival of herring larvae. Depending on the currents leading through them, which are induced by large-scale processes, the small- and large-scale processes act together forming a general network of factors providing the forces required for successful herring recruitment. These are summarised in Fig. 24. In support of our findings and the trophic relationships is the increased recruitment of plaice from the eastern English Channel between 2009 and 2014 (ICES, 2017). Plaice larvae from the eastern English Channel were transported in a similar way and at a similar time as the North Sea autumn spawning herring larvae. It is very likely that the plaice larvae were subject to the same conditions as the herring larvae. For recruitment assessment, we need to investigate the spatio-temporal location of plankton prey fields even further. Drift models need to estimate the chance of reaching these prey fields and, using size spectrum theory (Hufnagl et al., 2015; Kühn et al., 2008), it is possible to calculate prey availability. These calculations, in addition to larvae surveys, can help project the recruitment for the current year and give better estimates for scientific advice. Prey field modelling has proven to be complicated, especially in a spatio-temporal context (Hinrichsen et al., 2002). Plankton analyses remain time consuming and labour intensive and often lack the spatio-temporal extend to be used for validation of models and monitoring. Particularly for the latter, indicators often prove to be handy (Beaugrand and Kirby, 2010). For plankton however, indicators are often based on taxonomic composition, which involves considerable labour and knowledge. That there are other options is what I showed in Chapter III.

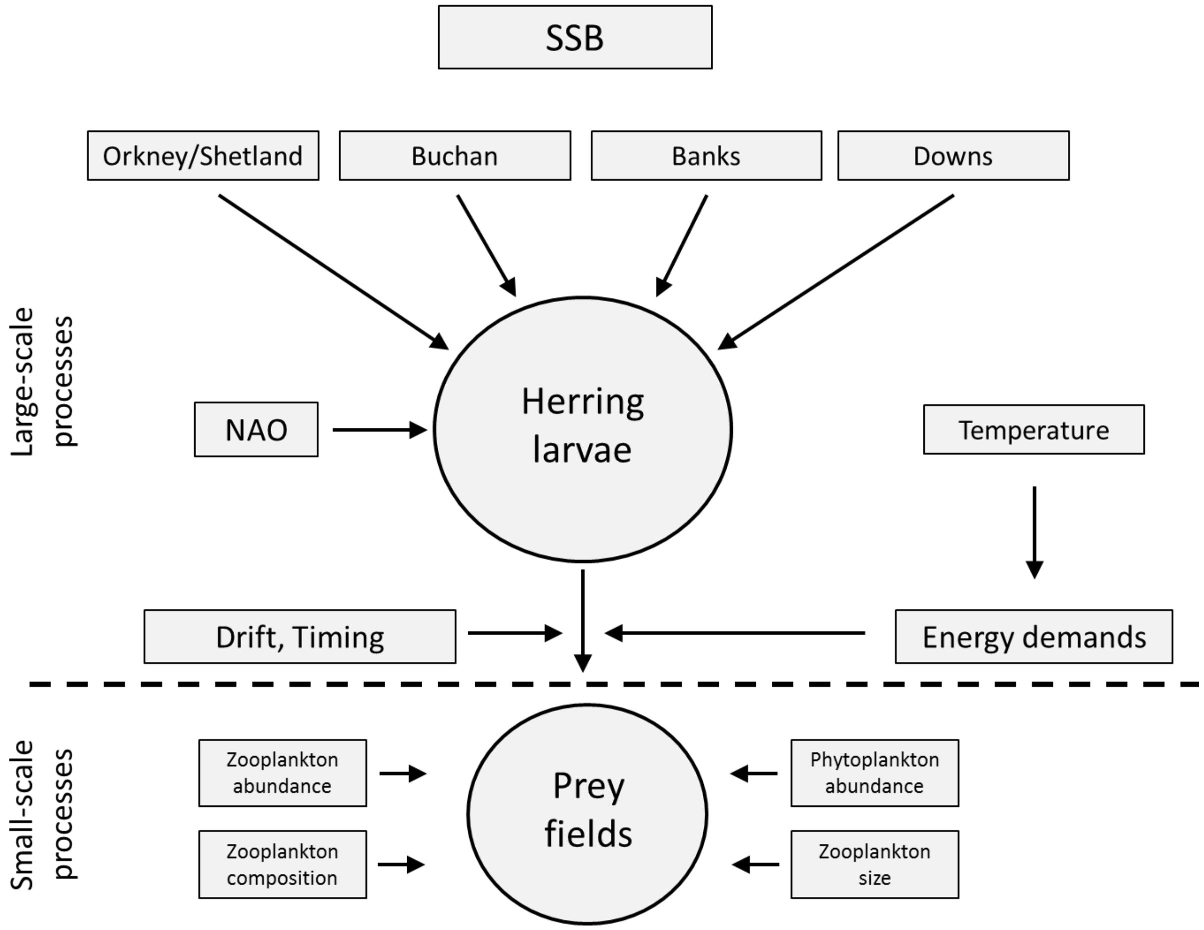

Fig. 24. Influence of small-scale and large-scale processes affecting herring larvae directly and indirectly through prey fields.

8.4 Size diversity and its potential as indicator for lower trophic levels

I related taxonomic biodiversity to size diversity in order to look for a new indicator that could be applied to ecosystem models and ecological assessment. The use of size for lower trophic levels has several advantages over taxonomic composition: It can be measured automatically, faster and it can be linked to other trophic levels in a continuous rather than factorial way. In comparison, cross-taxon congruence is one of the limitations of taxonomic biodiversity indicators (Heino, 2010). When considering larval survival and growth, the herring and plaice larvae have a certain prey size spectrum that they feed within. Size diversity can indicate the probability that there is sufficient food available to the larvae within their spectrum. Taxonomic diversity may also achieve this, but is based on the assumption that the larvae preferentially feed on a single or few species (Beaugrand et al., 2002). However, in case of changing ecosystems and projected shifts in species distributions the use of taxonomic biodiversity may be useful for detecting general change (Hooff and Peterson, 2006; Beaugrand et al., 2010). But for projections of fish larvae survival it is not. If one restricts larvae to feeding on only a few life stages of a few copepod species, for example, the probability of survival shifts with the location of these prey species. The spawning of fish is not solely environment driven, but rather subject to evolutionary constraints (Ciannelli et al., 2014). It is likely, if the prey's distribution changes, that the larvae cannot follow due the fixed starting position that is the spawning ground. In order to survive, larvae must then switch prey. The new prey must be in the same size spectrum as the previous. Size diversity or size spectra analysis can detect changes in the availabilities of prey sizes while taxonomic diversity cannot. The restriction by gape size of the larvae is more fundamental than the restriction by prey taxon or behaviour. A combination of both indicators could help detecting negative change in regard to good environmental status for fish larvae. Taxonomic diversity could detect a fundamental change and size diversity would than evaluate whether this change is critical to larvae survival. Although there have been recent efforts to include zooplankton size as a potential indicator (HELCOM, 2017), the assumption for good environmental status is different. It is thought that larger mean zooplankton sizes increase energy transfer efficiency to higher trophic levels compared to smaller zooplankton. This seems logical for adult planktivore fish like herring. For fish larvae though, smaller sized zooplankton may unveil options for prey switching and be advantageous in the end. It shows clearly that indicator choice and development is not an easy task. One indicator works for some trophic levels, some are plausible for certain seasons. Size, through the manifold relationships to physiological processes, behaviour and trophic interactions, has so far not been considered in a way that resembles its meaning in ecology. New instruments and procedures allow us to overcome this and incorporate size-structured data in ecosystem assessments.

9. Concluding Remarks

In summary, this thesis presents the bottom-up processes that take place in winter. Being so disregarded in the scientific community I can visualise the dynamics already starting at the beginning of the year before the rise of the annual spring plankton bloom. Winter blooms have been documented before, but very rarely so. It was surprising how little work has been done on that matter. As mentioned in all chapters of this thesis one of the main reasons is the lack of consistent data. While it is understandable that harsh sampling conditions in winter require good fortune and a wise survey plan, it is astounding how few surveys have been conducted in winter in Europe, when many commercially important fish species spawn and their recruitment success has been variable. Even more so, of those surveys conducted, samples have not been fully analysed and still contain much more information. This was one of the goals of my thesis: To show how much data is stored on shelves and provide information about uncommon events or locations. In chapter I I could show that the information contained in samples of the International Herring Larvae Survey gave rise to a rare time series of zooplankton in winter. In addition, I could measure individual zooplankton size, which is also a rare trait in datasets. Lastly, the dataset comes from a region that has not been sampled regularly, despite Continuous Plankton Recorder surveys at the northern margin of the study region and the fact that it is such a dynamic and ecologically important area. In chapter I and II it was possible to show that ecosystem changes occurred in winter. Zooplankton size decreased since the early 1990s and abundance increased abruptly in 2010 and 2011. The increase was related to the presence of primary production, especially in the vicinity of the Rhine-Meuse delta. My analysis in chapter I concluded that this unusual increase could have major implications for the successive cycle of phytoplankton-zooplankton-higher predator abundance, which would naturally start some weeks later. Abundances were of course much lower than during the spring bloom, yet, such early productive periods have largely gone unnoticed, although they would favour the overwintering standing stock of zooplankton with all its cascading links in the trophic pyramid. For further investigations, I recommend studying the phytoplankton and zooplankton development at the beginning of the year, leading from January to the start of the spring bloom in March/April. This would allow for investigations on match/mismatch scenarios and shifts in the timing of plankton blooms in the southern North Sea that may otherwise go unnoticed. It would also allow for the influence of the waters of the English Channel entering the North Sea and the effects of the riverine output of the Rhine-Meuse on the local ecosystem.

That herring larval survival is controlled by prey availability is not a new finding. But this thesis is the first study to correlate field data of zooplankton with data on phytoplankton and herring larvae. Variability of herring recruitment remains a phenomenon with too many possible reasons, but I could present evidence that a large portion of this variability can originate in the prey conditions early during the drift. Especially the potential of local prey fields such as the productive area of the Rhine-Meuse delta has not been considered before and needs further investigation. When considering prey for herring larvae survival, I advise to pay attention to size spectra of lower trophic levels. The reduction in herring larvae and zooplankton may show complementary patterns, but the occurrence of large quantities of small copepods indicates that prey size is crucial. With large variabilities in herring larvae size and availability of suitable prey temperature might become another important factor in the future that needs integration into research. Prey suitability is often investigated using species composition. Here, I showed that size also matters. Using size diversity in addition to biodiversity and perhaps normalised size spectra it is possible to monitor the availability of suitable prey. Using new plankton sampling devices size diversity provides opportunities as an indicator for environmental change and prey availability in the southern North Sea.

Size and winter abundances of zooplankton have largely been disregarded in science. With this thesis and the results therein I show the necessity to integrate zooplankton size and abundance as well as phytoplankton concentration in assessments of fish larvae feeding in winter and early spring in the southern North Sea. Monitoring the trophic relations can help detect changes in environmental status early and raise the options for coping with the challenges that climate change and fisheries management hold for us in the future.

10. References

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12. Eidesstattliche Versicherung, Declaration on oath

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hamburg, 29. September 2017