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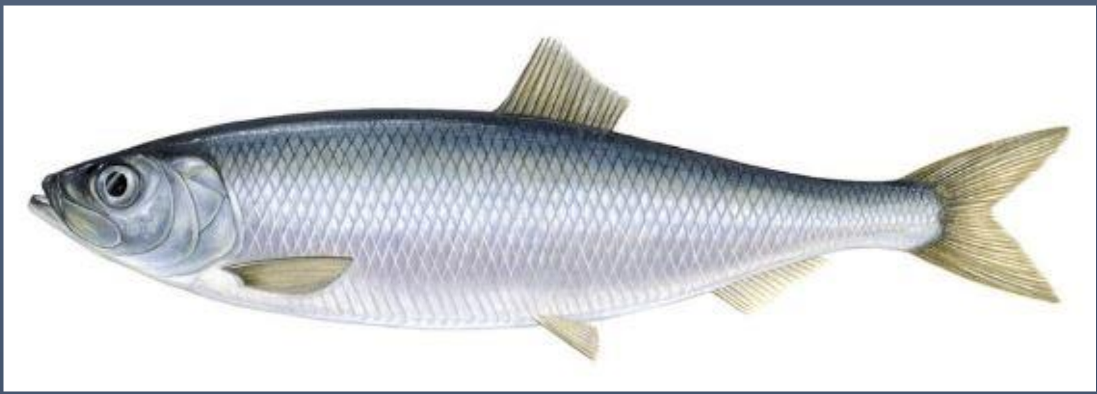

Identifying bottlenecks and knowledge gaps in the lifecycle of Wadden Sea herring for future management: A review

A bottleneck analysis on *Clupea harengus* for the Swimway Action Programme to build upon

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swimway
wadden sea

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Cover: *Clupea harengus* (Marine Stewardship Council, n.d.)

Preface

Before you lays a complete bottleneck analysis on Atlantic herring (*Clupea harengus*) within the Wadden Sea, which is written on behalf of the Swimway Action Programme, established by the Wadden Sea Board. This document may be used by the Swimway Action Programme to achieve their Trilateral Fish Targets and provides a basis for successive research on other fish species.

The results in this literature study could not be achieved without the help and cooperation of a small group of researchers and lecturers of Van Hall Larenstein, University of Applied Sciences. Special thanks go to our supervisors dr. Peter Hofman and David Goldsborough, who aided us in the making of the analysis and provided constructive feedback. Paddy Walker, Head of Science at the Dutch Elasmobranch Society and, in case of the analysis, client; put a lot of time and effort in helping to provide structure to the analysis. All three experienced and accommodating researchers helped out, as fast as possible, whenever problems occurred. This study was executed as part of our thesis, with which we finalized our bachelor's degree. We want to thank Alwin Hylkema, our opponent, in advance for testing our skillset acquired during Coastal and Marine Management (BSc).

Subsequently, we want to express our appreciation towards dr. Andreas Dänhardt (University of Hamburg) who was kind enough to provide feedback on the sources used within the analysis and provided additional information. He did not have to help us, but he chose to provide his services, increasing the credibility of this analysis.

Finally, special thanks go to all the researchers included in the analysis. Without their results, the creation of an overview of the lifecycle of herring, including bottlenecks within, would have never been possible.

Abstract

Due to the recent trend of fish stock decline in the Wadden Sea, conservation objectives on fish (Trilateral Fish Targets) have been set by the Wadden Sea Board, in a project called 'Swimway Action Programme'. However, lack of precise knowledge on the lifecycle of target fish species is largely missing, making it impossible for Swimway to manage fish stocks successfully. Therefore, this analysis was focused on the lifecycle of Atlantic Herring (*Clupea harengus*), encountered in the Wadden Sea, including bottlenecks identified within. Of the four main spawning stocks in the North Sea area, only the Banks stock and the Downs stock utilize the Wadden Sea during their lifecycle. Herring spawning in the North Sea begins in September in the North, seizing in the South at the end of January. The timing of spawning is fixed, occurring at the same time every year. After hatching, Downs and Banks herring larvae passively drift towards the southern North Sea, including the Wadden Sea, by means of currents created by winds and the North Atlantic Oscillation. After herring larvae reach the nurseries during Spring, they take advantage of plankton blooms which commonly appear during this part of the year. In these nurseries, in which the herring reside for the first 2-3 years of their life, larval herring morph into juveniles and, subsequently, adults. After reaching adulthood, herring move into the deeper central North Sea to feed. When spawning occurs between September and January, inexperienced herring will follow experienced herring to their spawning ground, to which they will return for spawning in the upcoming years. Within this lifecycle, both natural bottlenecks (temperature changes, hydrodynamics and salinity changes) and men-induced bottlenecks (eutrophication, gravel extraction, fishing, oil exploitation, construction of wind turbines, military activity and dredging) were considered. After an intensive literature study, global warming seems to be the main driver of ecological changes within the North Sea area. However, it is unclear if this is due to a direct effect of temperature increase, forcing herring into cooler waters, or an indirect effect in which the main prey species of herring is decreasing in biomass. However, due to the fixed nature of herring spawning, a change in the duration and timing of plankton blooms, caused by increased temperatures, might have catastrophic consequences. Upcoming increases in temperature are expected to further accelerate changes in the area and might go along with a decrease in salinity, due to expected increases in fresh water runoff, and an increase in water mass stratification. Some even expect a future increase in harmful algal- and jellyfish blooms. While changes in hydrodynamics are not responsible for the overall problem, they have the potential to either amplify or reduce the effect of climate change. Currently, most men-induced stressors in the area either pose limited or no threat to the different life stages of herring. This mostly has to do with strict management policies (extraction & fishing) or the implementation of impact reducing measures and continuous improvements (oil exploration, construction/use of wind turbine parks and military activity). However, within the Wadden Sea, dredging activity and military activity are high but poorly studied. Since the Wadden Sea is an important nursery area for Banks and Downs herring, more research on the effect of intensive dredging and heavy metal input by military activity is required. Also, the Wadden Sea is called a 'eutrophication problem area' by the OSPAR Commission and both monitoring intensity and research, on the effect of eutrophication on herring, should increase. With more data on the effect of eutrophication, intensive dredging and ongoing military activity in the Wadden Sea, additional management can be introduced, if necessary. Though ongoing climate change cannot be countered by human management, the eutrophication and lack of knowledge on human activity can be, to optimize the nursery function of the Wadden Sea for Atlantic herring and other pelagic species. The outcome of this analysis may be used by the Swimway Action Programme as a preliminary piece of information and provides a basis for successive research on the other Swimway species. Ultimately, this analysis might aid in the completion of the Trilateral Fish Targets within the Wadden Sea.

Table of contents

Glossary

ACL - *Annual Catch Limit*

CFP - *Common Fisheries Policy*

ICES - *International Council for the Exploration of the Sea*

MSFD - *Marine Strategy Framework Directive*

NAO - *North Atlantic Oscillation*

NIOZ - *Koninklijk Nederlands Instituut voor Onderzoek der Zee*

NMFS - *National Marine Fisheries Service*

NOAA - *National Oceanic and Atmospheric Administration*

OSPAR - *The Convention for the Protection of the Marine Environment of the North-East Atlantic*

TAC - *Total Allowable Catch*

TGC - *Trilateral Governmental Conference*

USA - *United States of America*

WFD - *Water Framework Directive*

WSB - *Wadden Sea Board*

1. Introduction

The Wadden Sea is one of the largest intertidal wetlands in the world (Wadden Sea Board, 2018). It provides a lot of different ecological functions for about 150 different fish species (Bolle et al., 2009; Walker, 2015), and is primarily used as a spawning and nursery area. It also provides a location to acclimatise and is used as a transition route for long distance diadromous fish (Walker, 2015). Because of these important ecological roles, the Wadden Sea is legally protected. The Wadden Sea is protected within the Bird and Habitat directive of Natura 2000, the Water Framework Directive (WFD), Marine Strategy Framework Directive (MSFD) and is listed in the World Heritage list (UNESCO, 2009). Since 10-12 million migratory birds utilize the Wadden Sea area every year as an important roosting spot, a lot of attention is focused on the conservation of different bird species (Tulp et al., 2008). However, due to the illusive nature of fish, conservation of fish is less developed. Since the Wadden Sea covers both Dutch, German and Danish surface area, it is protected by a trilateral cooperation of the Netherlands, Germany and Denmark (Wadden Sea Board, 2018).

In recent decades, fish populations have steeply declined (Sguotti et al., 2016) or shifted away from the Wadden Sea (Tulp & Bolle, 2018). The causes of these declines in fish stocks is only partially known or understood and has not been fully recorded (Wadden Sea Board, 2018). These declines can be due to various causes. Causes vary from human induced factors such as overfishing, pollution or habitat degradation (Lotze, 2005; Seitz, 2013) to the influence of environmental factors or climate change (Rose, 2005). Well studied environmental factors, which are known to have an effect on fish movement, are temperature, salinity, seasonal variation and food availability (Schlaff, 2014). These factors can also be the cause of bottlenecks in the lifecycles of different fish species. A bottleneck is a constraint on a species ability to survive, reproduce or recruit to the next life stage (Atlantic States Marine Fisheries Commission, 2016). Bottlenecks have the potential to drastically reduce the size of a population.

In the Wadden Sea alone, multiple methods of collecting data on fish take place. Methods range from large-scale beam trawling to local placement of fykes by research institutes NIOZ and Wageningen Marine Research. Consistent data collection in the Wadden Sea started as early as 1960 and multiple methods are used to assure that the fishing is not selective in nature. Trends suggest that commercially important species, which use the area as a nursery, are declining in numbers throughout the years, while small commercially unimportant species are increasing in numbers (Tulp et al., 2017). A demersal Fish Survey conducted by Wageningen Marine Research, shows a decrease in biomass of fish that use the area as a nursery ground. Between 1970 and 1980, off the Wadden Sea coast, roughly 15 kg/km^2 of juvenile fish was towed on a regular basis. Between 2011 and 2014, at the same location, regular catch rates are closer to 5 kg/km^2 of juvenile fish. Similar decreases in biomass are encountered in all parts of the Wadden Sea (Tulp et al., 2008). Surveying started earlier in the North Sea, at the beginning of the 20th century, making data on the North Sea plenteous for most species of fish (Rijnsdorp et al., 1996; Sguotti et al., 2016).

The surveys regarding teleost fish species did also continue in, and cover all of, the North Sea (Daan et al., 2005). This paper describes that, of all commercial species between 0 and 120 cm in length, large individuals decreased in numbers throughout the years. Intensive fishing is the expected driving factor for this phenomenon. However, changes in distribution and numbers of fish are not all directly caused by human impact. A paper written by Dulvy et al., (2008) shows the effect of temperature on distribution of teleosts. Papers like these indicate that species which prefer warmer waters are moving to shallow, coastal areas while cold water species are migrating to deeper waters. Overall, the North Sea demersal fish assemblage (28 species) has moved to deeper waters at a significant rate of ~3·6 m decade−1, indicating that global warming has profound effects on fish stocks (Dulvy et al., 2008). Consequently, a northward movement of specific fish species in the North Atlantic, as a result of warming temperatures, has also been recorded (Corten, 2001a; Rose, 2005).

Because of the decline in many fish populations within the Wadden Sea, Danish; Dutch and German fish experts have proposed that changes need to be made to reverse current trends in fish diminution. As a result, conservation objectives for fish were developed. These objectives were called Trilateral Fish Targets and were adopted at the 11th Trilateral Governmental Conference (TGC) as a part of the revised Wadden Sea Plan 2010. In the 12th TGC it was agreed that these Trilateral Fish Targets where to be further implemented. During this conference, the targets where passed to the Wadden Sea Board (WSB). The WSB then developed the Swimway Action Programme, in which the problems responsible for the fish decline in the Wadden Sea will be researched and, if possible, tackled. The Swimway Action Programme was signed at the Ministerial Conference in 2018 in Leeuwarden and focuses on 4 pillars: research/monitoring, management, counter measures and communication/education. The WSB now carries the responsibility to further implement these targets (Wadden Sea Board, 2018).

The Trilateral Fish Targets are to **maintain or improve**:

- *robust and viable populations of estuarine resident fish species within the Wadden Sea;*
- *the nursery function of the Wadden Sea and estuaries;*
- *the quality and quantity of typical Wadden Sea habitats;*
- *passage ways for fish migrating between the Wadden Sea and inland waters;*
- *conservation of endangered fish species within the Wadden Sea* (Wadden Sea Board, 2018).

The ultimate goal of Swimway is to implement these fish targets in real live (Wadden Sea Board, 2018). However, to realise these targets, first research needs to be done. Basic understanding on the functioning of the Wadden Sea within the lifecycle of different fish species is lacking. Without this knowledge, conservation cannot be specified, which makes it less likely for the Trilateral Fish Targets to be implemented. These targets include different fish species which all utilise the Wadden Sea in their own way. The different ways in which the Wadden Sea is used by fish species is shown in figure 1. Multiple species need to be evaluated because different species require different circumstances to thrive. Because of this, Swimway has divided fish, which utilise the Wadden Sea, into 5 different groups. For each group, a flagship species has been chosen which represents a fleet of species with a similar lifestyle. With this approach, management aimed at the flagship species will also be applicable for species which have a similar lifestyle as the flagship species. These groups and flagship species were chosen by Swimway experts, following Elliott et al., (2007).

The groups and their flagship species are (Wadden Sea Board, 2018):

- *Pelagic marine juvenile species* (Herring, *Clupea spp.*)
- *Demersal marine juvenile species* (Plaice, *Pleuronectes spp.*)
- *Wadden Sea residents* (Eelpout, *Zoarces spp.*)
- *Diadromous species* (Smelt, *Osmerus spp.*)
- *Marine adventitious species* (Tope, *Galeorhinus galeus*)

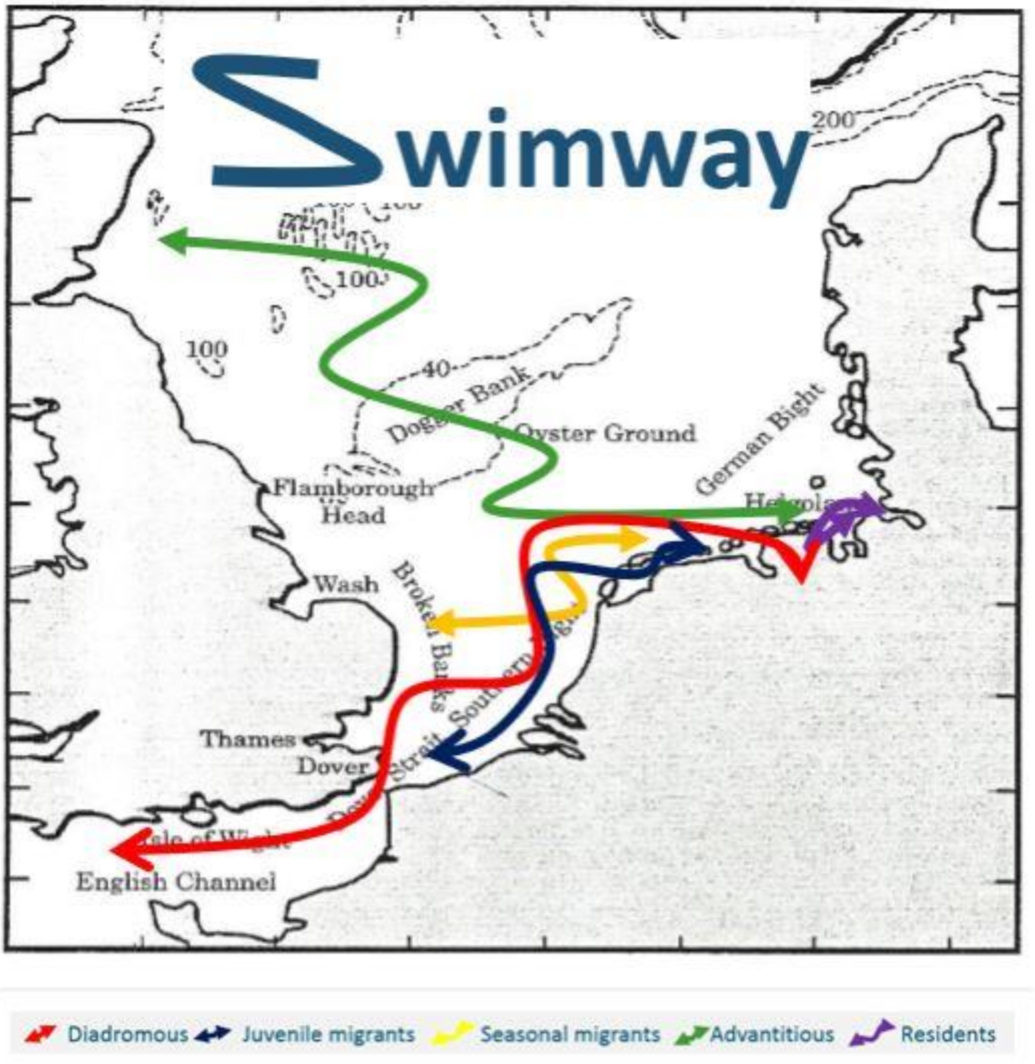

Figure 1: *Map showing the migratory paths of different fish species within the North Sea and Wadden Sea (Tulp & Bolle, 2018).*

This study focuses on Atlantic herring (*Clupea harengus*) which represents the 'Pelagic marine juvenile species' in the Wadden Sea. Only one Swimway species was chosen because of the limited timeframe set for this research. It is expected that the herring utilizes the Wadden Sea as a nursery ground (Coull et al., 1998). It has traits like fast maturity rates and a high fecundity and only small migrations between spawning and feeding grounds are documented (Ellis et al., 2012; ICES, n.d.; Petitgas et al., 2010). This means that the scope of North Sea herring includes the English Channel, Wadden Sea and North Sea but will probably not extend further than this (Dickey-Collas et al., 2010). There is abundant research available on herring (Ellis et al., 2012; Haslob et al., 2009; ICES, n.d.; Lindegren et al., 2011; Petitgas et al., 2010). However, information on the importance of the Wadden Sea within the lifecycle of herring is largely missing, preventing a complete lifecycle description.

In general, a lot of information on catch rates and changes in fish stocks is already present (Tulp et al., 2017). However, research is not linked together to form a complete lifecycle overview. Therefore, it is impossible to attempt to manage herring fish stocks and achieve results as described in the Trilateral Fish Targets, since further progression of the Swimway Action Programme is hampered by a lack of information. This is why a bottleneck analysis was conducted, using the available data and information. Where a shortage of knowledge was found, knowledge gaps were identified instead. This analysis, including recommendations on future measures and knowledge gaps, can be used for, and might support, management decisions and research in the future. Primarily, this analysis provides an overview of current as well as missing knowledge on one of the Swimway flagship species, which can be used by the project to realize the Swimway targets.

This study was conducted for the Lectorate Coast & Sea of the Van Hall Larenstein, University of Applied Sciences, and can serve as basis for Swimway. It may be used as preliminary research on one Swimway group (Pelagic marine juvenile species) and can subsequently be used as a guide for research into the other Swimway groups.

To aim and provide structure to the analysis, multiple research questions were formulated.

The main question is:

- *What bottlenecks and knowledge gaps occur within the lifecycle of herring (Clupea harengus) in relation to the Wadden Sea and how can these be countered?*

Which is divided into different sub-questions:

- *What does the lifecycle of herring look like within the North- and Wadden Sea?*
- *What are the bottlenecks and knowledge gaps encountered within the lifecycle of herring in relation to the Wadden Sea?*
- *How can the identified bottlenecks and knowledge gaps for herring be countered in relation to the Wadden Sea?*

2. Justification of material & methods

In this chapter, the methods of acquiring data are elaborated. This includes a small description of the study area, general rules on online searching and used methods for answering each sub-question.

2.1. Study area

The focus of this study was on the bottlenecks and knowledge gaps within the lifecycle of the herring, within the Wadden Sea (Figure 2). This includes the Dutch, German and Danish part of the Wadden Sea. In the lifecycle description, areas outside the Wadden Sea, mainly the North Sea, are also identified when said areas turn out to be important within the lifecycle of herring. However, efforts to counter found bottlenecks did only take place when a bottleneck was located in, or could be countered within, the Wadden Sea itself since project Swimway specifically acts in the Wadden Sea and not outside of this area. Whenever specific data on herring within the Wadden Sea was scarce or absent, information from the Gulf of Maine (USA) was used since the same species occurs in the area and, at this side of the Pacific, research on herring is plentiful as well.

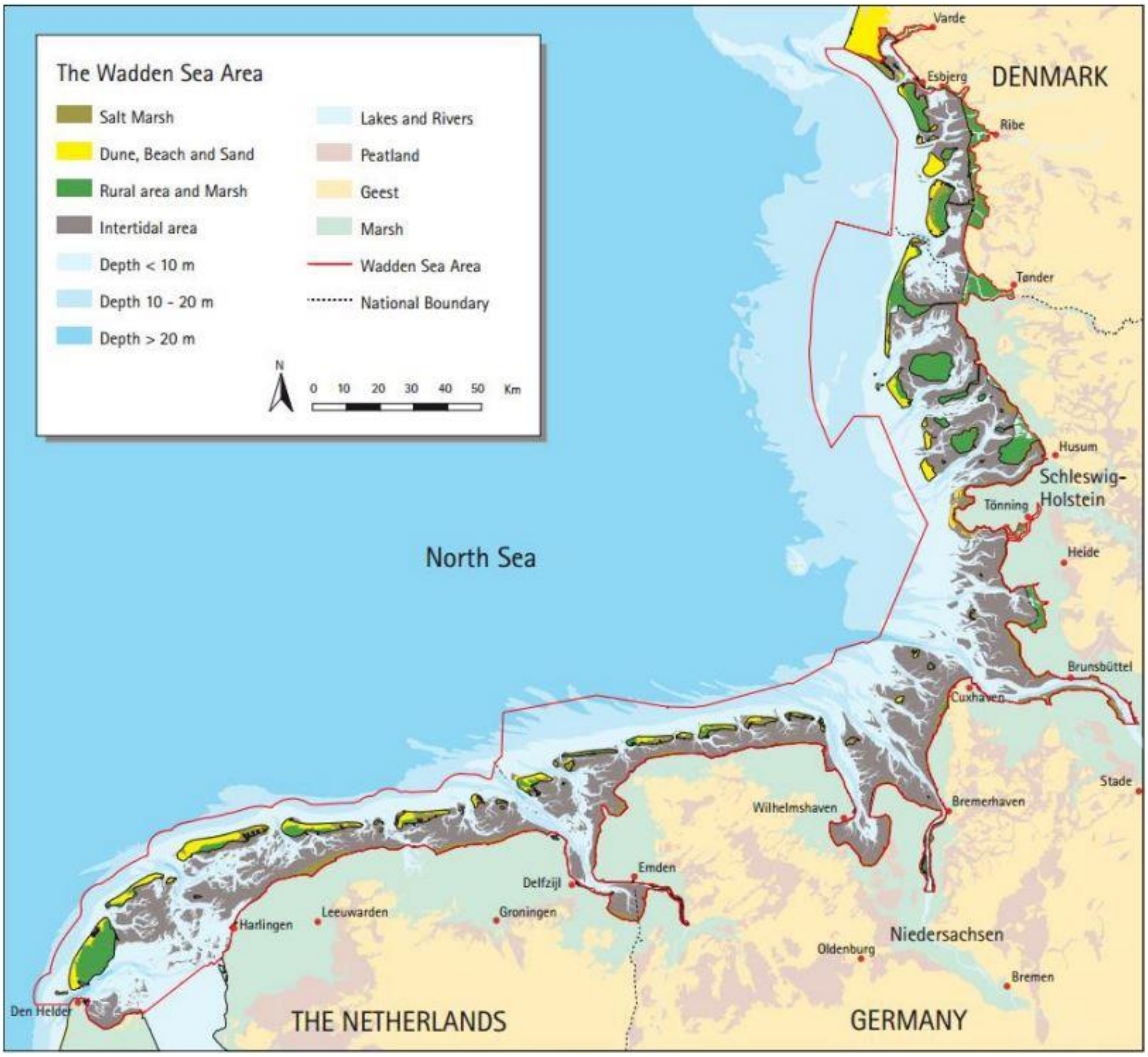

Figure 2: *Wadden Sea area and conservation areas within the Wadden Sea (Wadden Sea World Heritage, 2018).*

2.2. Research matrix

To aid this analysis, a research matrix was created (Choguill, 2005). A research matrix is a useful tool for the identification of key processes, bottlenecks and knowledge gaps within the lifecycle of herring. An example of the research matrix, and some of the themes within, is shown in table 1.

Table 1: *Example research matrix.*

	Key aspects				
Authors	*Spawning grounds*	*Larval distribution*	*Nursery grounds*	*Feeding grounds*	*Migratory paths*
Corten, 2013.				"The larvae take advantage of the spring plankton bloom."	"The precise migration of adult herring is unknown; presumably they migrate in a dispersed manner."

In a research matrix, key aspects of the lifecycle (or other subject) are written down according to different (online) articles. In this matrix, only the main findings of each source are included and compared. Are there any key aspects which are reoccurring? Do all sources agree on the same key aspects or are there differences between sources (and what is the cause for these differences)? This matrix will help to make (online) articles more accessible for the analysis and it will create a solid database. The final research matrix can be found in the Appendix.

2.3. Literature review

To answer the different sub-questions, a literature review, focusing on ecology, distribution and management of the fish species was executed. The availability of data determined if either bottlenecks or knowledge gaps were identified, with knowledge gaps being identified when data was scarce and a full lifecycle description could not be produced. To achieve the best possible result, primarily peer-reviewed scientific articles were used, especially for the ecological background. These articles had to be:

- *Posted by a(n) writer/organization adequate to the subject;*
- *Peer-reviewed (in case of issued scientific articles);*
- *The latest available version.*

However, grey sources like ICES databases and management plans were also used, since management is seldom peer-reviewed in the way scientific articles are.

Different search engines were used to search for online literature on the subject. The search engines used in this study included Google Scholar, Greeni and the ICES database. To make accurate searching possible, certain general keywords were used among multiple sub-questions. These keywords can be found in table 2.

Table 2: *Keywords used during literature research.*

General Keywords (included but were not limited to):
Adult, Atlantic, Bottlenecks, *Clupea harengus*, Counter measures, Decline, Disturbance, Effect (of), Estuary, Function, Herring, Human impact, Juvenile, Larval, Larvae, Lifecycle, Life stage, Migration, Mortality, North Sea, Recovery, Reproduction, Requirements, Stock, Substrate, UK/ Great Britain, Wadden Sea.

These keywords were used in combination with each other while searching for online literature. Latin names were used over the English names since it might provide useful Dutch literature that would otherwise be hidden, and it bypasses the inconsistency in common name use. Beside these general keywords, specific key aspects were used for the different sub-questions in the analysis. For this reason, all sub-questions are independently elaborated.

Sub-question 1: ***What does the lifecycle of herring look like within the North- and Wadden Sea?***

While answering the first sub-question, the focus was on available knowledge on ecology, biology and behaviour of herring. Most of the online searching was aimed at important lifecycle aspects of herring within the North- and Wadden Sea. This part was of great importance since it is impossible to discover problems in an animals' lifecycle when the lifecycle itself is undocumented.

For this part of the analysis, the most important aspects are the animals':

- *Spawning grounds;*
- *Larval distribution;*
- *Nursery grounds/nurseries;*
- *Feeding behaviour;*
- *Migratory patterns.*

In combination with the general keywords previously described, these aspects were used to accurately acquire online information. Examples of such search queries are: 'Migratory patterns among different life stages of *Clupea harengus* in the North Sea' or 'Nursery function of the Wadden Sea within the lifecycle of *Clupea harengus'*. During active online searching, 'spawning grounds' were identified first and the next lifecycle aspect was actively searched for after completion of the first. However, when found articles cover multiple aspects, all important findings were added to the research matrix.

When all five key aspects of the lifecycle of herring are identified, a complete lifecycle description can be provided by linking the different aspects together within the North Sea and Wadden Sea region. As is expected with herring, knowledge will be plenteous enough for the lifecycle to be identified within this area. During online searching, the focus was on the Wadden Sea, North Sea and the English Channel, since these bodies of water are used within the lifecycle of Wadden Sea herring (Dickey-Collas et al., 2010). Thus, data from the North Sea and English Channel was included in the analysis since data on herring within the Wadden Sea alone is insufficient for a complete lifecycle description. Useful articles, including the main findings which were used in the analysis, were inserted into the previously described research matrix to ensure that the various findings can accurately be linked together (Appendix 1).

Sub-question 2: ***What are the bottlenecks and/or knowledge gaps encountered within the lifecycle of herring (Clupea harengus) in relation to the Wadden Sea?***

While answering the second sub-question, the focus was on the bottlenecks and knowledge gaps encountered within the previously identified lifecycle of herring. Bottlenecks were pinpointed from literature and thereafter processed in the research matrix to structure the information found. For the identification of bottlenecks, five stressors were used which are known to impact fish populations and marine habitats on a global scale (Bonsdorff et al., 1997; Lotze, 2005; Rose, 2005; Seitz, 2013).

The key themes used in the research matrix are:

- *Climate change (temperature, hydrodynamics and salinity);*
- *Eutrophication;*
- *Food availability;*
- *Fishing pressure;*
- *Other human activities.*

The effects of each stressor were primarily researched in articles covering the Wadden Sea and the North Sea since the Wadden Sea herring resides in this area. When information on the effects of each stressor, on herring as a species, was missing, another species with a similar lifestyle was used instead. Research outside of the area was also used if it includes herring and the effects of different stressors elsewhere. However, the research area needed to be comparable to the Wadden Sea or found stressors needed to be present in the Wadden Sea to make the article useful for the analysis. Important findings were added to the research matrix (Appendix 2).

After stressors (and their effect range) were identified through this literature study, the earlier acquired knowledge on the lifecycle of herring was used to pinpoint the bottlenecks in which a stressor collides with an important aspect of the lifecycle of herring. If climate change turned out to be responsible for the bottlenecks within the lifecycle of herring, no further recommendations are made since the problem is unlikely to be reversed by human hand if it is forced by global warming. However, if other stressors are responsible for potential bottlenecks **and** said bottlenecks can be countered within the Wadden Sea, possible conservation or management is further discussed in sub-question 3.

Sub-question 3: ***How can the identified bottlenecks for herring (Clupea harengus) be countered in relation to the Wadden Sea?***

The third sub-question was answered via literature review and by using the results found in the previous sub-questions. By reviewing the results found in the previous sub-questions, possible bottlenecks and knowledge gaps within the lifecycle of the herring have become clear. Subsequently, possible solutions were looked at. First, current management on herring, and possibly on the existing bottlenecks, within the North Sea and Wadden Sea were reviewed. What kind of management on herring does already exists and is there already existing management for the potential bottlenecks found earlier? By which management bodies are these already existing policies employed? Are there policies elsewhere in the world that prove to be more effective than the current ones employed in the Wadden Sea and could these policies also counteract the bottlenecks found in the Wadden Sea? These questions aided in assessing the effectiveness of current management and policies. Currently most of the Wadden Sea is managed under the WFD and the Natura 2000 by the EU and the trilateral cooperation. The management policies differ per country, resulting in different management objectives being set. After assessing the management policies on herring, both in the Wadden Sea area as well as elsewhere in the world, suggestions were made on how current management can be reformed to relieve pressure of the identified bottlenecks.

After answering all 3 sub-questions, the main question was answered by combining the results.

3. Results

3.1. Sub-question 1: *What does the lifecycle of herring look like within the North- and Wadden Sea?*

The lifecycle of North Sea/Wadden Sea herring is described in this chapter. A complete description of the lifecycle is given, starting at the hatching of larval herring till the spawning of adult herring. It explains what requirements are necessary for herring to thrive during different life stages and how it migrates during different life stages.

3.1.1. Spawning grounds:

To better understand the lifecycle of herring in the North Sea, it must be noted that there are big differences among herring populations which utilize the North Sea during their spawning and feeding migrations. For this analysis, the focus was on herring which, at some point in their lifecycle, reside in the Wadden Sea. However, part of the North Sea herring population does not utilize this area at all. This has to do with the fact that the North Sea population comprise four main spawning components which all differ in spawning grounds, migration routes and growth rates (Dickey-Collas et al., 2010; Herdson & Priede, 2010). These components are the: Shetland/Orkney stock, Buchan stock, Downs stock and the Banks stock (figure 3). Together they are known as the North Sea autumn spawning herring. There is also the smaller Norwegian spring spawning herring stock which is located near the Norwegian coast, however, this stock is of lesser importance to the North Sea fisheries and is not connected to the Wadden Sea. Spawning of the main North Sea herring population begins in the north at the Shetland/Orkney stock in September and then progresses southwards with time, usually ceasing in January in the eastern English Channel where the Downs stock is located (ICES, 2015; Payne et al., 2009). It is a common hypothesis that the timing and duration of spawning of the different herring stocks is based on the time necessary to complete the larval phase and metamorphose within a time period of sufficient food availability and suitable seasonal variables. Stocks spawning in areas which are good for larval retention can sometimes spawn in the spring and still metamorphose within the seasonal envelope. However, stocks with larval retention areas that are less suitable for larval growth must spawn earlier, or the two requirements will not be satisfied, resulting in mortality (Sinclair & Tramblay, 1984). Research by Secor (2007) shows that seasonal egg and larval production is often mistimed with periods of favourable survival conditions, indicating that it is unlikely that autumn-spawning herring can avoid unfavourable conditions by delaying their spawning time or by spawning on more northern located grounds because of limitations in daylength to larval growth and survival (Hufnagl & Peck, 2011). This results in something called the match-mismatch theory (Sinclair & Tramblay, 1984) in which herring has fixed spawning periods while the timing of phytoplankton blooms shows yearly variation, resulting in either good or bad yearly population strength.

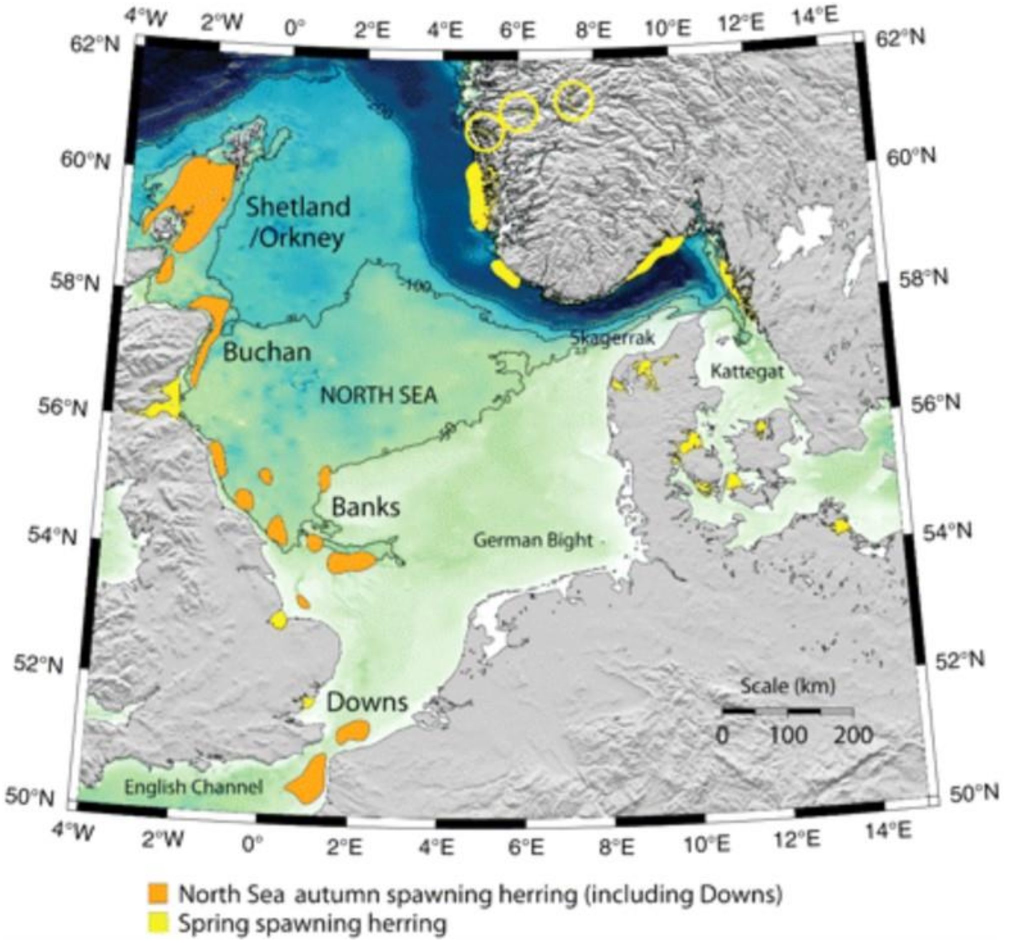

Figure 3: *An overview of the North Sea showing the different herring stocks. The yellow circles denote locations of spring spawning herring which utilize fjords for spawning (Dickey-Collas et al., 2010).*

North Sea herring are synchronous batch spawners that deposit mats of benthic eggs on coarse sand, gravel, shells and small stones (Fässler et al., 2011; ICES, n.d.; Reid et al., 1999). Of these different spawning substrates, gravel is preferred (Reid et al., 1999) and utilized by herring within the North Sea. Preferred spawning temperature slightly vary between different herring populations (10°-14°C: North Sea; 5°-15°C: Gulf of Maine) forcing most spawning areas to be in relatively shallow waters between 15-40 meters deep, though spawning in deeper waters does occur (De Groot, 1979a; ICES, n.d.; Reid et al., 1999). Around these ranges, adaptive flexibility to temperature has been documented among different stocks (Jennings & Beverton, 1991). During spawning, shoals of mature herring congregate near the seabed, where females perform specialized movements to adhere a ribbon of eggs to the substratum, after which the males shed the surrounding area with milt. The result is an area, up to one hectare, which is covered in multiple stacked layers of eggs (Gulf of Maine Research Institute, n.d.; ICES, n.d.; Stratoudakis, 1998). The (potential) large number of offspring ensures that at least a few survive, despite high mortality (Gulf of Maine Research Institute, n.d.). Average size, weight and number of eggs per female vary between stocks (ICES, n.d.). Eggs on the bottom layer are often less developed due to a process called retardation. Retardation occurs due to a decrease in oxygen supply and insufficient flushing of waste products resulting from a restriction in water circulation in the lower egg layers. As a result, juveniles hatched from these layers tend to be smaller in size (Gulf of Maine Research Institute, n.d.; Stratoudakis, 1998). However, eggs on the bottom layer are less vulnerable to predation than eggs in the upper layer (Gulf of Maine Research Institute, n.d.). Depending on temperature and location, North Sea herring eggs hatch between 7-15 days after which they enter a yolk-sac stage lasting another 10-15 days (Gulf of Maine Research Institute, n.d.; Dickey-Collas et al., 2010; ICES, 2015; Reid et al., 1999). It is at this stage that herring larvae are dispersed to their nursery grounds by means of ocean currents (Gulf of Maine Research Institute, n.d.; ICES, n.d.) of which only the Banks and the Downs stocks are expected to reach the Wadden Sea, as is stated by herring expert A. Dänhardt (personal communication, 6 June 2018). Research has shown that North Sea herring, from hatching to the end of the yolk-sac stage, can temporarily deal with temperatures up to 23,5°C; rendering the pre-hatching phase as the most temperature vulnerable phase (Yin & Blaxter, 1987). However, years with low recruitment were sometimes associated with higher temperature resulting in higher larval growth rates and increased consumption of the yolk-sac (Dickey-Collas et al., 2010). Salinity seems to be less important than temperature for the development of young herring, since the larvae and eggs of herring near the coast of Maine can withstand a wide salinity range (Gulf of Maine Research Institute, n.d.). Even though most adult North Sea herring engage in seasonal mixing in search of food, birth site fidelity is relatively fixed and natal homing occurs among the different stocks (Ruzzante et al., 2006; Sinclair & Power, 2015).

3.1.2. Larval distribution:

Larval and adult stages of herring are very different in appearance. Larval herring have a long and slender body, are transparent and entirely lack scales. Larvae are approximately 5 to 7 mm long when they hatch and carry a yolk-sac that provides a mobile food reserve for up to 15 days after hatching, during which the mouthparts develop (Gulf of Maine Research Institute, n.d.). During the mouthpart development, the larvae start to feed on *Artemia* sp. Nauplii, and other small prey (Batty et al., 1990; Gulf of Maine Research Institute, n.d.; ICES, n.d.; Kellnreitner, 2012), in the light by filtering as well as (occasionally) snapping towards food, while in the dark they can only filter feed (Batty et al., 1990). Vertical migrations of herring larvae are observed as a way to optimize feeding efficiency in the water column. Minor changes in salinity and temperature during this vertical migration do not negatively affect the larvae (Haslob et al., 2009). At this feeding-phase, mortality is catastrophically high, especially for larvae which got transported to improper areas which lack the requirements for larval survival (Gulf of Maine Research Institute, n.d.).

After mass-hatching has taken place in the Western North Sea between September and January, larvae are dependent on hydrographical conditions for successful dispersion, which may vary from year to year (Philippart et al., 1996). As a result, dispersion patterns strongly depend on hatching location. For example, in the Gulf of Maine some larvae are retained for several months after hatching on or near the spawning site, while other larvae are dispersed by residual currents soon after hatching (Reid et al., 1999). In the North Sea, larvae are transported in winter across the western North Sea towards the nursery areas in the eastern North Sea, like the German Bight, which surviving larvae arrive at in February (Corten, 2013; Dickey-Collas et al., 2010; Fässler et al., 2011; ICES, n.d.). Some researchers estimate that only about 1% of herring larvae survive to become juvenile fish (Gulf of Maine Research Institute, n.d.). Inshore areas which are located in the path of prevailing North Sea currents (figure 4), like the Wadden Sea, are also populated. For both Downs and Banks herring in particular, this passive transport by ocean currents to suitable nursery habitat (figure 5) is an important aspect of the lifecycle (Sinclair & Power, 2015) and forms a critical factor for larval survival (Corten, 2013). The southern North Sea, in which these two stocks reside, receives only a limited input of Atlantic water due to the narrow passage through the Strait of Dover. This results in a big contribution of wind conditions in the area on the dispersal of these herring larvae. Not only wind conditions affect the hydrographical conditions in the North Sea, also the North

Atlantic Oscillation (NAO) has pronounced influence and these two even go together (Corten, 2001a; Rafferty, 2011). The NAO is an irregular fluctuation in atmospheric pressure over the North Atlantic Ocean which can occur on a yearly basis or can take place decades apart. It has a 'positive' mode (high NAO-index) in which a strong high-pressure system is located over the Azores islands while a strong low-pressure system is centred over Iceland, and a 'negative' mode (low NAO-index) in which these pressure systems are weak (Rafferty, 2011). This phenomenon affects local winds, which subsequently affect the shelf edge current, ultimately influencing the Atlantic inflow into the North Sea which distribute herring larvae to their nursery habitats (Corten, 2001a). Winters with a low NAO-index and low water temperature often coincide with high recruitment numbers of herring (Philippart et al., 1996). This might have to do with reduced metabolic rates during lower temperatures (Dickey-Collas et al., 2010). Commercial stocks in the North Sea show a high inter-annual variability in their biomass and productivity due to these fluctuations. Together with fishing pressure, this has led to stock collapses or recoveries in the past (Akimova et al., 2016).
When herring larvae do successfully make it to a suitable nursery ground, it typically takes 6 months for the larval stage to be completed, though this can take either shorter or longer depending on local temperatures (Gulf of Maine Research Institute, n.d.).

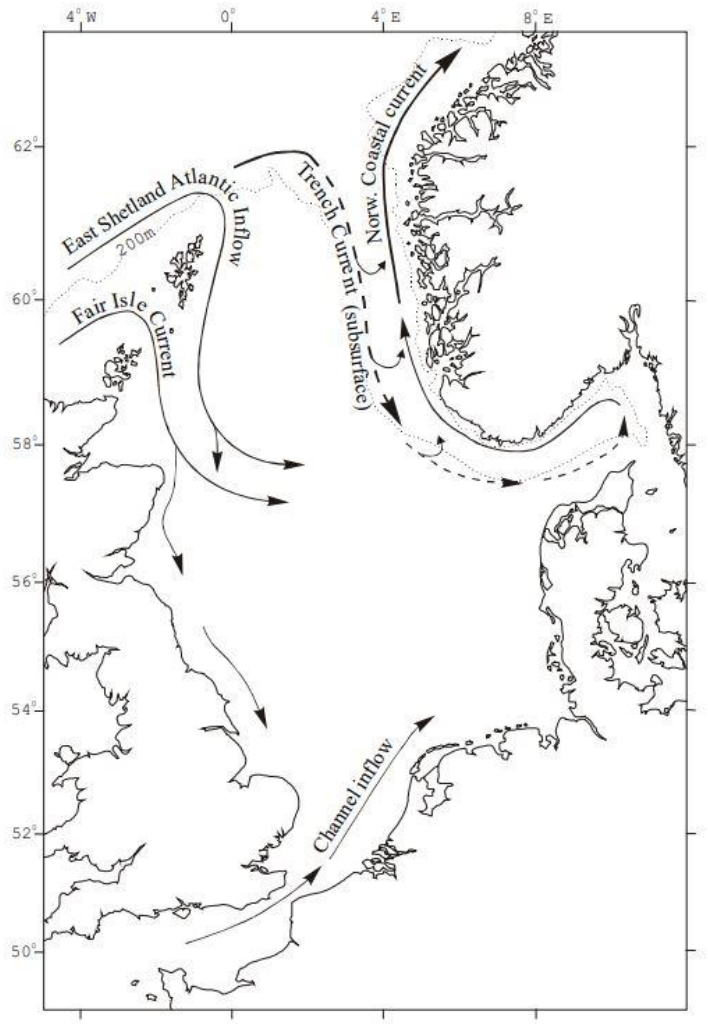

Figure 4: *The main hydrographical conditions in the North Sea which drive recruitment strength of North Sea herring on a yearly basis. Banks and Downs herring are transported to the Wadden Sea, and adjecent areas, by the Channel inflow which is subsceptible to changes in NAO-index and wind conditions (Corten, 2001a).*

3.1.3. Nursery grounds:

The Wadden Sea and eastern North Sea are used by herring as nursery areas (figure 5) (Corten, 2013; Coull et al., 1998; Couperus et al., 2016; ICES, n.d.; Kellnreitner, 2012; Philippart et al., 1996; Rijke Waddenzee, 2015). As mentioned before, the stocks that use the Wadden Sea as a nursery ground are herring from the Downs and Banks stocks. However, due to variable larval drift, herring larvae of one stock could be present in lesser numbers than the other. Due to the variability in oceanic circulation, some years, the larvae might not reach the traditional nursey areas in the Wadden and eastern North Sea (ICES, n.d.). This, in contribution with other factors, has led to stock collapses in the past (Corten, 2013; ICES, n.d.). Larval herring arrive on the nursery grounds via passive drift in early spring (February/March) and take advantage of the spring phytoplankton bloom. Here they metamorphose at an approximate length of 4.8 to 5 cm from larvae into juvenile herring (ICES, n.d.). The Wadden Sea and eastern North Sea are considered to be the most important nurseries for the North Sea herring population (Corten, 2013). This is because of different qualities of the Wadden and eastern North Sea respectively.

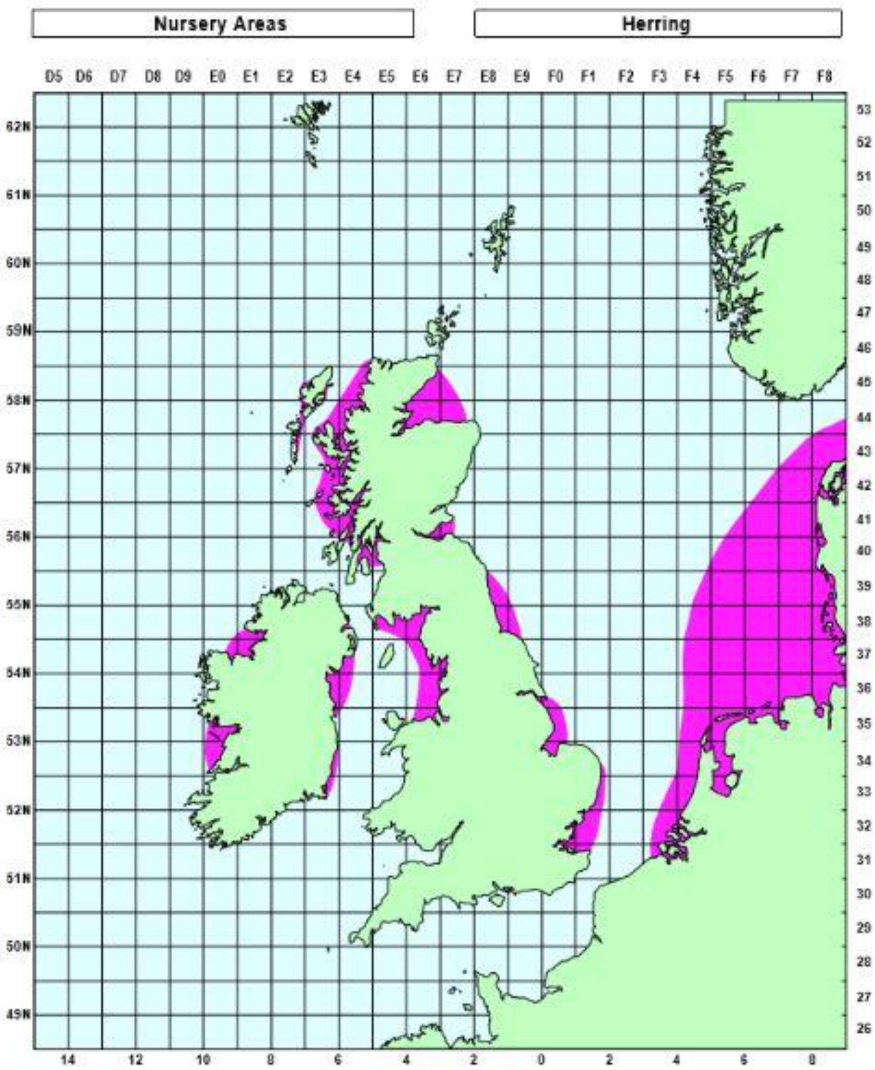

Figure 5: *Documented herring nursery areas in the Wadden Sea, North Sea and on the British Coast (Coull et al., 1998).*

The Wadden Sea is such an important nursery area because it provides increased protection from large predatory fish, due to the shallow and turbid waters. Due to the relative protection that the Wadden Sea offers, the mortality rate in the Wadden Sea is lower than it is in surrounding areas. Apart from protection, the Wadden Sea also provides juvenile herring (and other species) with abundant food sources, like copepods, to feed upon. This results in a considerable increase in the survival of juveniles (Cabral et al., 2007; Maes et al., 2005). Because of these qualities, juvenile herring thrives in this intertidal area and they are one of the most abundant species within the Wadden Sea (Couperus et al., 2016; Rijke Waddenzee, 2015). However, juvenile herring can also grow up outside of the safe estuarine conditions of the Wadden Sea. Mortality outside of estuaries is higher but it does offer more growth opportunities due to better food conditions. As a result, herring growing up in deeper waters tends to become larger than juvenile herring growing up into safe estuarine conditions like those found in the Wadden Sea (Maes et al., 2005). Juvenile herring also prefers the oligohaline salinities of estuaries, often occurring in salinities of around 16 to 32 parts per thousand. Preferred salinity slightly varies between different herring populations. The preferred salinity of juvenile herring increases when the juveniles grow older. The preferred temperature of juvenile herring is around 10 to 16 °C (Reid et al., 1999). This also varies between different populations but will be around this range. Due to this temperature preference, juvenile herring will usually leave estuarine waters right before summer to avoid warmer estuarine waters, since this is above the optimum temperature of growth for juvenile herring. The average temperature in 2015 measured in the Marsdiep (Wadden Sea) was 11.5°C (NIOZ, 2016). Because there is a time lag between the estuarine waters and seawater temperatures, the juvenile herring will use this cue in temperature difference to adjust in the coastal zone before moving back into estuarine waters again (Maes et al., 2005).

Similar to adult herring, juvenile herring have a mostly pelagic lifestyle. In the estuaries of the Wadden Sea, the juvenile fish tend to stay around the upper part of the water column. Here they have vertical migrations in response to the light cycles. During day time, juvenile herring is more dispersed throughout the water column, however, at night; they school in the surface waters to feed upon zooplankton (Gulf of Maine Research Institute, n.d.).

The average length of juvenile herring in the Wadden Sea ranges between 9,1 cm and 12,5 cm, though larger individuals up to 30 cm can be found. After living for about 2 to 3 years in the nursery grounds, the juvenile herring will move out of the nursery grounds to join the adult population in the North Sea (Couperus et al., 2016; ICES, n.d.). Here the juvenile herring will join in the spawning and feeding migrations of the adult population.

3.1.4. Feeding behaviour:

Due to the different life stages of herring throughout their lifecycle, herring uses different methods of feeding depending on life stage and food items which are available. Because of this, herring makes use of different feeding grounds during its lifecycle. During larval distribution, herring larvae carry a yolk sac that provides a mobile food resource which depletes in +/- 10 days, after which the larval herring starts foraging for themselves. Larval herring are no active predators, since they are very weak swimmers and thus mainly gain their food intake from whatever food is available. Due to this opportunistic feeding method, this is a very critical life stage within the lifecycle of the herring and mortality is usually very high (Gulf of Maine Research Institute, n.d.). Once the larvae reach the nurseries, they take advantage of the spring phytoplankton blooms (Corten, 2013). After the larval herring have grown into juvenile herring, they gain an additional feeding option. Both juvenile and adult herring have two different feeding methods. These two methods are filter and particulate feeding. Herring is known to switch foraging behaviour and select food items depending on different factors like prey size, visibility and particle concentration (Kellnreitner, 2012). The predominant food items of the juvenile herring are calanoid copepods like *Calanus finmarchicus*, however, euphausids, hyperiid amphipods, juvenile sandeels and fish eggs are also consumed (ICES, n.d.). Due to zooplankton being the main food source of herring, herring seem to have a sort of diel migration, following their food source wherever it goes. This is at least hypothesised since herring are commonly encountered at the same depth as their prey items (Haslob et al., 2009). At dusk, herring moves upwards in the water column and stays here when light intensity is low, and they move downwards in the water column when light intensity becomes high again. The activity of the herring is highest at dawn and dusk (Haslob et al., 2009; Reid et al., 1999). When juveniles become adults, they join the adult population in the North Sea in their spawning and feeding migrations. All herring populations in the North Sea share a common feeding ground in the northern North Sea. Although the southern originating populations do not trek up as far north as the northern populations do (Corten, 2001b). The predominant food items of adult herring are also copepods. However small fish, arrow worms and ctenophores are also consumed (ICES, n.d.).

Feeding grounds of herring seem to be mainly affected by environmental factors such as phytoplankton and zooplankton production. Due to this, herring tend to be in abundant numbers wherever chlorophyll levels are high (Dickey-Collas et al., 2010; Philippart et al., 1996). Phytoplankton levels are regulated by inflow of oceanic nutrients, river runoff into the Wadden- and North Sea and light. Changes in the composition of plankton dependents on said nutrient inflow (Corten, 2001a; Skogen et al., 2004). The abundance and location of herring is thus partially regulated by yearly inflow of nutrients and phytoplankton production.

3.1.5. Migratory patterns:

During their lifecycle, the different life stages of herring also have different migration routes. Herring have a “triangular” migration pattern that is typical for many pelagic schooling fish. In this migration pattern the larvae passively drift with the currents from the spawning grounds to the nursery grounds. From the nursery grounds the juvenile herring will eventually move out into the open water to join the adult herring in the pursuit of food. When the time is right, adult herring will migrate back towards the spawning grounds where they can lay their eggs and start the cycle all over again (Gulf of Maine Research Institute, n.d.; Clausen, 2007).

After spending years in the nursery grounds, juvenile herring will finally move away to join the adults in the spawning and feeding migrations in the western deeper waters of the North Sea (ICES, n.d.). This migratory pattern seems to be caused by the plankton blooms that start in the eastern North Sea and over time move westwards (Corten, 2000). Herring will initiate their yearly migrations based on the timing of this bloom during previous years. Meaning that the herring have some kind of conservationism by not only following the food production of the current year but also by taking the average timing of food production of previous years into consideration (Corten, 2000). The migratory patterns adapted by herring (including their timing) are considered to be fairly constant over several years of environmental variation, even after becoming mobile adults (ICES, n.d.).

Once larval herring hatch, they start to drift along on the currents from the spawning grounds towards the nursery grounds. Due to this passive migration, the larval herring do not have a natal imprint of their original spawning ground. As a result, first time spawners must learn the routes to the spawning grounds from experienced adult herring. This may or may not be the original location of their hatching. After the first time spawners have learned the route to their respective spawning grounds, they will return here for the subsequent years (Nash, 2009; Sinclair & Power, 2015).

Adult herring have a couple of different migratory patterns. They perform extensive seasonal migrations between feeding and spawning grounds. Some adult herring also make use of wintering grounds. These wintering grounds are warmer than the feeding grounds and are used as transition areas between the spawning grounds and the feeding grounds. The wintering grounds for the Downs and Banks herring are in the south of the North Sea close to the spawning grounds (Clausen, 2007). Even though the exact migratory pathways of adult herring between the spawning grounds and wintering grounds are not fully known, it is assumed that the herring migrate in a dispersed manner (Corten, 2013). Although the spawning grounds of the different stock components are fixed, different stocks often mix on feeding or wintering grounds (Clausen, 2007). The feeding grounds are located in the northern North Sea and central North Sea. The adult herring migrate to these feeding grounds in spring. Southern populations like the Downs and Banks herring do not migrate up as far north as more northern populations, of which the Skagerrak is the most northern range in which they can be found (Clausen, 2007; Corten, 2001b).

A summarized overview of the lifecycle of Downs and Banks herring, including the general steps which are described in the text, can be seen in figure 6.

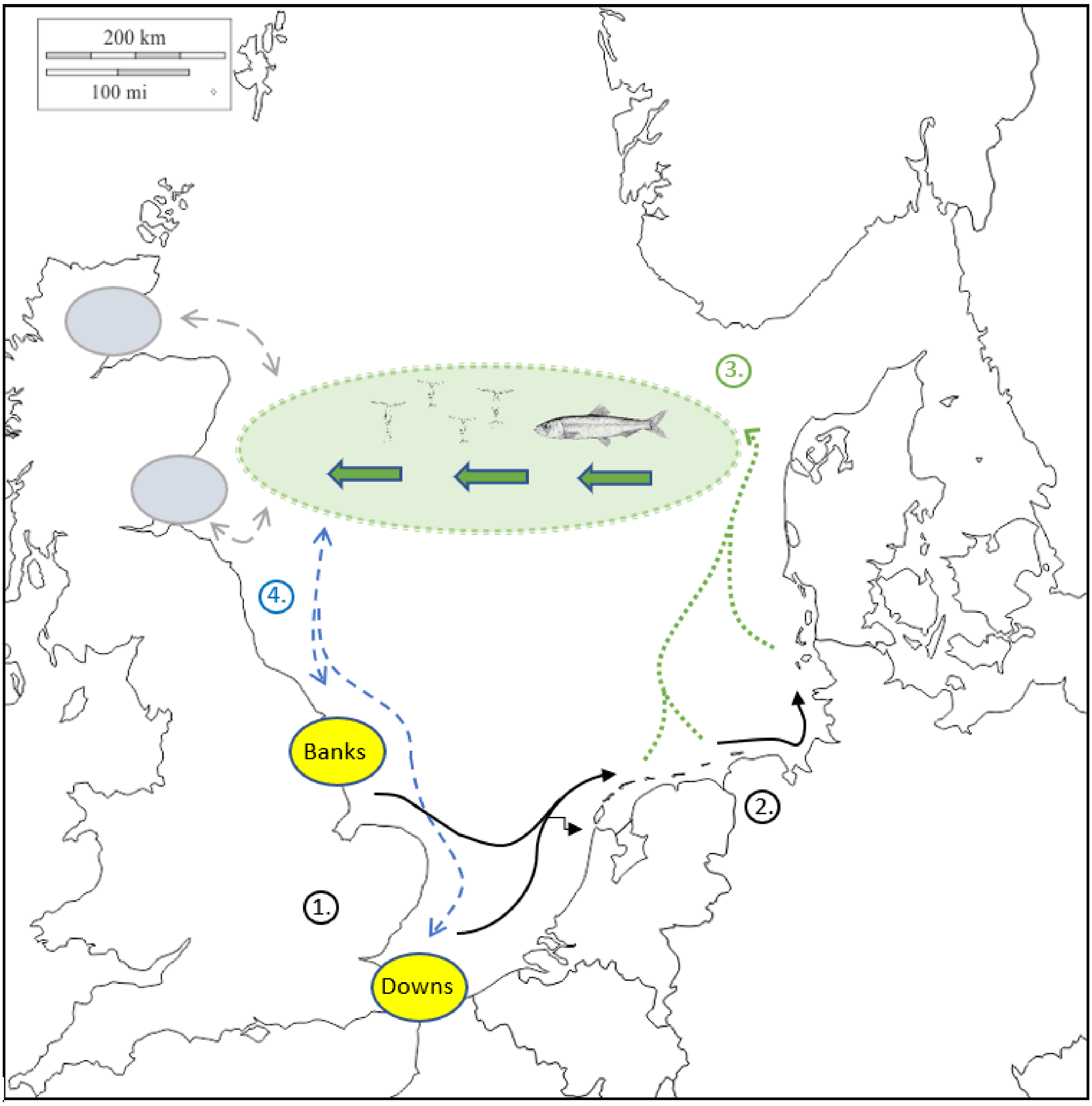

Figure 6: *General steps in the lifecycle of Downs and Banks herring in the North Sea.* ***1.*** *spawning occurs in September/ October (Banks stock) and November – January (Downs stock) after which larvae passively drift to the nursery grounds in the eastern North Sea (solid black arrows);* ***2.*** *After spending 2 to 3 years in the Wadden Sea (or other coastal nurseries), herring move out of the shallow waters to join the adult population in deeper parts of the North Sea (dotted green arrow);* ***3.*** *Adult herring starts feasting on copepods, which are a result of plankton blooms starting in the eastern North Sea and seizing in the western North Sea;* ***4.*** *Between September and January, when spawning starts, the new generation of adult herring follows experienced herring to the different spawning grounds (striped blue and grey arrows), of which the Banks and Downs larvae will continue the cycle.*

3.2. Sub-question 2: *What are the bottlenecks and/or knowledge gaps encountered within the lifecycle of herring in relation to the Wadden Sea?*

The outcomes discussed in this chapter describe potential bottlenecks during the lifecycle of the herring. Here is explained what bottlenecks the North/Wadden Sea herring might stumble upon during its lifecycle and what effects these bottlenecks could have on the herring stocks.

3.2.1. Climate change - *Temperature:*

"Species can only tolerate a specific range of environmental conditions that, among other factors, places constraints upon their range of distribution" (Rijnsdorp et al., 2009, p. 1572). Temperature might as well be the most often studied environmental factor on marine animals and their ecosystems. During the past 40 years, water temperatures in the German Bight increased by 1.13°C. Cold winters with sea surface temperatures around –1°C used to occur about once every 10 years up to 1944 but has only occurred once since 1960. Models predict further sea surface temperature warming for the next 90 to 100 years, by about 1.6° to 3.0°C in the northern and even by 3.0° to 3.9°C in the shallower southern North Sea in which Downs and Banks herring reside (Pörtner & Knust, 2007). Other sources also expect future temperature increases over the next century, with varying expectations from a 0.5°C up to 5.8°C increase in North Atlantic sea-surface temperatures (Peperzak, 2003; Sims et al., 2004). Corten (2001a) shows that temperatures in deep parts of Skagerrak have risen consistently over the last 50 years, which means that winter temperatures on the North Sea plateau must also have increased over this period. During high winter/spring temperatures, a northern distribution of herring has already been detected (Corten, 2001a; Rijnsdorp et al., 2009). Temperate (northern) marine species which already live close to the limits of their range of physiological tolerance, as is the case with the most southern herring populations, will be more vulnerable to changes in abiotic conditions than populations living in the centre of their distribution area (Rijnsdorp et al., 2009).

Temperature affects almost every biological step leading to recruitment, from larval growth till adult maturity and mortality (Ottersen et al., 2001). It is expected that climate change will have pronounced effects on the distribution and abundance of fish through its influence on recruitment, which is quite worrying for these southern fish stocks which utilize the Wadden Sea during their life cycle (Rijnsdorp et al., 2009). However, temperature does not seem to affect all life stages in the same way. Temperature increase seems to influence the growth rate of herring and thereby causes enhanced stock biomass in warmer years (Akimova et al., 2016; Fässler et al., 2011; Gröger et al., 2009) possibly through enhanced gonad development (Corten, 2001a). As a result, larval biomass is higher during these years. However, larval mortality also increases with temperature (Corten, 2013; Fässler et al., 2011; Gröger et al., 2009; Hufnagl & Peck, 2011), often resulting in weak year classes even though the original spawning biomass is high. There are multiple hypotheses on what drives this increase in larval mortality since not all research indicates a direct influence of temperature. Some research does indicate a direct effect of temperature, like lab results showing that less than 10% of the simulations including larval herring where successful at temperatures ≥11°C (Hufnagl & Peck, 2011). During an ICES meeting in 2007, it was concluded that the low larvae survival during warm years is the result of less developed yolk-sacs and faster consumption of this food supply due to higher metabolic rates (Corten, 2013), and the sensitivity of larvae may be further increased due to their small body size and inability to select areas with better characteristics (Gröger et al., 2009; Rijnsdorp et al., 2009). However, other researchers believe other factors, which are often linked with temperature, to be responsible. Payne et al., (2013) does not support the temperature-hypothesis since temperature did not show significance during statistical testing. Instead, food availability and quality are expected to drive larval mortality (Akimova et al., 2016; Möllmann et al., 2008; Payne et al., 2013; Rijnsdorp et al., 2009). In the period between 1988±1990, a northern distribution of adult herring was not only linked with high water temperatures but also with low abundances of copepod *C. finmarchicus*, main food item of North Sea herring (Corten, 2001a). In earlier work, it was already concluded that *C. finmarchicus* is sensitive to temperature changes (Corten, 2000) and this statement did not change throughout the years (Akimova et al., 2016). It is suggested that the North Sea, and especially the coastal Wadden Sea, is slowly shifting to a warm temperate ecosystem, due to a decrease in sub-Arctic zooplankton, like *C. finmarchicus*, and an increase in warm-temperate plankton species (Edwards et al., 2006). It is even speculated to be a possible Atlantic wide climatic change (Reid & Edwards, 2001; Rijnsdorp et al., 2009). The warming of the North Sea area also has the potential to accelerate water mass stratification, resulting in earlier plankton blooms. This might negatively affect herring recruitment though the match-mismatch theory, missing the critical period of food production in the Wadden Sea (Rijnsdorp et al., 2009; Sinclair & Tramblay, 1984).

An additional, though less often considered, hypothesis is an increase in jellyfish blooms as a result of sea water warming, either direct through temperature or through increased plankton production (Lynam et al., 2004; Purcell, 2005; Richardson et al., 2009). This phenomenon can have a huge impact on local ecosystems, especially near the coast (Richardson et al., 2009). Jellyfish blooms can either affect an ecosystem through top-down (medusae prey on fish eggs and larvae) as well as bottom-up (medusae limit fish populations through competition) processes (Lynam et al., 2004). For most temperate species, sexual reproduction increases at warm temperatures, with the speed of production being greatest at the warmest temperatures tested (Purcell, 2005).
Jellyfish *Mnemiopsis leidyi*, a temperate species which is commonly encountered in the North- and Wadden Sea, is known to thrive under warm conditions (Kellnreitner, 2012; Purcell, 2005). This species is held responsible for diminishing zooplankton abundance and overall diversity in multiple invaded habitats whenever conditions are good. At some locations, it is hypothesized to be responsible for the collapse of fish stocks. Right now, the probability of competition between herring and *M. leidyi* is low, since winter temperatures are often too low for the survival of this species of jellyfish (Kellnreitner, 2012). However, the recent climatic trend towards higher winter temperatures might change things in the future.

Though temperature is expected to be a driving factor in many of these scenarios, it must be noted that matters are often more complicated. It is nearly impossible to be sure if a change in sea water temperature is truly caused by global warming or if it is caused by North Atlantic Oscillation based changes, since the NAO is generally linked with temperature changes which can last for long periods of time (Fässler et al., 2011; Rafferty, 2011). Some say that the changes documented in the North Sea and the Wadden Sea are a combination of changes in the NAO and global warming (Reid & Edwards, 2001; Weijerman et al., 2005).

3.2.2. Climate change – *Hydrodynamics:*

The NAO is known to have a strong influence on ecological dynamics, causing diverse responses in multiple ecological processes, ranging from spawning time to spatial distribution of biological communities (Weijerman et al., 2005). Rather than climatic changes showing a progressive trend, changes in NAO-index are not necessarily continuous, forming ‘clusters’ of unusually high or low temperature intervals alternated by intervals with 'normal’ characteristics (Rafferty, 2011; Reid & Edwards, 2001). The North Sea area has undergone noticeable changes over the last decades, affecting all trophic levels (Reid & Edwards, 2001). By now it is generally believed that these changes are largely driven by environmental variability (Akimova et al., 2016; Lynam et al., 2005). However, primary causes of true ‘ecosystem shifts’ may be a combination of different factors, since big shifts in the North Sea area are getting progressively more prominent through sudden noticeable changes from year to year (Weijerman et al., 2005). Many researchers assumed that reduced larval survival during different time periods were caused by either unusual hydrological conditions or by temperature changes (Gröger et al., 2009; Kellnreitner, 2012; Rijke Waddenzee, 2015; Payne et al., 2009). Most of the past changes in pelagic fish stocks in the North Sea (particularly the dramatic decline of herring in the late 1970s) could be explained by a reduced inflow of Atlantic water and changes to the circulation of the North Sea area. Even if the water circulation is strong enough for the successful dispersion of larvae, the origin of the water can also differ between years, changing the plankton composition and the overall temperature in the North Sea area (Reid & Edwards, 2001; Edwards et al., 2002). However, specific periods of exceptionally long and high NAO-index, which resulted in long timespans of above average sea water temperature (1988) are expected to be a direct consequence of global warming (Reid & Edwards, 2001). The exact way in which these two factors affect each other, and therefor herring stocks, is still unknown (Edwards et al., 2002). This is further complicated by the fact that it is difficult to link changes in herring stocks to specific climate variations due to 3 specific reasons (Corten, 2001a). First of all, it is difficult to isolate natural changes in fish stocks from man-induced effects like fishing. Second, it is difficult to identify hydrographic variation since this is area specific and often the combined effect of several processes including moon-cycles and tides. Lastly, while there is information available on long-term hydrographical changes, the information is limited and area specific (Scharfe & Callies, 2010). However, due to the far-reaching consequences of the recent NAO shifts on the North Sea ecosystem, it is suggested that the principal causes are anomalous ocean climate conditions, rather than common changes in atmospheric oscillations like the NAO (Edwards et al., 2002).

Both the shifts in NAO-index and climate change through global warming primarily seem to influence the distribution and composition of the primary production in the North Sea and the Wadden Sea. Reduced biomass of zooplankton appears to be responsible for a decline in North Sea herring from 6 million tonnes to 50.000 tonnes in the early 1950s, showing the importance of food items (Reid & Edwards, 2001). Even though the length of the phytoplankton growth season will likely increase with an increase of warm winters, cold water prey species will most likely be replaced by warm water species (Beaugrand et al., 2002; Ottersen et al., 2001). Global warming could thus stack with (elongated) periods of high NAO-index, slowly surpassing the temperature threshold of prey species commonly consumed by North Sea herring (Weijerman et al., 2005). Of these areas, warmer coastal water bodies, like the Wadden Sea, are expected to lose their suitable characteristics the fastest. It is unknown if the removal of *C. finmarchicus* makes it impossible for herring to thrive since it will be replaced by other, warm water, copepod species (Beaugrand et al., 2002; Ottersen et al., 2001).

However, previous northern movements of herring were also linked with a decrease in *C. finmarchicus* biomass in the southern North Sea (Corten, 2001a) and herring, specifically larvae, do prefer some copepod species over others, indicating quality differences between food items (Alvarez Fernandez, 2015). As a result, the wrong distribution and composition of zooplankton might result in starvation in larval herring.

Jellyfish blooms are also linked with changes in NAO, of which climate change can increase the likelihood during periods of high NAO-index (Purcell, 2005). As a result, blooms might become more abundant in the future, especially near the coast. As mentioned before, this could result in a higher competitive pressure on herring and could thus be negative for the herring stocks.

3.2.3. Climate change – *Salinity:*

The Wadden Sea is an area with relatively low salinity, since it has limited oceanic water inflow and it has a surplus of freshwater runoff (Madsen, 2009). However, due to the profound temperature changes in the North Sea area during the last decades, rarely any research has been focused on salinity changes throughout the years. This partly has to do with the fact that research has indicated that herring is much more sensitive to temperature changes than it is to changes in salinity (Gulf of Maine Research Institute, n.d.). Due to the periodical variation in NAO circulation, which brings saline waters into the North Sea, and the runoff of multiple rivers, local animals are already adapted to endure specific ranges of salinity. A prime example is the low salinity requirement of most marine species in the adjacent Baltic Sea, which has a permanent halocline due to the limited inflow of oceanic water (Madsen, 2009). Even though herring prefers salinities between 26-32 ppt, herring is commonly seen up to a threshold of 16 ppt. However, lower salinities can be endured for short periods of time, especially by young herring. When herring matures, the preferred salinity range changes to higher salinities with a lower limit of 28 ppt (Reid et al., 1999). Besides the Great Salinity Anomaly (1960), in which an increased distribution of sea ice from the northern North Atlantic resulted in extremely low salinity within the North Sea area, salinity has been relatively stable throughout the years (Dima & Lohmann, 2011). Though the resent threat of climate change is expected to influence salinity as well. Several climate models, both global and regional, indicate an increase in the runoff of the northern latitudes due to proceeding climate change, resulting in reduced salinity (Peperzak, 2003; Vuorinen et al., 2014). A future critical shift in salinity of 5-7 ppt is expected, possibly rendering certain coastal areas, like the Wadden Sea, unsuitable for herring distribution (Vuorinen et al., 2014), if temperature increases have not done that already by then. These salinity shifts are expected to stratificate the water column near the coast and, in combination with higher (winter) temperatures, increase the occurrence of harmful algal (dinoflagellates and raphidophytes) and jellyfish blooms (Peperzak, 2003; Purcell, 2005) and might even change the timing of the much-needed algal blooms (Rijnsdorp et al., 2009).

Overall, it seems that the slight salinity decrease is unlikely to be responsible for the apparent ecosystem shifts in the North Sea area since, unlike temperature, salinity mediated migrations have not been documented in the North Sea or Wadden Sea. Though it is possible that the early stratification of the water column, due to decreased salinity, might have more severe consequences in combination with global warming.

3.2.4. Eutrophication:

Another factor that has been known to limit fish stock size is eutrophication. Eutrophication is usually caused by a water body getting too much of a specific nutrient. The phytoplankton in this body of water cannot process the amount of nutrients, which leaves the water vulnerable to different phytoplankton species or other algae which can cause the reduction of oxygen in the water body, leading to general poor water quality. This is usually caused by having an overload of nitrogen, however, this can also be due to an overload of phosphorus (Van Beusekom et al., 2017). An overload of nutrients can originate from different kinds of sources, either natural or anthropogenic. Natural sources include weathering of minerals, decomposition of materials, lightning and geothermal emissions. Anthropogenic sources include wastewater, agriculture products such as fertilizers and animal waste, atmospheric decomposition of fossil fuels and other similar sources (Paerl, 1997). The nutrients from these sources are transported through rivers, groundwater and precipitation and end up into the sea. An overload of nutrients could pose a threat to coastal ecosystems, like the Wadden Sea, since the nutrients stay in this system for longer periods of time. The main input of nutrients is the large amount of riverine discharge in to the Wadden Sea. During the last century, nutrient concentration in the Wadden Sea increased. This is presumably caused by an increase in wastewater and agricultural waste ending up in rivers and being transported to the Wadden Sea. In the 1970's and the 1980's, measures were taken to combat the increased nutrient input into the North and Wadden Sea to combat the negative effect eutrophication can have on a coastal ecosystem (Van Beusekom et al., 2017; Skogen et al., 2004; Tulp et al., 2008). Measures like the reduction of nutrient inputs from industries, agriculture and sewage treatment plants where taken and laws have been made for these industries to reduce their nutrient input into rivers (De Jong, 2007). Within the framework of the WFD, Denmark and Germany have agreed on a chlorophyll-A percentile threshold of 7,5 µg per liter. Currently the chlorophyll levels in the Northern Wadden Sea are a least 50% higher than this threshold (Van Beusekom et al., 2017).

Eutrophication is universally known to cause jellyfish blooms (Richardson et al., 2009). As is previously stated, jellyfish blooms could cause problems to herring stocks due to the increased competition between these species (Kellnreitner, 2012). Another known aspect of eutrophication is its tendency to create harmful algae blooms. This is also dependant on temperature and salinity conditions (Edwards et al., 2006; Paerl, 1997; Peperzak, 2003). These blooms have caused mass mortality of fish elsewhere in the world, however, no records of mass mortality, due to harmful algae blooms, have been recorded in the Northeast Atlantic (Rijnsdorp et al., 2009). Future effects of harmful blooms on herring population in the North/Wadden Sea are not yet known.

Eutrophication also has the potential to cause a decrease in sea grass in the Wadden Sea, which is known to negatively affect many species of fish, especially juvenile stages (Van Beusekom et al., 2017). However, herring is almost exclusively found outside patches of sea grass, rendering this species unaffected by this effect (Polte & Asmus, 2006). The importance of sea grass differs between species and should be identified on species specific level for future Swimway targets.

Nowadays, nutrient input via rivers seems to have decreased in comparison with last century (Tulp et al., 2008). However, nutrient discharge from rivers is still high. It seems that the measures taken to combat eutrophication are working, since total nutrient input in the Wadden Sea has reduced since the last century. However, the entire south eastern part of the North Sea (including the Wadden Sea) is still considered a problem area (Almroth & Skogen, 2010) and continuous monitoring of nutrients and chlorophyll is still necessary.

Although current nutrient input in the Wadden Sea seems to decrease and eutrophication is not seen as a current major thread, exact effects of eutrophication on the herring stocks are not known. More research on this subject needs to be conducted to get a clear view of the potential thread eutrophication forms on the herring stocks, especially in the future when fresh water runoff is expected to increase (Peperzak, 2003; Vuorinen et al., 2014).

3.2.5. Food availability

Food availability is a major parameter which determines whether a population is doing well or not. When abundant amounts of food are available, the herring population will often thrive better than when food availability is low (Polte et al., 2013). From the end of the yolk sac stage till death, herring is dependent on the food availability in the North Sea. Especially the mismatch of primary production, previously explained in larval distribution, could thus result in a large mortality rate of larval and juvenile herring (Gröger et al., 2009). For example, the copepods: *Paracalanus* spp., *Pseadocalanus* spp. and tintinnids, which usually had a relatively high abundance during autumn, have declined since a regime shift in the 2000s in the North Sea. From 1960 till 2009, an overall increase in tintinnids in the Northeast Atlantic could be seen in a research from Hinder et al., (2011). In 1960, the tintinnid occurrence in all samples was <20% while in 2009 an occurrence of tintinnids could be found in >50% of the samples. Although tintinnid occurrence increased from 1960 till the early 2000's in the North Sea as well, a drop of tintinnid occurrence could be seen from 2003 onwards where tintinnids occurred in <10% of all samples. Coincidentally with the decrease in prey items of herring throughout the Wadden Sea, the herring also saw a decline in numbers from 2000 till 2010 (Payne et al., 2009; Payne et al., 2013.). It is not sure if this drop is connected to the drop in tintinnids due to the 3-year difference between the decrease in herring and the decrease in tintinnids. Especially for the Downs herring, food availability is critical due to limited inflow. In the northern North Sea, on the contrary, new nutrients are easily supplied by currents from the Atlantic. Plankton production is greatly dependant on the inflow of these nutrients and herring feeding conditions rely on this inflow of nutrients as well (Corten, 2001a). Since the main food source of herring consists of zooplankton, during all the different life stages, herring is also dependent on zooplankton composition and size distribution. Managing the herring stock thus starts with the incorporation of zooplankton dynamics in the stock assessments of North- and Wadden Sea herring (Lindegren et al., 2011). As mentioned before, one of the main prey items of herring, *C. finmarchicus* is sensitive to temperature changes and food availability for herring greatly depends on this species (Akimova et al., 2016; Corten, 2000).

The food availability of herring is not only reliant on how well their prey items are doing but also on how well competitors are doing. Herring might have to compete with other pelagic fish species for food and some (earlier mentioned) jellyfish species like *Mnemiopsis leidyi*, *Aurelia aurita* and *Cyanea capillata* also have dietary overlap with herring (Kellnreitner, 2012; Lynam et al., 2005; Purcell & Arai, 2001; Richardson et al., 2009). Jellyfishes like *Aurelia aurita, Cyanea capillata and M. Leidyi* are usually abundant in the North Sea during summer. This means that a jellyfish bloom in the summer could result in less food available to herring larvae, which hatch in the autumn and winter. The result could be a weak year class of herring, since the larval period is seen as the most critical period (Lynam et al., 2005). *M. leidyi* and juvenile herring are both common in the Wadden Sea. Luckily herring and *M. Leidyi* do not usually occur in the Wadden Sea within the same time span and in the same abundance numbers. Kellnreitner (2012) found that juvenile herring where most abundant during June and July, whereas *M. leidyi* abundance was relatively low during this period. In August and September, the abundance of herring dropped whereas abundance of *M. leidyi* increased. This research also showed that herring could switch to alternative sources of food when *M. leidyi* abundance was high. Competition between these species could, however, cause a problem should their common food source be limited in the Wadden Sea for long periods of time (Kellnreitner, 2012).

Lastly, low food abundance could cause herring to resort to cannibalism. However, this is rarely seen and not a likely case. This is mainly seen if adult herring extended residence in shallow waters (Gröger et al., 2009). However, due to future temperature increases, this is not to be expected.

Currently the Wadden Sea is subjected to change and food availability of herring should be further monitored while managing herring in the Wadden Sea (Rijke Waddenzee, 2015).

3.2.6. Fishing pressure:

Fishing pressure is known to influence fish population size. This is also the case for herring, being an important species of commercial interest in the North Sea. Herring plays a key economic role with ~0.3 to 0.4 million tons landed yearly between 2007 to 2012 (Alvarez Fernandez, 2015). Fisheries have seen, and been part of, long and short-term fluctuations within the herring stock over the years. Within these periods, there have been times in which the herring stock size thrived and periods in which the stock size came to a dangerous low (Corten, 2001a). Before the second world war, research on herring was mainly focussed on the natural effects on the herring stock. However, in the 1950's till the 1970's there was a severe overexploitation of the herring, causing a low abundance in herring stocks all around the North Sea. It is estimated that the spawning stock biomass dropped from around 4,5 million tonnes in the late 1940's to lows of 100000 tonnes in the late 1970's (ICES, 2016b). This stock collapse was caused (among other factors) by heavy fishing pressure on the herring stocks in the North Sea (Corten, 2013; Herdson & Priede, 2010; Rijke Waddenzee, 2015). New fishing techniques, like purse seine fishing, combined with the schooling behaviour of herring, created opportunities for the herring stock to be effectively targeted. As a result, it became viable to fish on the herring stock, even when the stock is at a relative low (Bjørndal, 1989). Figure 7 shows a map of the average annual herring catches in the North Sea region from 2011 to 2015. This catch data is only from Dutch fisheries. As can be seen, pelagic fishing is most common in the northern North Sea and the English Channel. No commercial fishing on herring is done in the Wadden Sea (Acton, 2017; Rijke Waddenzee, 2015).

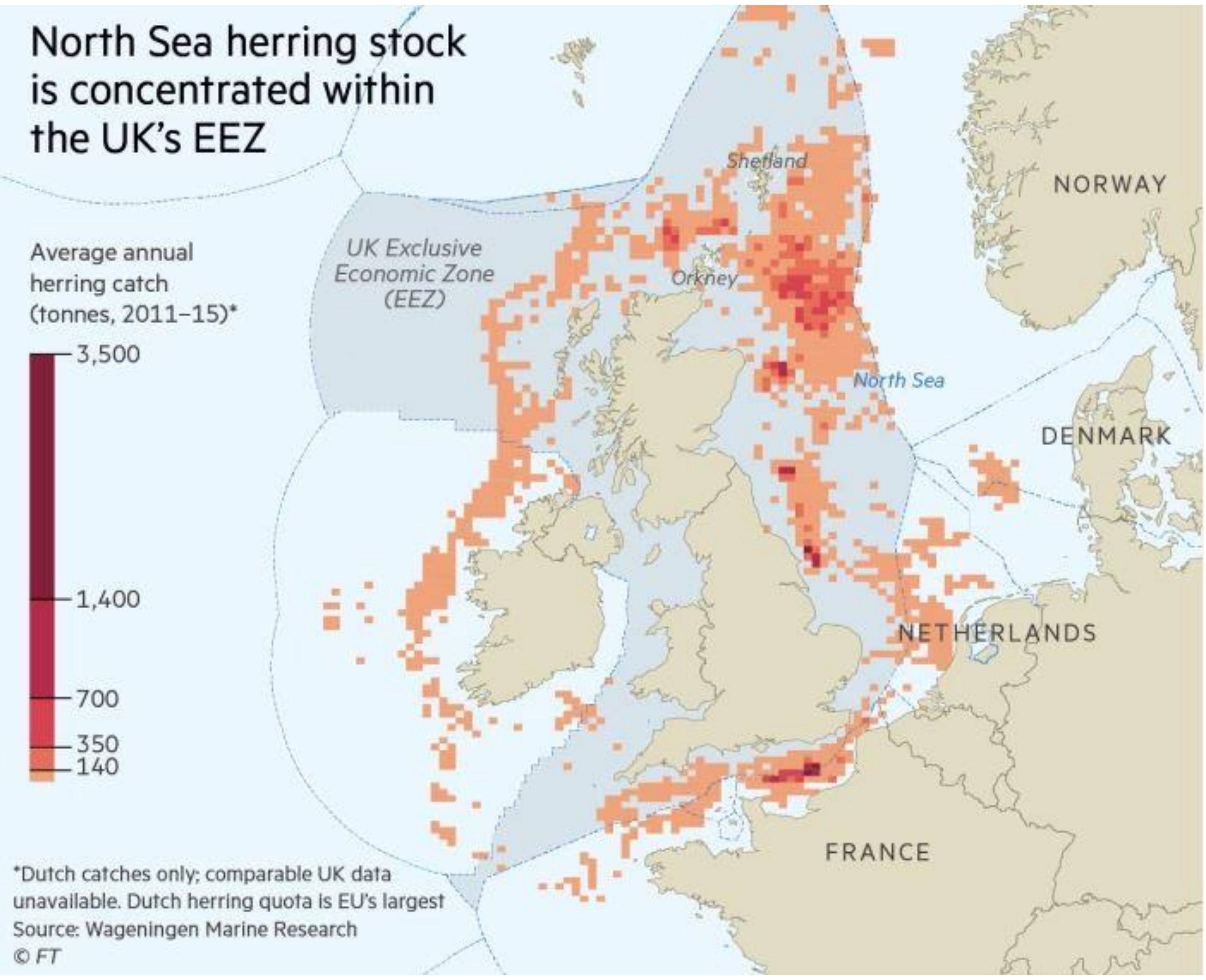

Figure 7: *Average annual herring catch from Dutch fisheries in tonnes from 2011 till 2015 (Acton, 2017).*

With the advances in fishing techniques, the effects of fishing pressure started to surpass the natural changes in the herring stocks. Since this period, human actions have been taken account in herring and fisheries sciences as well (Corten, 2001a). Due to multiple crashes in herring stocks, total allowed catches (TAC's) where implemented to regulate the total amount of herring caught, in an attempt to rebuild the stocks to a healthy status. To further prevent future stock collapses, herring stocks are consistently monitored and researched (ICES, n.d.). Current estimates of the herring stock suggest that the stock is close to its pre-collapse state and that only about 10% of the total herring stock is being exploited (Herdson, & Priede, 2010; Rijke Waddenzee, 2015). To aid in the rebuilding of the North Sea herring stocks, fisheries are also closed during spawning season, enabling the recruitment of the next generation of herring by leaving more adult herring alive. This way herring will be protected, even though the clustered nature of herring on their spawning grounds makes fishing considerably easier during spawning (Overzee & Rijnsdorp, 2015). Having a healthy amount of adult herring is important because the younger fish must learn the routes to the spawning grounds from the experienced adults, as is mentioned before. If there are no experienced adults, the younger fish would have to find suitable spawning areas themselves, which might not be as suitable for future stock survival as the currently known spawning grounds (Nash, 2009; Overzee & Rijnsdorp, 2015). Also, the selective removal of older age classes will increase the truncation of the age and size classes of the herring stocks. Larger fish tend to produce more and larger eggs than smaller adult fish, of which the larger individuals are thought to be more advantageous as they result in larger hatchlings which are physiologically more likely to survive (Overzee & Rijnsdorp, 2015; Rijnsdorp et al., 2009.). A spawning disturbance might also cause a forced delay in fertilization of the eggs or destroy the demersal egg mats of herring. It is known that females who cannot get rid of their ovulated eggs, causes the eggs to come into a process of decline. This process is known as overripening and causes the eggs to decline in quality, making fertilization less likely. This process may, however, be a bigger problem for other fish species since overripening already starts in multiple other fish species after a few hours, whereas in herring this may occur after a couple of days (Overzee & Rijnsdorp, 2015). In previous research, the stock collapse has been monitored closely. Here it has been shown that herring have a density-dependence and thus need a sizable frequency of good year classes in order for the stock to continue this trend in the future. For this reason, current measures where needed to avoid overfishing of the herring stock (Gröger et al., 2009).

Another indirect effect caused by overfishing is that it is known to contribute to jellyfish blooms. Reducing the stock of competitors (like herring) gives jellyfishes a chance to flourish. Jellyfish blooms can have severe consequences to the ecosystem. Especially on a coastal ecosystem like the Wadden Sea (Lynam et al., 2005; Richardson et al., 2009).

However, despite the negative effects that overfishing can have on the herring stock, current management and monitoring of herring fisheries seems to be sufficient in keeping the herring stocks healthy. Even though overfishing does not seem to be a current problem for the North Sea herring population, it can attribute to other factors that prove a larger thread to the herring stocks in the area. Clupeidae species, in general, exhibit schooling behaviour and, due to wide fluctuations in year class strength, are far more susceptible to overfishing than commercially important demersal species are (i.e. gadoids - cod, haddock), since a significant portion of a school may be removed in a single net haul, leaving behind a population that may not be able to rebound. This is especially true if intense fishing pressure occurs during a period of a natural population fluctuations (Möllmann et al., 2008; Payne et al., 2009; Pasche, 1993). As a result, continuous monitoring of herring stocks will always be important for herring fisheries. Currently, it can be stated that, in comparison with the past, awareness is much higher.

3.2.7. Other human activities:

Even though fisheries are often responsible for most damage done to the marine ecosystem in the North Sea, other human activities are also known to have harmful effects. Human activities can be grouped into several different types of pressure to describe the specific ways that ecosystems and their components are perturbed, ranging from physical damage to contamination by heavy metals. Human activities operating in the North Sea consist of the extraction of marine aggregates, oil and gas exploration and production, cable laying, windfarm construction and operation, Eutrophication caused by pollution, fishing with mobile seabed gear, and wrecks at sea arising from military activity (Eastwood et al., 2007). Since both the effects of eutrophication and fishing have already been described, the focus will be on the other activities.

Since gravel beds are of such great importance for the spawning of herring, major spawning grounds became protected in 1974 (De Groot, 1979a). So even though gravel extraction does take place in the North Sea, it is prohibited to do so during spawning season, preventing it from becoming a bottleneck at this moment. In the Belgian part of the North Sea, the maximum amount of gravel which can be harvested by each permit holder is decreasing on a yearly basis within specific areas, reducing the risk of overexploitation (FOD Economie, 2014). However, the demand in gravel (and other aggregates) is still increasing. In 1976, about 29000 m^3 of gravel and sand was harvested in the Dutch part of the Wadden Sea, which has increased to 5,82 million m^3 in 2014 (Van Lancker et al., 2015). If this demand does not abate, herring spawning grounds might be lost in the future.

As for the exploitation of oil, hydrocarbons have been shown to have negative effects on various species, including herring. Larvae drift with currents from the western North Sea across the oil fields in the central North Sea to the eastern nursery areas, including the Wadden Sea. As larvae pass these oil fields, exposure to hydrocarbons may occur. Although most of the larvae die due to starvation and predation, further decreases may occur due to oil contamination either to the larvae themselves or to their planktonic food source. Elevated levels of AHH and P450 monooxygenase have been detected in fish caught within a radius of 4000 meters away from production platforms. Increased mortality, decreased oxygen uptake and both reduced swimming and feeding activity have all been detected in herring larvae due to exposure to production water. Though it might be impossible to separate the effects of natural processes and the effects of hydrocarbons, the combination of the two may reduce condition factor to a critical point of disease susceptibility. However, the waste water disposal of oil refineries might be more problematic since most of the coastal refineries of the North Sea are located close to either a spawning ground or a nursery area. To understand the full extent of these pollutants on North Sea herring population, continuous water quality monitoring is vital (Pasche, 1993). Studies on the subject show varying results, some of which indicate negative effects (MacLachlan et al., 1981) while others show no effect at all (Føyn & Serigstad, 1988). However, it must be stated that the oil industry is constantly working on measures to reduce the impact on the marine ecosystem, further reducing chance of exposure (Carpenter, 2018). At this point, the effect of pollution, because of oil exploitation, is not expected to drive the changes in herring stocks but might contribute to the mortality of larvae in a weakened condition. The extraction of gas does not seem to have the same complications as oil extraction does (Pasche, 1993).

When larvae get closer to the Wadden Sea, they cross other human activities, one of which are wind turbine parks. Wind turbines are known to have negative effect on marine birds which utilize a flight route crossing these turbines, risking collision or higher metabolic rates when they stray from their flight path (Exo et al., 2003). However, the effect it has on fish is studied to lesser extent. There are two aspects of wind turbine parks which are expected to negatively influence marine fish in the area. These aspects are the construction of the park, including the sound of construction, and the transmission of electricity through cables. It is assumed that the construction of a wind turbine park itself only has minor environmental impact, as is based on the construction of the fixed link across the Øresund sound between Denmark and Sweden. This 12 km long artificial peninsula consists of two parts, a tunnel and a bridge. To prevent reduced water flow in the Øresund by the construction, additional compensating dredging operations were performed. Subsequently, a monitoring program was set up to monitor the effects of the construction. The overall results show no impact, major or temporal, of the construction on water quality, sediment characteristics, benthic vegetation, mussel populations, benthic fauna, migratory fish (herring), or on a nearby seal population.

Many species of fish rely on acoustics to survive in their marine ecosystems, either for predation (avoidance), mating or spatial orientation. Construction sounds might interfere with these acoustic based aspects of the lifecycle. Due to limited research on the subject, exact effects of anthropogenic sounds on fish remains unclear. However, in a lab experiment; sea bass, thicklip mullet, pout, horse mackerel and Atlantic cod all got startled by sounds below 2 kHz, while herring possess a threshold closer to 4 kHz (Kastelein et al., 2008). Most activities in the North Sea area, including pile driving during construction and transport by boats, do not often surpass this range (Ainslie et al., 2009). So, it seems that that herring can tolerate a wide array of anthropogenic sounds and it, as a mobile pelagic species, has the potential to avoid noisy areas. Other Swimway species might be more vulnerable to loud sounds since vulnerability varies between species (Kastelein et al., 2008).

Transmission of electricity through cables, associated with wind turbines, will lead to the generation of electric and magnetic fields to which some species are sensitive. Though the use of mitigating measures such as improved cable armor and sheath or burial of the cables can reduce the impact. In conclusion, with the present knowledge, it can be assumed that these effects are of minor importance and that technological improvements may further reduce the impact. (Petersen & Malm, 2006)

The Wadden Sea is also known to be the main center of Dutch marine military activities, especially the 'Vliehorst', 'Mokbaai' and 'Marnewaard' areas. This involves shooting ranges for ground forces and aircraft, testing areas for military equipment and air target areas. Military activity is higher in the Dutch part of the Wadden Sea than it is the Danish and German parts (figure 8). However, munition; torpedoes and ballast droppings are recorded in both the Dutch and the Danish part of the Wadden Sea (Brenner et al., 2017). Continuous shooting can contaminate the surrounding waters with lead and other heavy metals. Most of these heavy metals are toxic to marine animals and have a tendency to get recycled in the food chain (Polak-Juszczak, 2009). High levels of heavy metals can also enter the marine ecosystem during exercises with high-powered weapons, though 'dummy' rounds have been developed to lessen the environmental impacts. Finally, possible wreckage caused by military training may pose certain risks for the environment they are found in, due to corrosion and degradation (Lawrence et al., 2015). Due to the small scale of the military trainings in the Dutch part of the Wadden Sea (and the inconsistency of the military trainings in Germany and Denmark), the effect on the ecosystem is expected to be neglectable (Brenner et al., 2017). However, exact research on the matter is missing in the Wadden Sea.

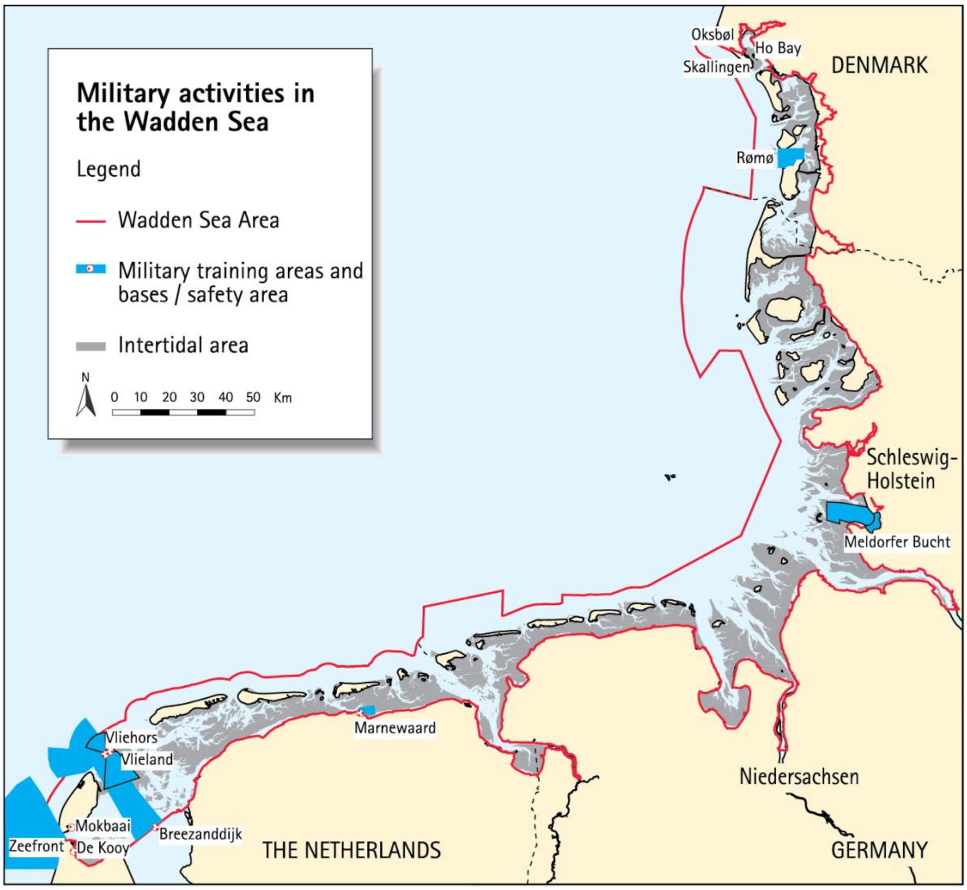

Figure 8: *Military hotspots within the Wadden Sea area. While Dutch military grounds are used every working day, military areas in Germany and Denmark are commonly used once a year (Brenner et al., 2017).*

The final human activity which takes place in the swimway of herring is dredging (figure 9), which can create temporary sediment plumes in the water column. Dredging is expected to cause serious problems when executed near spawning areas, though this is not the case for herring, which experiences dredging near the nursery grounds (De Groot, 1996). On these nursery grounds, larval development is unaffected by silt. Mortality rates varied significantly between aquaria in lab experiments but was unrelated to silt treatment (Kiørboe et al., 1981). It is thus concluded that suspended particles pose no harmful effects to herring on their nursery grounds, especially when larvae start to show avoidance behaviour. The Wadden Sea is an intertidal area in which turbidity is already high, even without dredging, which makes herring larvae naturally resistant to turbid waters, at least temporally. The more likely complication on herring survival is the effect of dredging on zooplankton. Since zooplankton obtains its food by filtration, it can be proposed that an unnatural increase of suspended matter will result in detrimental effects, which negatively affect herring larvae through their food source (De Groot, 1979b; Phua et al., 2002). However, effects at higher trophic levels are not well studied (Phua et al., 2002). Finally, dredging has the potential to release 'trapped' heavy metals from the sediment, after which it can affect pelagic species like herring. If bioaccumulation of these metals continues for longer amounts of time, mortality rate rises (Taylor, 2014). An increase in heavy metals also goes along with a local decrease in oxygen, due to oxygen binding (Phua et al., 2002). Though elevated levels of heavy metals have been registered in the area even before large scale changes in fish stocks occurred, it may amplify the effect of other factors like global warming and stratification, especially in the Dutch Wadden Sea, where military activity and dredging are more common.

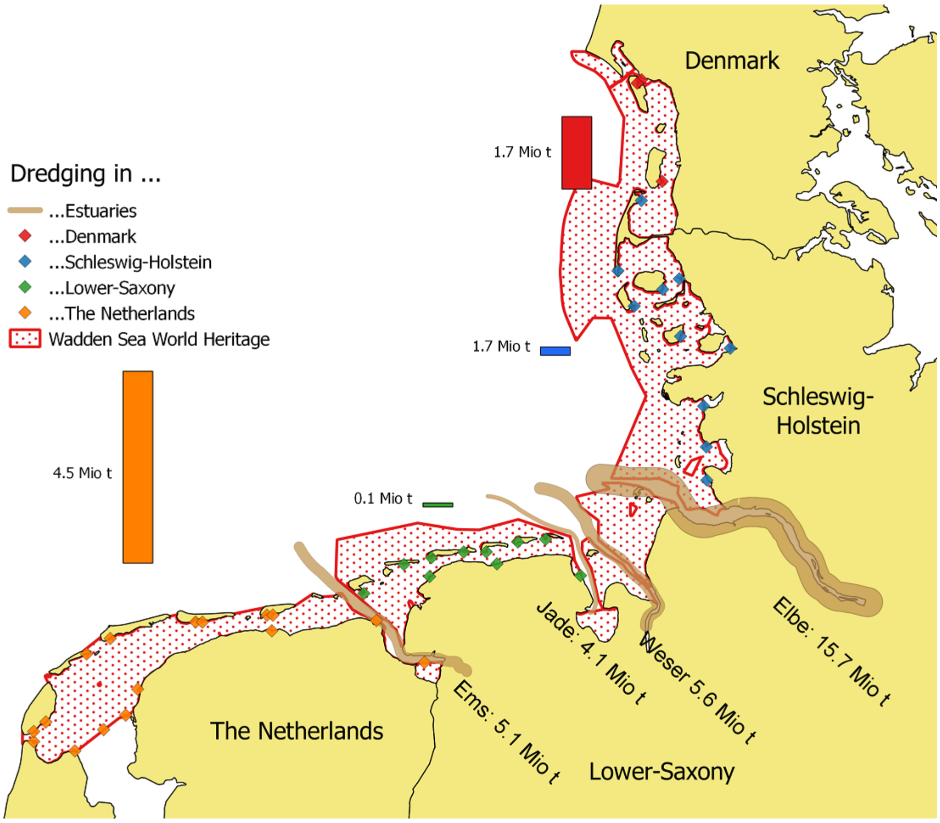

Figure 9: *Both the locations of dredging and average amount of dredged sediment in the different parts of the Wadden Sea between 2006 and 2013 (Schultze & Nehls, 2017).*

3.2.8. Bottleneck overview:

In this paragraph, a short overview of potential bottlenecks is given. Global warming seems to be the main driver in ecological changes in the North Sea area, through direct impact on herring or bottom-up effects including plankton distribution and composition. This effect of global warming can either be toned down or amplified by varying NAO intervals. Further increases in temperature, and an expected increase in fresh water runoff, are expected to continue this sequence of change through additional effects like reduced salinity in coastal areas and water mass stratification, resulting in eutrophication and other detrimental effects. In the past, fisheries have resulted in collapses of herring stocks, predominantly after ‘weak’ years with low recruitment or high larval mortality. However, the continuous monitoring of herring stocks is now a crucial part of the North Sea herring fishery, making sure that exploitation is sustainable, even in years of low stock size. Other stakeholders in the North Sea area are generally aware of the effects which their activities have on local ecosystems, regularly implementing new measures to reduce negative impacts. Consequently, effects on herring are often minimal and might only be significant when the animal is in a weakened and vulnerable state. On many of these activities, including oil exploitation, construction of wind turbines and gravel extraction; research does not indicate a clear detrimental effect, as is seen in most research on global warming. However, this is not the case for military activity and dredging, of which local effects are monitored in lesser extent. Military activities and dredging are common in the Wadden Sea (especially the Dutch part), which is used as a nursery during a critical period of development for herring larvae and juveniles. Research on these activities in the Wadden Sea are either limited, including a plethora of knowledge gaps, or absent. Jellyfish blooms and harmful algal blooms might occur in the future, though this is mostly speculation.

3.3. Sub-question 3: *How can the identified bottlenecks for herring be countered in relation to the Wadden Sea?*

In this chapter, existing management on herring in the North and Wadden Sea is explained and compared with management in the USA to see if adaptations on current management can be made to improve on bottlenecks specified in the second sub-question.

3.3.1. Existing management and regulations inside the North- and Wadden Sea:

The North Sea and Wadden Sea are protected via many framework policies and directives, as has been mentioned in the introduction. These different policies have all sorts of management objectives to protect the animals and environments included. Herring is also stated in some of these management objectives. Measures on herring have been taken after earlier collapses of the herring stock in the North Sea. As mentioned before, the herring stock collapsed around the 1970's and another dip in the herring stock was seen in the 2000's. The Common Fisheries Policy (CFP) was introduced in the 1970's to protect fish stocks against overexploitation. TAC's (total allowable catches) where introduced in 1983 to set a maximum amount of fish to be fished upon. For economically important species, these TAC's are set annually to prevent overfishing. For less important species, TAC's are set once every two years. The changes made to the herring TAC are based on scientific research on herring. This research, and advice on the TAC, is provided by ICES. In 2018, the TAC set for herring is 435 000 tonnes for the Northeast Atlantic and Greenland (European Commission, 2013; ICES, 2016a). The latest change of the CFP in 2014 also states that all herring should be landed, even when they are below the minimum landing size. This landing obligation is for scientific purposes and is counted against the quota (European Commission, 2013).

Although herring itself is not specifically included in the habitat directive or any of its annexes, it is protected though the protection of the Wadden Sea and through other protected animal species which utilize the Wadden Sea. Herring is a prime user of habitat type: permanently flooded sandbanks, mentioned in the Natura 2000 habitat profile: permanently flooded sand banks (H1110) (2014), which in turn is part of the habitat directive. Here herring is used as an indicator for a good abiotic state and good biotic structure. No specific measures regarding herring have been taken here (Altera, 2014).

Herring is also used as an indicator species for the WFD. This is done in the Wadden Sea and used mostly in transitional waters. The herring is used an indicators species for river mouths or estuaries like the Elbe (2006), Weser (2006) and the Ems (2007). At these locations, juvenile herring abundance is classified as bad when there are 0-100 individuals or as very good when there are 1120-2000 individuals per 80 m^2 per hour caught by stow net. This species is thus included in the ecological quality of these places (Kranenbarg & Jager, 2009).

Additionally, herring is protected though the MSFD. In here it is stated that, in certain places, disturbance of sediments should be limited to a minimum. Spawning grounds of herring are considered one of these places and no sediment disturbances are allowed here during spawning time (OSPAR, 2012). This enables herring to spawn safely without limiting recruitment. As mentioned before, it is also prohibited to fish on herring on the spawning grounds during the spawning season, to enhance recruitment of the next herring generation. Especially since adult herring are more clustered on the spawning grounds than on the feeding grounds, making them more vulnerable to overfishing (Overzee & Rijnsdorp, 2015).

Through the framework of OSPAR and the WFD, measures have also been taken to combat eutrophication in the Northeast Atlantic. These measures are not targeted at herring directly, however, they do address the thread of eutrophication to herring. These measures state that industries, like agriculture and sewage treatment plants, cannot dump their waste into rivers but should first filter and control the amount of, and chemical composition of, their waste to acceptable levels (De Jong, 2007). The aim for "a Wadden Sea that can be regarded as a eutrophication non-problem area" (Van Beusekom et al., 2017, p. 141) has also been set by the framework of OSPAR in 1997. Denmark and Germany have agreed on a chlorophyll-A percentile threshold of 7,5 µg per liter. However, no agreements have been made on the eutrophication status between the Netherlands and Germany. The aim of the MSFD is that the Wadden Sea reaches a "Good Environmental Status" and the aim of the WFD is that the Wadden Sea reaches a "Good Ecological Status". These factors are based on different biological and chemical parameters. These parameters differ per region and are thus dependant on the area itself, however, these parameters mostly include phytoplankton biomass or chlorophyll production or other similar parameters (Van Beusekom et al., 2017). So far the requirements for a "Good Environmental Status" and "Good Ecological Status" have not been met. Among the 3 Wadden Sea countries, management on herring slightly differ but are uniformly the same.

3.3.2. Existing management and regulations in the USA:

Herring is not only present in the North- and Wadden Sea but also occurs in the Atlantic Ocean next to North America, Greenland and in the ocean above Scandinavia and Russia. This chapter breaks down management on Atlantic herring in the USA, to compare with management being executed in the North Sea area.

In the USA, the Atlantic herring stock is managed in state and federal waters by the Atlantic States Marine Fisheries Commission, National Oceanic and Atmospheric Administration (NOAA Fisheries) and the New England Management Council. The herring management area is divided into 4 districts, named area 1 to 4. Fisheries require permits to exploit herring, in each individual area, and different permits allow fisheries to fish in either one or a couple of these areas. Some of these permits (Permits A, B and C) require the fisheries to report their catches on a weekly basis to the National Marine Fisheries Service (NMFS) (NMFS, 2011). Fisheries are managed similarly to TAC's in the Northeast Atlantic, however this is done via a stock wide annual catch limit (ACL). The ACL is set once every 3 years and the annual catch limit set for 2018 is 49900 mt. This catch limit has only been in effect since the 23rd of August, since the limit lowered half way through the year because of an updated stock assessment made by the New England Fishery Management Council. This was done since herring recruitment in 2018 has so far been poor and measures were required to prevent large cuts in the upcoming years. The reduction in ACL is expected to reduce the probability of overfishing in 2018 and increases the herring stock biomass for 2019 till 2021. There are no minimum or maximum fish sizes set in the USA. Once fisheries reach 92% of the ACL for that year, fisheries are not allowed to have more than 907,18 kg of herring per trip (NOAA, 2018). The ACL and management thereof lies with the NMFS (NMFS, 2011). Discarding or slippage of bycatch is not allowed, unless retrieving the herring from the nets, for whatever reason, results in unsafe conditions.

In the USA, the herring fisheries are also linked to the quota of haddock. Here the herring fisheries are allocated 1% of the acceptable biological catches for each haddock stock in the Gulf of Maine and Georges Bank. When the quota of haddock has been reached in a specific area, herring fisheries are limited in that same area, to prevent the overexploitation of haddock. If the ACL for haddock is reached, all herring fisheries with mid-water trawling gear are not allowed to land more than 907,18 kg of herring (NOAA, 2018).

3.3.3. Overview and comparison of management on herring

The management of herring in the USA must be compared with the European management to find if adaptations can be made to protect the herring stock in the North- and Wadden Sea. Between the management policies of the USA and Europe, some similarities and differences can be found in how they manage fishing pressure. In Europe, a TAC is set, whereas in the USA, an ACL is set. Both measures set the maximum amount of herring which is allowed to be caught and are thus quite similar. One of the differences between the measures is the amount of time they are set for. In Europe this is done annually, but in the USA, this is set once every 3 years. Even though, in the USA, ACL is set once every three years, the management in the USA does seem more reactive, since the management was adapted half way through 2018 to prevent overexploitation of the herring stock. There might be a difference in the speed in which the USA can develop new adaptations, in reaction to stock changes, compared to Europe. The USA is a single country with different legislative organs, however, it is still based on the same legislative system. This is different in comparison to Europe, which must deal with multiple different countries and legislative systems. This results in complications while managing shared areas like the North Sea. Another difference between the USA and Europe is the linkage between different fish stocks in the USA, like the link between the haddock stock and the herring stock. In Europe, every stock is seen separately. As conclusion of the comparison, there is no real evidence that proves that management in Europe is better than the management in the USA or vice versa. The annually set TAC in Europe seem like a better implementation since research on the stock is done on a regular base and adaptations are made every single year, while adaptations in the US commonly occur once every three years. However, the legislative system of the USA allows management organs to react quickly to changes in the herring stock and adapt accordingly. In Europe this sort of system would be near impossible since management must deal with multiple countries with different laws, regulations and interests. However, no suggestions for management improvement can be concluded by comparing management from Europe with management in the USA, due to their striking similarities.

4. Discussion

This study provides an insight in the potential bottlenecks during the lifecycle of herring in the North- and Wadden Sea. While monitoring of the herring stock in the North Sea is commonly executed, monitoring of the herring stock within the Wadden Sea is rather scarce and knowledge from within the Wadden Sea is limited (Kellnreitner, 2012; Rijke Waddenzee, 2015). However, by combining the profound knowledge on herring in the North Sea, available knowledge of the Wadden Sea and knowledge of herring expert, Dr. Andreas Dänhardt, a profound lifecycle description of herring has been made. A description of potential bottlenecks that could be found during the lifecycle of herring is also provided.

Due to the nature of a literature review, there is always a chance that important information is not included in the analysis. This is due to the fact that not every single paper on herring in the North- and Wadden Sea has been read due to time constraints. To reduce the chance of missing important information, the reference list of this analysis has been checked by herring expert Andreas Dänhardt. Dr. Dänhardt concluded that no important authors on the subject where missing from the literature list (personal communication, 17 October 2018).

The research matrix used during this study helped gaining structure and made it easier to decide which factors were considered important and which were considered unimportant. Decisions made in the research matrix where still made though human decisions and errors could have been made as a result. Examples of these errors could include: overlooking important information from a scientific article, unknowingly excluding information from the research matrix or wrongly deciding which research paper holds the most realistic information between two conflicting pieces of information (Choguill, 2005). To reduce human error, all conflicting information has been discussed between the authors of this analysis. Added to this, reoccurrence and date of publishing helped deciding which of the conflicting information seemed more plausible. An example of conflicting information is the effects of temperature on larval mortality. Hufnagl & Peck (2011) suggest that the driving factor of larval mortality is temperature. Whereas Payne (2013) does not support this hypothesis and suggest that other factors, linked with temperature, are the driving factor.

Other conflicts can be found in the expected temperature increase in the North and Wadden Sea during the next century. Models from Pörtner & Knust (2007) suggest an increase by about 1.6° to 3.0°C in the Northern North Sea and 3.0° to 3.9°C in the Southern North Sea, while Peperzak (2003) and Sims et al., (2004) expect an increase from 0.5°C up to 5.8°C in the North Sea area. It is still unknown which temperature increase will eventually take place and, thus, to which extent herring will be affected. As mentioned in Reid et al., (1999), the preferred temperature of juvenile herring is around 10 to 16 °C. Since the average temperature of the Marsdiep (Wadden Sea) was 11,5°C in 2015, a temperature increase of 5.8°C could potentially be stressful for juvenile herring, resulting in higher metabolic rates (NIOZ, 2016). However, an increase of 0.5°C might be neglectable.

Another point up for discussion is that it is near impossible to know if a change in sea water temperature is caused by global warming or by the NAO (Fässler et al., 2011; Rafferty, 2011). Although changes in temperature are likely caused by a combination of the two (Reid & Edwards, 2001; Weijerman et al., 2005). Temperature and salinity ranges are both important for herring. However due to limited research on salinity in the North and Wadden Sea, salinity ranges from the USA where used to specify which ranges herring prefer. This was done as a comparison since no specific salinity ranges of the North and/or Wadden Sea could be found. Research on temperature is overall more prevalent than research on salinity.

Due to the sensitivity of *C. Finmarchicus* to temperature, the potential increase in temperature in the Wadden Sea could be bad for herring since *C. Finmarchicus* is one of the main prey items of herring and is usually consumed in large numbers. However, it is unknown if the increasing unsuitability of the Wadden Sea, for this copepod species, has a direct effect on herring. Even though movements of herring have been linked with a northern movement of *C. Finmarchicus* (Corten, 2001a), It is unknown if herring will adapt to another species or follow the movement of *C. Finmarchicus*. Furthermore, the stock decrease of herring in the 2000's is mismatched with the drop in tintinnids seen in Hinder et al., (2011) (Hinder et al., 2011; Payne et al., 2009; Payne et al., 2013). The decrease in tintinnids could have amplified the decrease of the herring stock but is most likely not the main cause, as this drop in tintinnids started in 2003 while the herring stock already dropped in 2000.

This research also concludes that there are some bottlenecks of which the potential effects are not yet completely known or understood. This is partially due to the limited monitoring of herring within the Wadden Sea and partially because some (potential) bottlenecks have not been fully researched, or no research has been done, on their effects on herring. Examples of this are the heavy metal input by military activity, the effect of the release of trapped heavy metals in the Wadden Sea due to dredging and the effects of jelly fish and harmful algal blooms. Even though harmful blooms do not pose a problem right now, it might in the future, when jellyfish blooms are, by some researchers, expected to occur due to warmer winters. So far only speculation is possible. Currently, no final statements on these effects can be made due to limited research or uncertainty in upcoming temperature increases.

5. Conclusion

By combining the results from all the sub questions, the main question can be answered. 'What bottlenecks and knowledge gaps occur within the lifecycle of herring (Clupea harengus) in relation to the Wadden Sea and how can these be countered?'.

A lot of activities and phenomenon, affecting the local herring population, are occurring in the North Sea and the Wadden Sea. Though most of the described factors are shown to have the ability to negatively influence fish stocks, some only pose minor thread in comparison with larger drivers of change in the area. Even though fisheries are known to be responsible for stock collapses in the past (Corten, 2013; Herdson & Priede, 2010; ICES, 2016b; Rijke Waddenzee, 2015), they are generally problematic when herring year class is already low, due to other stressors. Even though the introduction of better fishing techniques was a major threat at the time, during the last decade, awareness has been rising. Through the years, management of herring fisheries have been refined to a point where stock collapses are unlikely to happen due to monitoring and preservation of stocks. With the monitoring of herring populations integrated in the fisheries, fishing pressure should not be responsible for the ongoing changes in the North Sea area. Instead, latest changes in the North Sea area might predominantly be caused by, a possibly Atlantic wide, climate change (Akimova et al., 2016; Corten, 2001a; Möllmann et al., 2008; Payne et al., 2013; Peperzak, 2003; Pörtner & Knust, 2007; Reid & Edwards, 2001; Rijnsdorp et al., 2009; Sims et al., 2004; Weijerman et al., 2005). In the upcoming decennia, temperature increases between 1.6 and 3.9°C (Pörtner & Knust, 2007), or even up to 5.8°C (Peperzak, 2003; Sims et al., 2004), are expected throughout the North Sea area. It has been shown that this climatic change has multiple effects on the Wadden Sea, both direct and indirect. The direct effects of climate change are the exceedance of the temperature limit for both herring or their main food item. This is expected to drive big future changes in the North Sea herring stocks, with Wadden Sea herring being affected fist, due to their shallow coastal habitat. Northern migrations have already been documented and are expected to increase in frequency (Corten, 2001a; Rijnsdorp et al., 2009; Rose, 2005). The timing of these migrations suggests that *C. finmarchicus* migrate further North, forcing herring to go with them (Dickey-Collas et al., 2010; Philippart et al., 1996). Especially since this copepod is highly sensitive to temperature changes (Akimova et al., 2016; Corten, 2000). However, warming of coastal nurseries will, at a certain point, increase stress and metabolic rate to such high levels that these areas lose their suitability for northern species like herring (Corten, 2013; Fässler et al., 2011; Gröger et al., 2009; Hufnagl & Peck, 2011; Rijnsdorp et al., 2009; Weijerman et al., 2005). Though a consistent water temperature increase is expected to be the main driver, the indirect effects of climate change might also pose a problem to species, like herring, which are inflexible in the time of spawning (Hufnagl & Peck, 2011; Secor, 2007; Sinclair & Tramblay, 1984). Temperature increase and stratification of the water column, which might be amplified by future salinity changes and eutrophication, provide perfect conditions for premature algal blooms (Peperzak, 2003; Rijnsdorp et al., 2009). In combination with NAO changes, this phenomenon already causes complications, resulting in weak year classes of herring. It is expected that North Sea herring cannot adapt spawning time to match the new timing of algal blooms (Hufnagl & Peck, 2011; Secor, 2007).

The other described stressors within the North Sea area do not directly cause, but might amplify the weakening of herring stocks, when combined with climate changes. Hydrocarbons introduced by the oil industry have been proven to affect larval herring up to 4000 meters away from production platforms and refineries are often located near spawning grounds or nurseries. However, effects of hydrocarbons seem to be close to zero since they cannot be separated from the effect of natural processes and research on the subject shows varying results (Pasche, 1993).

In the Wadden Sea itself, military activity releases heavy metals into the ecosystem which might be trapped in the sediment and consequently be released again by the intensive dredging in the area (Phua et al., 2002). Though not enough data is available on this interaction to state the effect on juvenile herring. While measures on countering eutrophication are taken, the Wadden Sea is still seen as a problem area (Van Beusekom et al., 2017). With increasing temperatures in the area, eutrophication should be monitored on the combined effect with climate change. These, commonly by Wadden Sea herring encountered, stressors might have bigger effects on herring when metabolic rate is already high and condition is weak due to climate change and high NAO-index.

While gravel extraction is currently not a thread, the increasing demand of gravel might eventually deplete local gravel beds (Van Lancker et al., 2015). However, maximum aggregation loads are known to decrease with the decreasing resource, indicating conservatism of the aggregate (FOD Economie, 2014). This makes it unlikely for the resource to be depleted before climate change have already had drastic effects on the local stocks. The construction of wind turbine parks did not indicate any harm to herring (Ainslie et al., 2009; Petersen & Malm, 2006) and jellyfish and harmful algal blooms have not yet been sighted in the northeast Atlantic (Rijnsdorp et al., 2009). While the latter might turn problematic somewhere in the future due to warmer winters, it is currently not responsible for big changes in the North Sea herring population.

To reflect on the main question, herring comes across a few main bottlenecks within the Wadden Sea, which are: climate change induced temperature increases, eutrophication and a lack of knowledge on the (combined) effects of military activity and dredging in the area. Global warming is expected to be the main driver of the deterioration of the Wadden Sea (Akimova et al., 2016; Corten, 2013; Edwards et al., 2006; Hufnagl & Peck, 2011; Möllmann et al., 2008; Payne et al., 2013; Rijnsdorp et al., 2009), as a habitat for herring, and this problem is near impossible to be countered by human management. However, measures towards countering the other bottlenecks and knowledge gaps within the nursery are discussed in the recommendations.

6. Recommendations

In this chapter, recommendations are made for the Wadden Sea Board in light of the Swimway Action Programme. Recommendations made are focussed upon the Wadden Sea.

Since bottlenecks discovered in the lifecycle of herring are primarily driven by climate change, the problem is mostly out of human hands. While it might be near impossible to reverse the warming of the North Sea, especially since the warming and cooling of seas and oceans are a natural phenomenon, it will be possible to reduce other stressors which might amplify the impact of climate change on herring. Since oil exploration and refineries are located outside the Wadden Sea, only military activity, dredging and eutrophication are stressors which threaten the successful survival of juvenile herring in this area. Close monitoring of eutrophication in the Wadden Sea is the backbone of keeping the nutrient input in the area on a stable level. While there are multiple monitoring stations in the Wadden Sea, the utilization of these resources varies on a yearly basis (Van Beusekom et al., 2017). For the most optimal results, all stations should be active each year. This way, critical nutrient levels can quickly be acted on when they do occur. Additionally, more research on the effect of eutrophication on herring must be conducted. Due to the limited knowledge on the effect of military activity in the Wadden Sea, partially due to the lack of knowledge on precise military activities in the area and their extent of their pollution, it is impossible to assess the effect on juvenile herring. Even though the small-scale heavy metal input is expected to pose minor problems, it should still be researched to make sure that this does not pose bigger problems when combined with temperature increases, stratification and dredging. This lack of data is especially daunting in the Dutch part of the Wadden Sea, were military activity is a daily routine (Brenner et al., 2017). Recommendations go to doing more precise research on the effect of heavy metals on juvenile herring, as a result of military activity in the Wadden Sea. While dredging plumes do not negatively affect juvenile herring in the area, it might negatively affect primary production which is of great importance to herring and other species of fish (De Groot, 1979b; Phua et al., 2002). Since dredging activity is more than three times as high in the Dutch part as it is in the other parts of the Wadden Sea, all should be known about the consequences of dredging in the area (Schultze & Nehls, 2017). Thus, more research on the effect of dredging on both herring and their prey, focusing on increased water turbidity and the release of trapped heavy metals, must take place. It is likely that possible problems, other than climate change, will primarily occur in the Dutch part of the Wadden Sea due to relatively intensive use of this area (Brenner et al., 2017; Schultze & Nehls, 2017). To manage herring in the Wadden Sea in the most effective way possible, these activities should be focused upon.

With this acquired knowledge, Swimway will have a better chance of successfully implementing the targets to maintain or improve: '*robust and viable populations of estuarine resident fish species within the Wadden Sea*' and '*the nursery function of the Wadden Sea and estuaries*' for pelagic juvenile species, like herring. Since juvenile herring exclusively uses (mobile) sand banks, on which human activity poses minor threats due to the habitats' durable nature and commonness (Vorberg et al., 2017), and herring itself is neither a diadromous or protected species, the other Swimway targets are less important for this species in particular. For the other Swimway species, a similar approach can be used to define bottlenecks and knowledge gaps in the lifecycle of these species. While the temperature increases in the Wadden Sea probably affects all fish species utilizing the area (Dulvy et al., 2008), other bottlenecks on herring might have little or no effect on the other Swimway species. On the other hand, found bottlenecks might affected other Swimway species even more. Final recommendations go towards performing similar (successive) research on other Swimway species, to aid the Swimway Action Programme in achieving the Trilateral Fish Targets in the Wadden Sea.

7. References

Acton, M. (2017). *Britain seeks to take back control in Brexit fisheries fight*. Accessed on 9 October 2018, from https://www.ft.com/content/4f21072a-c87f-11e7-ab18-7a9fb7d6163e.

Ainslie, M. A., De Jong, C. A. F., Dol, H. S., Blacquière, G., & Marasini, C. (2009). *Assessment of natural and anthropogenic sound sources and acoustic propagation in the North Sea*. Den Haag: TNO.

Akimova, A., Nunez-Riboni, I., Kempf, A., & Taylor, M. H. (2016). Spatially-resolved influence of temperature and salinity on stock and recruitment variability of commercially important fishes in the North Sea. *PloS one*, *11*(9), e0161917.

Almroth, E., & Skogen, M. D. (2010). A North Sea and Baltic Sea model ensemble eutrophication assessment. *Ambio*, *39*(1), 59-69.

Altera. (2014). *H1110 Permanent Overstroomde zandbanken*. Accessed on 26 September 2018, from https://www.synbiosys.alterra.nl/natura2000/documenten/profielen/habitattypen/profiel_habitattype_1110_2014.pdf.

Atlantic States Marine Fisheries Commission. (2016). *Habitat bottlenecks and fisheries management*. Accessed on 30 May 2018, from http://www.asmfc.org/files/Habitat/HMS13_Habitat_Bottlenecks2016.pdf.

Batty, R. S., Blaxter, J. H. S., & Richard, J. M. (1990). Light intensity and the feeding behaviour of herring, Clupea harengus. *Marine Biology*, *107*(3), 383-388.

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., & Edwards, M. (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, *296*(5573), 1692-1694.

Bjørndal, T. (1989). Production in a schooling fishery: The case of the North Sea herring fishery. *Land Economics*, *65*(1), 49-56.

Bolle, L. J., Neudecker, T., Vorberg, R., Damm, U., Diederichs, B., Jager, Z., & Marencic, H. (2009). *Trends in Wadden Sea Fish Fauna, Part I: Trilateral Cooperation* (No. C108/08). IMARES.

Bonsdorff, E., Blomqvist, E. M., Mattila, J., & Norkko, A. (1997). Coastal eutrophication: causes, consequences and perspectives in the archipelago areas of the northern Baltic Sea. *Estuarine, coastal and shelf science*, *44*, 63-72.

Brenner M., Bostelmann A. & Klöpper S. (2017) Military activities. In Kloepper S. et al., (Eds.), *Wadden Sea Quality Status Report 2017*. (Eds.) Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Cabral, H. N., Vasconcelos, R., Vinagre, C., França, S., Fonseca, V., Maia, A., & Freitas, V. (2007). Relative importance of estuarine flatfish nurseries along the Portuguese coast. *Journal of Sea Research*, *57*(2-3), 209-217.

Carpenter, A. (2018). Oil pollution in the North Sea: the impact of governance measures on oil pollution over several decades. *Hydrobiologia*, 1-19.

Choguill, C. L. (2005). The research design matrix: A tool for development planning research studies. *Habitat International*, *29*(4), 615-626.

Clausen, L. A. W., Bekkevold, D., Hatfield, E. M. C., & Mosegaard, H. (2007). Application and validation of otolith microstructure as a stock identification method in mixed Atlantic herring

(Clupea harengus) stocks in the North Sea and western Baltic. *ICES Journal of Marine Science*, *64*(2), 377-385.

Common Wadden Sea Secretariat. (2018) *Wadden Sea World Heritage Map*. Accessed on 26 April 2018, from http://www.waddensea-worldheritage.org/node/1228.

Common Wadden Sea Secretariat. (2018). *Trilateral Wadden Sea Swimway Vision Action Programme*. Accessed on 20 April 2018, from http://www.waddensea-secretariat.org/sites/default/files/Meeting_Documents/WSB/WSB23/wsb_23.5.2.2_swimway.pdf.

Corten, A. (2000). A possible adaptation of herring feeding migrations to a change in timing of the Calanus finmarchicus season in the eastern North Sea. *ICES Journal of Marine Science*, *57*(4), 1270-2000.

Corten, A. (2001a). *Herring and climate*. (Dissertation). Rijksuniversiteit Groningen, Groningen.

Corten, A. (2001b). Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. *Fisheries Research*, *50*(1-2), 189-204.

Corten, A. (2013). Recruitment depressions in North Sea herring. *ICES Journal of Marine Science*, *70*(1), 1-15.

Coull, K. A., Johnstone, R., & Rogers, S. I. (1998). Fisheries sensitivity maps in British waters. *UKOOA Ltd*, *9*.

Couperus, B., Gastauer, S., Fässler, S. M., Tulp, I., van der Veer, H. W., & Poos, J. J. (2016). Abundance and tidal behaviour of pelagic fish in the gateway to the Wadden Sea. *Journal of Sea Research*, *109*, 42-51.

Daan, N., Gislason, H. G., Pope, J., & C. Rice, J. (2005). Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of marine Science, 62*(2), 177-188.

De Groot, S. J. (1996). The physical impact of marine aggregate extraction in the North Sea. *ICES Journal of Marine Science*, *53*(6), 1051-1053.

De Groot, S. J. (1979a). The potential environmental impact of marine gravel extraction in the North Sea. *Ocean Management*, *5*(3), 233-249.

De Groot, S. J. (1979b). An assessment of the potential environmental impact of large-scale sand-dredging for the building of artificial islands in the North Sea. *Ocean Management*, *5*(3), 211-232.

De Jong, F. (2007). *Marine eutrophication in perspective: on the relevance of ecology for environmental policy*. Berlin: Springer Science & Business Media.

Dickey-Collas, M., Nash, R. D., Brunel, T., Van Damme, C. J., Marshall, C. T., Payne, M. R., & Hintzen, N. T. (2010). Lessons learned from stock collapse and recovery of North Sea herring: a review. *ICES Journal of Marine Science*, *67*(9), 1875-1886.

Dima, M., & Lohmann, G. (2011). *Causes and consequences of the late 1960s great salinity anomaly* (pp. 213-230). London: InTech.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, 45(4), 1029-1039.

Eastwood, P. D., Mills, C. M., Aldridge, J. N., Houghton, C. A., & Rogers, S. I. (2007). Human activities in UK offshore waters: an assessment of direct, physical pressure on the seabed. *ICES Journal of Marine Science*, *64*(3), 453-463.

Edwards, M., Beaugrand, G., Reid, P. C., Rowden, A. A., & Jones, M. B. (2002). Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series*, *239*, 1-10.

Edwards, M., Johns, D. G., Leterme, S. C., Svendsen, E., & Richardson, A. J. (2006). Regional climate change and harmful algal blooms in the northeast Atlantic. *Limnology and oceanography*, *51*(2), 820-829.

Elliott, M., Whitfield, A. K., Potter, I. C., Blaber, S. J., Cyrus, D. P., Nordlie, F. G., & Harrison, T. D. (2007). The guild approach to categorizing estuarine fish assemblages: a global review. *Fish and Fisheries, 8*(3), 241-268.

Ellis, J. R., Milligan, S. P., Readdy, L., Taylor, N., & Brown, M. J. (2012). Spawning and nursery grounds of selected fish species in UK waters. *Science Series Technical Report., Cefas Lowestoft, 147*, 56.

European Commission. (2013). *REGULATION (EU) No 1380/2013 OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC*. Accessed on 27 September 2018, from https://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2013:354:0022:0061:EN:PDF.

Exo, K. M., Huppop, O., & Garthe, S. (2003). Birds and offshore wind farms: a hot topic in marine ecology. *Bulletin-Wader Study Group*, *100*, 50-53.

Fässler, S. M., Payne, M. R., Brunel, T., & Dickey-Collas, M. (2011). Does larval mortality influence population dynamics? An analysis of North Sea herring (Clupea harengus) time series. *Fisheries Oceanography*, *20*(6), 530-543.

Alvarez Fernandez, S. (2015). *Rhyme and reason: plankton changes in the North Sea ecosystem*. Wageningen: Wageningen University.

FOD Economie (2014). *Reglementering zand- en grindwinning in het Belgische deel van de Noordzee*. Accessed on 11 October 2018, from https://economie.fgov.be/nl/themas/ondernemingen/specifieke-sectoren/zand-en-grindwinning-op-zee.

Føyn, L., & Serigstad, B. (1988). Oil exploration in new offshore fields. Fish larvae as the critical component in the assessment of potential consequenses for the fish resources. *ICES Journal of Marine Science*, (E:18)

Gröger, J. P., Kruse, G. H., & Rohlf, N. (2009). Slave to the rhythm: how large-scale climate cycles trigger herring (Clupea harengus) regeneration in the North Sea. *ICES Journal of Marine Science*, *67*(3), 454-465.

Gulf of Maine Research Institute. (n.d.). *Herring Biology: Life-Cycle*. Accessed on 5 September 2018, from http://www.gma.org/herring/biology/life_cycle/default.asp.

Haslob, H., Rohlf, N., & Schnack, D. (2009). Small scale distribution patterns and vertical migration of North Sea herring larvae (Clupea harengus, Teleostei: Clupeidae) in relation to abiotic and biotic factors. *Scientia Marina*, *73*(S1), 13-22.

Herdson, D., & Priede, I. (2010). Clupea harengus. The IUCN Red List of Threatened Species 2010: e.T155123A4717767. Accessed on 5 May 2018, from http://dx.doi.org/10.2305/IUCN.UK.2010-4.RLTS.T155123A4717767.en.

Hinder, S. L., Manning, J. E., Gravenor, M. B., Edwards, M., Walne, A. W., Burkill, P. H., & Hays, G. C. (2011). Long-term changes in abundance and distribution of microzooplankton in the NE Atlantic and North Sea. *Journal of plankton research*, *34*(1), 83-91.

Hufnagl, M., & Peck, M. A. (2011). Physiological individual-based modelling of larval Atlantic herring (Clupea harengus) foraging and growth: insights on climate-driven life-history scheduling. *ICES Journal of Marine Science*, *68*(6), 1170-1188.

ICES. (2015). *Science and industry jump into a (gravel) bed*. HAWG. Accessed on 23 September 2018, from http://www.ices.dk/news-and-events/news-archive/news/Pages/Science-and-industry-jump-into-(a-gravel)-bed.aspx.

ICES. (2016a). *ICES Advice on fishing opportunities, catch, and effort Greater North Sea Ecoregion, 1 6.3.18 Herring (Clupea harengus) in Subarea 4 and divisions 3.a and 7.d, autumn spawners (North Sea, Skagerrak, Kattegat, and eastern English Channel)*. Accessed on 28 September 2018, from http://ices.dk/sites/pub/Publication%20Reports/Advice/2016/2016/her-47d3.pdf.

ICES. (2016b). *Stock Annex: Herring (Clupea harengus) in Subarea 4 and divisions 3.a and 7.d, autumn spawners (North Sea, Skagerrak and Kattegat, eastern English Channel) (her-47d3)*. Produced by Herring Assessment Working Group for the Area South of 62°N (HAWG). 65 pp. Accessed on 28 September 2018, from http://ices.dk/sites/pub/Publication%20Reports/Stock%20Annexes/2016/her47d3_SA.pdf.

ICES. (n.d.) Clupea harengus species factsheet. Accessed on 12 June 2018, from http://www.ices.dk/explore-us/projects/EU-RFP/EU%20Repository/ICES%20FIshMap/ICES%20FishMap%20species%20factsheet-herring.pdf.

Jennings, S., & Beverton, R. J. H. (1991). Intraspecific variation in the life history tactics of Atlantic herring (Clupea harengus L.) stocks. *ICES Journal of Marine Science*, *48*(1), 117-125.

Kastelein, R. A., Van Der Heul, S., Verboom, W. C., Jennings, N., Van Der Veen, J., & De Haan, D. (2008). Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz. *Marine Environmental Research*, *65*(5), 369-377.

Kellnreitner, F. (2012). *The trophic structure of a Wadden Sea fish community and its feeding interactions with alien species*. (Doctoral dissertation). Universitätsbibliothek Kiel, Kiel.

Kiørboe, T., Frantsen, E., Jensen, C., & Sørensen, G. (1981). Effects of suspended sediment on development and hatching of herring (Clupea harengus) eggs. *Estuarine, Coastal and Shelf Science*, *13*(1), 107-111.

Kranenbarg, J., & Jager, Z. (2009). *Maatlat vissen in estuaria. KRW watertype O2*. Accessed on 28 September 2018, from http://www.vliz.be/imisdocs/publications/148360.pdf.

Lawrence, M. J., Stemberger, H. L., Zolderdo, A. J., Struthers, D. P., & Cooke, S. J. (2015). The effects of modern war and military activities on biodiversity and the environment. *Environmental Reviews*, *23*(4), 443-460.

Lindegren, M., Östman, Ö., & Gårdmark, A. (2011). Interacting trophic forcing and the population dynamics of herring. *Ecology*, *92*(7), 1407-1413.

Lotze, H. K. (2005). Radical changes in the Wadden Sea fauna and flora over the last 2,000 years. *Helgoland Marine Research, 59*(1), 71.

Lynam, C. P., Hay, S. J., & Brierley, A. S. (2004). Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography*, *49*(3), 637-643.

Lynam, C. P., Heath, M. R., Hay, S. J., & Brierley, A. S. (2005). Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series*, *298*, 157-167.

MacLachlan, P., Seaton, D., & Gamble, J. (1981). Developmental patterns of experimentally enclosed populations of autumn and spring spawned Atlantic herring larvae. *International Council for the Exploration of the Sea (CM. Papers and Reports)*.

Madsen, K. S. (2009). *Recent and future climatic changes in temperture, salinity, and sea level of the the North Sea and the Baltic Sea*. (Doctoral dissertation). Museum Tusculanum, Copenhagen.

Maes, J., Limburg, K. E., Van de Putte, A., & Ollevier, F. (2005). A spatially explicit, individual-based model to assess the role of estuarine nurseries in the early life history of North Sea herring, Clupea harengus. *Fisheries Oceanography*, *14*(1), 17-31.

Marine Stewardship Council. (n.d.). *Faroese Pelagic Organisation Atlanto-Scandian herring*. Accessed on 20 October 2018, from https://fisheries.msc.org/en/fisheries/faroese-pelagic-organisation-atlanto-scandian-herring/about/.

Möllmann, C., Müller-Karulis, B., Kornilovs, G., & St John, M. A. (2008). Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES Journal of Marine Science*, *65*(3), 302-310.

Nash, R. D., Dickey-Collas, M., & Kell, L. T. (2009). Stock and recruitment in North Sea herring (Clupea harengus); compensation and depensation in the population dynamics. *Fisheries Research*, *95*(1), 88-97.

NIOZ. (2016). *Wadden Barometer | Seawater temperature*. Accessed on 5 October 2018, from https://www.nioz.nl/en/expertise/waddencentre-1/wadden-barometer-seawater-temperature.

NMFS. (2011). *REGULATORY AMENDMENT TO REVISE CATCH REPORTING REQUIREMENTS IN THE ATLANTIC HERRING FISHERY*. Accessed on 1 October 2018, from https://www.greateratlantic.fisheries.noaa.gov/nero/regs/frdoc/11/11HerPRCatchReportingEA.pdf.

NOAA. (2018). *Atlantic Herring*. Accessed on 1 October 2018, from https://www.greateratlantic.fisheries.noaa.gov/sustainable/species/atlherring/index.html.

OSPAR. (2012). *MSFD Advice Manual and Background Document on Biodiversity A living document - Version 3.2 of 5 March 2012*. Accessed on 28 September 2018, from https://circabc.europa.eu/sd/a/68c36348-42b8-4181-98c4-1cb4fc67e0a4/OSPAR2001_Advice%20D1_D2_D4_D6.pdf.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., & Stenseth, N. C. (2001). Ecological effects of the North Atlantic oscillation. *Oecologia*, *128*(1), 1-14.

Paerl, H. W. (1997). Coastal eutrophication and harmful algal blooms: Importance of atmospheric deposition and groundwater as “new” nitrogen and other nutrient sources. *Limnology and oceanography*, *42* (5 part 2), 1154-1165.

Pasche, C. A. (1993). Conflicts in Use: The Impacts of the Oil and Gas Industry on the Herring Fishery in the North Sea. *Theses and Major Papers*. Paper 300.

Payne, M. R., Hatfield, E. M., Dickey-Collas, M., Falkenhaug, T., Gallego, A., Gröger, J., & Schmidt, J. O. (2009). Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. *ICES Journal of Marine Science*, *66*(2), 272-277.

Payne, M. R., Ross, S. D., Clausen, L. W., Munk, P., Mosegaard, H., & Nash, R. D. (2013). Recruitment decline in North Sea herring is accompanied by reduced larval growth rates. *Marine Ecology Progress Series*, *489*, 197-211.

Peperzak, L. (2003). Climate change and harmful algal blooms in the North Sea. *Acta Oecologica*, *24*, S139-S144.

Petersen, J. K., & Malm, T. (2006). Offshore windmill farms: threats to or possibilities for the marine environment. *AMBIO: A Journal of the Human Environment*, *35*(2), 75-80.

Petitgas, P., Secor, D. H., McQuinn, I., Huse, G., & Lo, N. (2010). Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. *ICES journal of Marine Science, 67*(9), 1841-1848.

Philippart, C. J., Lindeboom, H. J., Van der Meer, J., Van der Veer, H. W., & Witte, J. I. (1996). Long-term fluctuations in fish recruit abundance in the western Wadden Sea in relation to variation in the marine environment. *ICES Journal of marine science*, *53*(6), 1120-1129.

Phua, C., Van den Akker, S., Baretta, M., & Van Dalfsen, J. (2002*). Ecological effects of sand extraction in the North Sea*. Utrecht: Stichting De Noordzee.

Polak-Juszczak, L. (2009). Temporal trends in the bioaccumulation of trace metals in herring, sprat, and cod from the southern Baltic Sea in the 1994–2003 period. *Chemosphere*, *76*(10), 1334-1339.

Polte, P., & Asmus, H. (2006). Influence of seagrass beds (Zostera noltii) on the species composition of juvenile fishes temporarily visiting the intertidal zone of the Wadden Sea. *Journal of Sea Research*, *55*(3), 244-252.

Polte, P., Kotterba, P., Hammer, C., & Gröhsler, T. (2013). Survival bottlenecks in the early ontogenesis of Atlantic herring (Clupea harengus, L.) in coastal lagoon spawning areas of the western Baltic Sea. *ICES Journal of Marine Science*, *71*(4), 982-990.

Pörtner, H. O., & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *science*, *315*(5808), 95-97.

Purcell, J. E. (2005). Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United kingdom*, *85*(3), 461-476.

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

Rafferty, J. P. (2011). *North Atlantic Oscillation*. Accessed on 12 September 2018, from https://www.britannica.com/science/North-Atlantic-Oscillation.

Reid, P. C., & Edwards, M. (2001). Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenbergiana maritima*, *31*(2), 107.

Reid, R.N., Cargnelli, L.M., Griesbach. S.J., Packer D.B., Johnson. D.L., Zetlin. C.A., Morse. W.W. & Berrien P.L. (1999). Essential fish habitat source document: Atlantic herring, Clupea harengus, life history and habitat characteristics. *NOAA Tech Memo NMFS NE 126*; 48 p.

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

Rijke Waddenzee. (2015). *Species Fact Sheets for the Wadden Sea Fish Strategy*. Accessed on 05 September 2018, from https://rijkewaddenzee.nl/wp-content/uploads/2016/03/NHP0090-factsheets-DEF-ONLINE-LOW2.pdf.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., & Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. *ICES journal of marine science*, *66*(7), 1570-1583.

Rijnsdorp, A. D., van Leeuwen, P. I., Daan, N., & Heessen, H. J. (1996). Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *ICES Journal of Marine Science, 53*(6), 1054-1062.

Rose, G. A. (2005). On distributional responses of North Atlantic fish to climate change. *ICES Journal of Marine Science, 62*(7), 1360-1374.

Ruzzante, D. E., Mariani, S., Bekkevold, D., André, C., Mosegaard, H., Clausen, L. A., & Brigham, J. (2006). Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*(1593), 1459-1464.

Scharfe, M., & Callies, U. (2010). Long-term changes (1958-2004) in the hydro-climatic environment of the southern North Sea and consequences for the interpretation of observations on the island Helgoland (German Bight), 2010 AGU Ocean Sciences Meeting, Portland, USA, 22 February 2010 - 26 February 2010.

Schlaff, A. M., Heupel, M. R., & Simpfendorfer, C. A. (2014). Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. *Fish Biology and Fisheries, 24*(4), 1089-1103.

Schultze M. & Nehls G. (2017) Extraction and dredging. In Kloepper S. et al., (Eds.), *Wadden Sea Quality Status Report 2017*. (Eds.) Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Secor, D. H. (2007). The year-class phenomenon and the storage effect in marine fishes. *Journal of Sea Research*, *57*(2-3), 91-103.

Seitz, R. D., Wennhage, H., Bergström, U., Lipcius, R. N., & Ysebaert, T. (2013). Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science, 71*(3), 648-665.

Sguotti, C., Lynam, C. P., García-Carreras, B., Ellis, J. R., & Engelhard, G. H. (2016). Distribution of skates and sharks in the North Sea: 112 years of change. *Global change biology, 22*(8), 2729-2743.

Sims, D. W., Wearmouth, V. J., Genner, M. J., Southward, A. J., & Hawkins, S. J. (2004). Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology*, *73*(2), 333-341.

Sinclair, M., & Power, M. (2015). The role of "larval retention" in life-cycle closure of Atlantic herring (Clupea harengus) populations. *Fisheries Research*, *172*, 401-414.

Sinclair, M., & Tremblay, M. J. (1984). Timing of spawning of Atlantic herring (Clupea harengus harengus) populations and the match–mismatch theory. *Canadian Journal of Fisheries and Aquatic Sciences*, *41*(7), 1055-1065.

Skogen, M. D., Søiland, H., & Svendsen, E. (2004). Effects of changing nutrient loads to the North Sea. *Journal of Marine Systems*, *46*(1-4), 23-38.

Stratoudakis, Y., Gallego, A., & Morrison, J. A. (1998). Spatial distribution of developmental egg ages within a herring Clupea harengus spawning ground. *Marine Ecology Progress Series*, *174*, 27-32.

Taylor, H. (2014). *Dredging Up the Past: The Danger of Remobilizing Heavy Metals*. Accessed on 25 September 2018, from http://duwaterlawreview.com/dredging-up-the-past-the-danger-of-remobilizing-heavy-metals/.

Tulp I., & Bolle, L.J. (2018). Vis in de Waddenzee wat vertelt de monitoring ons (en wat niet)? Accessed on 6 April 2018, from https://rijkewaddenzee.nl/wp-content/uploads/2018/05/Swimway-stakeholder-workshop-6-april-2018.pdf.

Tulp, I., Bolle, L.J., & Rijnsdorp, A. D. (2008). Signals from the shallows: In search of common patterns in long-term trends in Dutch estuarine and coastal fish. *Journal of Sea Research*, 60, pp. 54- 73.

Tulp, I., Bolle, L.J., Dänhardt A., de Vries P., Haslob H., Jepsen N., Scholle J. & van der Veer H.W. (2017) Fish. In Kloepper S. et al., (Eds.), *Wadden Sea Quality Status Report 2017*. (Eds.) Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

UNESCO. (2009). *Wadden Sea*. Accessed on 29 April 2018, from https://whc.unesco.org/en/list/1314.

Van Beusekom, J.E.E., Bot P., Carstensen J., Grage A., Kolbe K., Lenhart H.-J., Pätsch J., Petenati T. & Rick J. (2017). Eutrophication. In Kloepper S. et al., (Eds.), *Wadden Sea Quality Status Report 2017*. (Eds.) Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Van Lancker, V., Lauwaert, B., De Mol, L., Vandenreyken, H., De Backer, A., & Pirlet, H. (2015). Zand- en grindwinning. In: Pirlet, H., Verleye, T., Lescrauwaet, A.K., Mees, J. (Eds.), *Compendium voor Kust en Zee 2015: Een geïntegreerd kennisdocument over de socio-economische, ecologische en institutionele aspecten van de kust en zee in Vlaanderen en België*. Oostende, Belgium, p. 109-118.

Van Overzee, H. M., & Rijnsdorp, A. D. (2015). Effects of fishing during the spawning period: implications for sustainable management. *Reviews in Fish Biology and Fisheries*, *25*(1), 65-83.

Vorberg R., Glorius S., Mascioli F., Nielsen P., Reimers H.-C., Ricklefs K. & Troost K. (2017) Subtidal habitats. In Kloepper S. et al., (Eds.), *Wadden Sea Quality Status Report 2017*. (Eds.) Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Vuorinen, I., Hänninen, J., Rajasilta, M., Laine, P., Eklund, J., Montesino-Pouzols, F., & Dippner, J. W. (2015). Scenario simulations of future salinity and ecological consequences in the Baltic Sea and adjacent North Sea areas–implications for environmental monitoring. *Ecological indicators*, *50*, 196-205.

Walker, P. (2015). *Wadden Sea Fish Haven*. Accessed on 26 April 2018, from www.rijkewadden.nl.

Weijerman, M., Lindeboom, H., & Zuur, A. F. (2005). Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Marine Ecology Progress Series*, *298*, 21-39.

Yin, M. C., & Blaxter, J. H. S. (1987). Temperature, salinity tolerance, and buoyancy during early development and starvation of Clyde and North Sea herring, cod, and flounder larvae. *Journal of Experimental Marine Biology and Ecology*, *107*(3), 279-290.

Appendix 1: Research matrix, Lifecycle of herring

Research matrix: Lifecycle of herring

	Key aspects				
Authors	*Spawning grounds*	*Larval distribution*	*Nursery grounds*	*Feeding grounds*	*Migratory paths*
Batty et al., 1990.		"The ability of herring Clupea harengus L. to feed on Artemia sp. nauplii in the light by filtering as well as biting (snapping) has been demonstrated by Gibson and Ezzi (1985). This species can now be regarded as a facultative filter-feeder when the density of prey is above a certain threshold. Herring can also feed on Artemia sp. nauplii in the dark but only by filtering (Batty et al. 1986), and because the fish swim more slowly in the dark the rate of removal of prey is lower than in the light."			
Clausen, 2007.					"Herring perform extensive seasonal

					migrations between spawning, feeding, and wintering areas (Slotte, 1998), and different stock components often mix on feeding and wintering grounds." "NSAS and Downs juveniles as well as adults of WBSS (western Baltic spring spawners) origin migrate into Division IIIa, where they feed in mixed stocks." "The large Norwegian spring-spawning (NSS) stock spawning along the west coast of Norway also migrates extensively (Slotte, 1998). However, an extensive literature search has not produced evidence for its migration into Division IIIa."
Corten, 2000.					"Herring starts feeding in the eastern North Sea and follow the plankton blooms going westwards."

					"There was a delay of one or two years between the shortening of the feeding season and the earlier departure of the herring from the eastern North Sea. This suggests the existence of a certain conservatism in the migrations of the herring." "It seems that the time of departure from the eastern North Sea is based not only on the food situation in the current year, but also on the average timing of food production in earlier years."
Corten, 2001a.		"Long-term changes in herring could be symptoms of variations in currents or other hydrographic parameters that have not yet been detected by hydrographic monitoring programmes. The observed changes in herring distribution, therefore, could be used to formulate new		"Bainbridge et al (1978) showed that the latitudinal shifts in the position of the herring fishery coincided with changes in the composition of the plankton on the fishing grounds. The changes in plankton distribution appeared to be related to variations in the inflow of	

		hypotheses about the existence of hydrographic changes that went unnoticed until now.” “Contrary to the northern North Sea, the southern North Sea receives only a limited input of Atlantic (or actually Celtic Sea) water. This is due to the restrictions posed by the narrow passage through the Strait of Dover. The inflow of Atlantic water into this area is strongly dependent upon the wind conditions over the English Channel and southern North Sea (Pingree and Griffiths 1980, Salomon and Bretton 1993). Variations in Atlantic inflow trough the Strait of Dover will affect the transport of herring larvae from the hatching grounds in the eastern Channel to the nursery grounds in the southern North Sea.		Atlantic water into the northwestern North Sea.”	

		Since local winds will be influenced by the NAO (North Atlantic Oscillation), the NAO will affect the SEC (Shelf Edge Current) and thereby ultimately the Atlantic inflow into the North Sea. This might affect larval distribution.”			
Corten, 2001b.				“All populations share a common feeding ground in the central and northern North Sea, although the southern population does not migrate as far north as the other two.”	“Herring of the southern population spawn in December ± January in the eastern English Channel, and then overwinter in the southern North Sea. In spring, the fish move directly to the feeding grounds in the central and northern North Sea.” “Herring is a northern species, for which the North Sea is a southern part of its distribution area.”
Corten, 2013.		“A critical factor for the survival of the larvae born in the central and northern North Sea is their transport in winter across the North Sea	“Although some larvae may be retained in coastal waters along the western board of the North Sea, the most important nurseries are found in the	“The larvae have to arrive in the eastern North Sea in early spring to take advantage of the spring plankton bloom.”	“The precise migration path of the adult herring is not known; presumably the fish migrate in a dispersed manner.”

		towards the nursery areas in the eastern North Sea.” “Normally, the bulk of the larvae should have reached the German Bight by February.”	shallow and productive waters of the eastern North Sea. This is evident from the high densities of juvenile (1-ringed) herring found in this area during the International Bottom Trawl Survey (IBTS). However, evidence for a disruption of larval transport in the earlier years is available from a sampling programme of late herring larvae in the inlets of the Dutch Waddenzee (Corten and Van der Kamp, 1979; Corten, 1986a). This region is part of the herring nursery area in the eastern North Sea (Figure 3), and larvae from the central North Sea spawning grounds normally arrive here in February–March.”		
Couperus et al., 2016.			“The Wadden Sea and the adjoining coastal area, both Natura 2000 sites (EC, 2002), are used by juvenile pelagic fish that later in life recruit to commercially exploited		

			adult populations (including herring *Clupea harengus*, pilchard *Sardina pilchardus*, anchovy *Engraulis encrasicolus*, sandeel *Ammodytes* sp.). Older life stages of some of these species stay in the shallow waters for feeding (Zijlstra, 1978)." "In October, sandeel was caught in low numbers and herring was the second most abundant species. The average lengths of herring ranged between 9.1–12.5 cm, but specimens up to 30 cm were caught."		
Dickey-Collas et al., 2010.			"As for the distribution of herring at other times of the year, the collapse seems to have had little effect, because feeding sites and nursery grounds appear to be governed by environmental factors, such as plankton production or physical transport."	"As for the distribution of herring at other times of the year, the collapse seems to have had little effect, because feeding sites and nursery grounds appear to be governed by environmental factors, such as plankton production or physical transport."	

Fässler et al., 2011.	"North Sea herring are synchronous batch spawners that lay mats of benthic eggs from which the larvae hatch."	"After hatching, the larvae are dispersed and drift in a counter-clockwise fashion towards nursery grounds in the German Bight and eastern North Sea."			
Gulf of Maine Research Institute, n.d. *U.S.A.	"At the other extreme, adults produce massive quantities of progeny, investing hardly any time or resources in any one offspring. Herring reproduction falls into the latter category, which is basically a number game: the large number of offspring ensures that at least a few survive despite high mortality." "Herring use external fertilization to produce masses of adhesive benthic (bottom-oriented) eggs that develop on the ocean floor and then metamorphose into transparent larvae which join the plankton drifting on ocean currents and eddies."	"Herring eggs that don't succumb to low oxygen levels or hungry predators hatch in about 7-10 days. Early development can take place over a wide salinity range, with the rate of development largely determined by water temperature." "Like many organisms, the larval and adult stages of herring are very different in appearance. Larval herring are elongated, transparent and entirely lacking scales. Larvae are approximately 5 to 7 mm long when they hatch and carry a yolk sac that provides a mobile food reserve. As they deplete their yolk reserve (+/- 10 days), their tiny mouthparts	"Aggregations of brit herring enter shallow bays and inlets, where they migrate vertically in the water column in response to light cycles. Dispersed throughout the water column during the day, they collect in surface waters at night to feed on their zooplankton prey. In the late summer and fall, when adults are migrating onshore to spawning grounds, the brit move offshore to spend winter close to the bottom."		"In general, the spawning pattern of herring conforms to the typical "triangular" migration pattern common in pelagic schooling fish. Adults migrate against currents from feeding grounds to spawning grounds. Larvae drift passively away with currents, and juveniles eventually swim back out to join adults at feeding grounds."

	“Mature eggs make up a large portion (20%+) of the female's body weight. The fecundity of herring females is typically in the range of 20,000-50,000 eggs per female, although a large female herring can lay as many as 200,000 eggs.” “Herring are iteroparous, meaning that spawning is not a death sentence and herring generally live to spawn repeatedly for several years. After spawning, their weight declines with the loss of reproductive material (gametes) and associated fat content.” “The sticky demersal eggs sink and adhere to the ocean bottom to form dense carpets that can be several centimeters thick. This egg mat contains eggs from numerous individual herring. In one square meter there can	develop enough to allow them to capture and swallow small prey. The transition to feeding in fish larvae is considered to be a "critical period" in which mortality is catastrophically high. [3] Larvae are weak swimmers, but are able to lunge at tiny larval plankton and eggs drifting nearby. Larval herring feed on a variety of tiny plankton. They can attack and fit in their mouths, including the eggs and larval stages of copepods, clams, barnacles, and shrimp. After hatching, the journey of the pelagic larvae is primarily at the mercy of the prevailing currents, tides and wind. Depending on environmental conditions like water temperature, the larval stage lasts from 3 to 11 (typically 6) months.”			

	be as many seven million eggs. Fertilized eggs hatch into larvae in 7-10 days depending on the water temperature. Egg mortality can be quite high. The mass of eggs lying on the bottom attracts an array of predators, for whom the egg mat simply represents a bonanza of protein covering the sea bottom. Cunner, tautog, flounder, cod, haddock, sculpin, and other fish as well as crabs, whelks, and starfish take advantage of this nutritive windfall. [1]" "Location in the egg mat may affect survival, with a trade-off between the effects of predation and oxygen-limitation. Eggs deposited on the upper level of the egg mat are more vulnerable to predatory fish and invertebrates. Alternatively, the top layer of developing eggs benefits from higher	"Not surprisingly, mortality levels are high during this vulnerable life-history stage - the odds of survival are stacked against these odd-looking transparent drifters. The pelagic phase is long and the young fish are potentially dispersed over a huge geographical area. Some researchers estimate that only about 1% of herring larvae survive to become juvenile fish."			

	oxygen levels as they are more exposed to the currents above.” “Preliminary research on herring egg beds off Scotland suggests that the herring eggs located deeper in the egg mat are less viable then those on top. In fact, researchers theorize that small, less developed larvae might hatch from eggs found lower in the egg mat.”				
Haslob et al., 2009.		“From the major spawning grounds of North Sea herring, located to the east coast of Great Britain, the herring larvae drift towards their nursery areas located in the German Bight (Corten, 1986).” “The temperature gradient from the surface to the bottom did not exceed 1.5°C. After Seliverstov (1974), this range does not affect the vertical migration of herring larvae. The same		“Ctenophores were recorded only sporadically in the depth range from the surface to 60 m and no conclusion regarding a possible diel migration could be made in this case.” “At least the results show that during the day herring larvae do occur in the same depth range as their potential prey.”	

		is considered for the minor changes in salinity from surface to bottom." "Heath et al. (1988) showed that herring larvae are mainly located in the mixed layer when the water column is stratified. However, in a totally mixed situation, herring larvae can be found throughout the water column." "In a study by Munk et al. (1989), herring larvae were observed to migrate into depth zones where they can prey successfully due to sufficient light and prey availability."			
Herdson & Priede, 2010.	"The species is divided into several subspecies, with separate spawning times; these include the winter spawning Norwegian and Icelandic herrings, the autumn spawning Icelandic and North sea herrings and the Baltic herrings."				

Hufnagl & Peck, 2011.	"It is unlikely that autumn-spawning herring will be able to avoid unfavourable conditions by delaying their spawning time or by utilizing more northern spawning grounds because of limitations in daylength to larval growth and survival."				
ICES, n.d.	"Herring are demersal spawners, depositing their sticky eggs on coarse sand, gravel, shells and small stones, all the members of a shoal spawning over a relatively short time period. The fish congregate on traditional spawning grounds, many of which are on shoals and banks and in relatively shallow water, approximately 15-40 m deep. Each female produces a single batch of eggs per year, releasing a ribbon of eggs that adheres to the substratum, and the male sheds milt while swimming a few	"The larval stage may be extended and passive drift may bring them to nursery areas that are far away from the spawning grounds." "Most autumn spawned herring larvae drift in an easterly direction, towards the important nursery grounds in the coastal waters of the eastern North Sea."	"Most autumn spawned herring larvae drift in an easterly direction, towards the important nursery grounds in the coastal waters of the eastern North Sea, and they metamorphose in the spring at a length of approximately 4.8 5.0 cm [14]. There are also nursery grounds in the Moray Firth and Firth of Forth. Larval drift is however variable, and in some years many larvae may not reach the traditional nursery areas."	"The pelagic larvae, which are 8-10 mm at hatching, feed on copepods and other small planktonic organisms [14,21]. Calanoid copepods are the predominant prey items during the early juvenile (< 3 cm) stage of life [12], but euphausids, hyperiid amphipods, juvenile sandeels, Oikopleura spp., and fish eggs are also eaten [20], with larger herring also consuming predominantly copepods with small fish, arrow worms and ctenophores aside."	"After spending their first few years in coastal nurseries, two-year-old herring move offshore into deeper waters [18], eventually joining the adult population in the feeding and spawning migrations to the western areas of the North Sea. These migration patterns, developed as juveniles, are generally regarded as being relatively constant over periods of several years despite environmental variation."

	centimetres above the female [11]. The resulting egg carpet, which can be 4-9 layers thick, may cover an area of up to one hectare. The number, size and weight of eggs produced by an average sized female vary between stocks [9]. For example, an average sized female (27.5 cm, 175 g) from the Downs stock (see below under stock structure) produces 42 000 eggs per annum (240 eggs per gram body weight) whereas a comparably sized fish from the Buchan stock may produce 67 000 eggs (380 eggs per gram) [13]." "It may take up to two weeks for the eggs to hatch, depending on sea temperature [14], and, after hatching, the pelagic larvae rise to surface waters where they are transported by the				

	prevailing water currents [15].”				
ICES, 2015.	“Spawning of the main North herring population begins in the north of the North Sea in September and then progresses southwards with time, ceasing in January in the eastern English Channel.” “As it takes about 10–15 days for the eggs to develop in the North Sea and the duration of the yolk-sac stage is 10–15 days, the total time for a spawning bed to remain undisturbed in order for allowing a successful survival of spawn will on average be around 30 days.”				
Kellnreitner, 2012.			“The importance of the Wadden Sea as nursery area for C. harengus and many other North Sea fish requires an early assessment of the possible threats induced by M. leidyi.”	“Although both species feed on zooplankton to a certain extent, they can differ in their feeding mode as the herring has the possibility to switch between filter- and particulate-feeding.”	

			"Atlantic herring (Clupea harengus) is the dominant pelagic fish using Wadden Sea waters as a nursery and is considered primarily recruiting from North Sea autumn and winter spawning populations (Corten 1986, Daan et al. 1990), although local stocks of spring spawners occur in the Wadden Sea."	"Herring is known to adjust feeding behavior and select prey according to prey size (Sandström 1980, Gibson and Ezzi 1985), visibility (Checkley 1982) and particle concentration (Gibson and Ezzi 1985, 1990)."	
Maes et al., 2005.			"Young herring pay for their migration into safer estuarine water by foregoing growth opportunities at sea. Accordingly, estuaries are regarded as nurseries for young-of-the-year fishes, providing abundant food resources and increased protection from predatory fishes (Boesch and Turner, 1984; Miller et al., 1985; Day et al., 1989; Blaber, 1997; Pihl et al., 2002; Ross, 2003). During spring, post-larval herring are predicted to utilize the turbid upper parts of the estuary,		"Herring assimilate more resources when forced to stay in the open sea than for an optimal or random migration strategy but they pay off with lower survival. Random movement between habitats results in both lower growth and survival. Herring migrate to another habitat only if the sum of metabolic costs inherent to the different habitat as well as migration costs to reach that habitat are lower than metabolic costs of

			which offer shelter and an abundance of copepods. To summarize, before summer young herring leave the estuary for the open sea to avoid warmer estuarine or coastal waters which are above the optimum for growth. Then follows a period of coastal residence before herring move into the estuary. Further, it is clear that the winter use of the turbid upper estuarine waters is facultative. In the second winter, the alternative use of the warmer coastal zone is suggested by our model, as high turbidities (>80 N TU) protect herring from predatory fish. First, estuarine residence results in fitter individuals through a considerable increase in survival probability of age-0 fish." "Secondly, model simulations indicate that temperature, and in particular the time lag		remaining in the first habitat."

			between estuarine and seawater temperatures, acts as a basic cue for herring to navigate in the heterogeneous space between the offshore spawning grounds at sea and the oligohaline nursery zone in estuaries.”		
Nash, 2009.					“McQuinn (1997) points out that in herring the larvae drift away from their spawning grounds and so do not have a natal spawning ground imprint. Therefore, they generally learn the location of spawning grounds from their peers by following them (Corten, 2001b). Thus recolonisation can be a slow process.”
Payne, 2009.	“The adults spawn along the east coast of Great Britain, and around Orkney and Shetland, from August to December.”	“The late stages of the larval phase are observed in February by a survey covering the entire North Sea, and are characterized by the MIK 0-group index (ICES, 2008a).”	“The International Bottom Trawl Survey (IBTS), performed concurrently with the MIK survey, gives an index of cohort strength at age 1-winter ring (wr) juveniles (ICES, 2008a).”		
Philippart et al., 1996.		“Successful transport of herring larvae has been	“Herring, like turbot and plaice, uses the Dutch	“Recruits of whiting, cod, plaice, sole, flounder, and	

		related to hydrographical conditions, which may deviate strongly from year to year.” “Coinciding high recruit numbers of herring, flounder, sole, plaice, and whiting in years with a low NAO index and low water temperatures in winter can therefore be caused by an enhancement of eastward transport of fish larvae across the North Sea.”	coastal zone as a nursery area.”	herring were abundant in periods when chlorophyll levels were above average and in years with low densities of predatory crustaceans.”	
Polte et al., 2013.			“After hatching, the sheltered, brackish lagoons (German: “Bodden”) represent particular retention areas where larvae are considered to perform most of the critical early life stage development.”		
Reid et al., 1999. U.S.A.*	“All spawning grounds are located in high energy environments, either nearshore shallows subject to wave/tidal flux, or deeper water with tidal action.”	“Occur in 9-16oC in the Gulf of Maine. Offshore waters in winter generally have higher temperatures than inshore waters (up to 5oC difference); may favor a more rapid development in offshore	“Preference for higher salinities with increasing age.”	“Juveniles (and adults) perform vertical migrations that are linked to changing light intensity, most likely in response to movements of their prey. They move up in the water column at	“Adults: Movements become sluggish at less than 4oC. Spawning occurs at temperatures of 7-15oC. Spawning in western Gulf of Maine

	"Spawning substrate varied (stones, gravel); free of fine sediments that might prevent gaseous exchange between eggs and environment. Bottom temp. of 5-15oC required. Average incubation time for autumn spawned eggs is 10-15 days. Developmental rate inversely related to temp.: 40 d at 4-5oC, 15 d at 6-8oC, 11 d at 10-12oC, 6-8 d at 14.4- 16oC. Herring deposit demersal eggs on a variety of substrates ranging from boulders, rocks, and gravel to sand, shell fragments, and macrophytes in 20 to 80 m of water in areas with strong tidal currents. Gravel is the preferred spawning substrate." "Larvae occur at temperatures of 9-16oC and salinities of 32 ppt in the Gulf of Maine."	waters, thereby reducing time of vulnerability to predation. Larvae that overwinter in estuaries typically experience reduced salinities. Some larvae are retained for several months after hatching on or near the spawning site, while other larvae are dispersed soon after hatching and drift with residual currents."		twilight and remain near the surface when light intensity is low; activity is highest just after sunrise and just before sunset. Larvae feed opportunistically on whatever zooplankton of appropriate size are abundant."	occurs at warmer temperatures than east. Enter bays and estuaries, but 28 ppt is lower limit of occurrence. Spawn at high salinities, ranging from 31.9 - 33.0 ppt; never brackish water."

Rijke Waddenzee, 2015.			"Found across estuarine, euryhaline, coastal, and continental shelf areas." "Herring is not sampled well by the DFS." "Juvenile herring occur in the Wadden Sea in considerable numbers and use gullies and intertidal for growth. They originate from different autumn (and winter) spawning herring stocks (e.g. Channel)." "Abundance reflects the processes that act during the larval phase on the North Sea, is thus mainly determined outside the Wadden Sea."		
Ruzzante et al., 2006.	"The existence of genetically and phenotypically diverse stocks in this region despite intense seasonal mixing strongly implicates natal homing in this species."				

	"Virtually all herring hatched in the autumn and winter were of NS origin (comprising NNS autumn spawners, English Channel winter spawners and Norwegian spring spawners)."				
Secor, 2007.	"Seasonal egg and larval production is often mistimed with periods of favourable survival conditions."				
Sinclair & Power, 2015.	"Although there is considerable evidence of mixing amongst populations of herring during the non-spawning components of the life history migrations (from both earlier tagging studies and more recent otolith micro-chemistry research), there is also considerable evidence of fixed spatial patterns of spawning. In this sense "plasticity" may well be an accurate characterization of some aspects of the life history migrations (juvenile nursery areas, adult	"Passive transfer of larvae is part of the life cycle." "The study (Heath & Rankine, 1988) concluded that the average drift rate for larvae in the coastal area was 9 Km per day, whereas the more offshore larvae were more rapidly advected to the North Sea."			"Under the Common Pool Hypothesis (Cushing, 1962), it is interpreted that first time spawners follow older adult herring to a particular spawning location (which may or may not be the location of their hatching). During subsequent years most individuals are interpreted to return the area of first spawning."

	feeding and overwintering areas), yet birth site fidelity could be relatively fixed (i.e. limited mixing amongst spawning components)."				
Sinclair & Tramblay, 1984.	"It is hypothesized that the timing of spawning of a herring population is a function of the time necessary to complete the larval phase and yet metamorphose within the acceptable seasonal envelope. Populations that have "'good" larval retention areas can spawn in the spring and still metamorphose within the seasonal envelope. Populations with larval retention areas that are less "good" for larval growth have to spawn earlier to satisfy the two constraints."				
Skogen et al., 2004.				"Results of this paper clearly show that the production estimates with the highest production are located along the continental coast. Here, the algal blooms start.	

				Oceanic inflow to the North Sea is the major source of new nutrients.”	
Stratoudakis, 1998.	“Herring Clupea harengus are unique among clupeoids and rare among teleost fish in having a demersal egg phase. During spawning, shoals of mature herring congregate near the seabed, where females perform specialised movements to deposit their eggs on the substrate, and males 'spray' the surrounding area with milt (Haegele & Schweigert 1985). Herring eggs have a slightly negative buoyancy and quickly stick to the sediment and to each other, gradually building a fairly uniform multi-layer mat (5 to 10 layers thick) along the spawning ground (Napier 1993).” “Developmental retardation in multi-layered herring spawn has been described in the				

	literature (Baxter 1971, Alderdice & Hourston 1985), and is believed to act through the restriction of water circulation in the deeper layers of the egg mat. This reduces oxygen availability and flushing of metabolic waste products (Napier 1993)."				
Yin & Blaxter, 1987.	"Clyde and North Sea herring, cod and flounder from hatching to the end of the yolk-sac stage, could withstand 21-23.5 "C, 20.5-23 "C, 15.5-18 "C and 21.5-24 "C, respectively. The temperature tolerance was reduced by about 3.5-4 "C for Clyde herring and cod, 4-4.5 "C for North Sea herring and 8-8.5 "C for flounder when the larvae reached the point-of-no-return (PNR, when 50% of larvae, although still alive, are no longer strong enough to feed)."	"The aim of the experiments was to stress the larvae in order to test whether there was a gradual decline of resistance during progressive starvation, or whether there was a sudden loss of resistance near the end of the starvation period. Although the high temperatures and low salinities used would not be experienced in the offshore marine environment, they might well be found in estuaries or shallow seas like the Baltic."			

Appendix 2: Research matrix, Bottlenecks herring

Research matrix: bottlenecks herring

	Key Aspects			
Authors	*Climate change*	*Eutrophication*	*Fishing pressure*	*Food availability*
Akimova et al., 2016.	“The North Sea is a complex shelf sea ecosystem, which has undergone strong changes over the last decades, mainly in zooplankton and fish communities. These changes are believed to be primarily driven by environmental variability and heavy exploitation of the commercial fishes.” “Commercial stocks in the North Sea are well documented and show a high inter-annual variability in their biomass and productivity. Together with fishing pressure this led to collapses and recoveries of the North Sea stocks, for instance, herring.” “The biomass of Calanus finmachicus (the main prey item of herring larvae) was shown to			

	be negatively correlated with the temperature and therefore could not cause the positive correlation between larvae abundance and temperature [29]. Therefore, Influence of Temperature and Salinity on Fish Stocks in the North Sea. One can conclude that the positive correlation between larvae abundance and temperature is probably a consequence of a positive relation between spawning stock biomass and temperature. Enhanced temperature may directly influence the growth rate of herring and thereby cause enhanced stock biomass in warm years. However, as we mentioned, the temperature amplitudes in this region are around 2°C on the inter-annual scale, therefore we rather suggest that temperature is a proxy for other mechanisms driving variability of herring spawning stock. One likely candidate might be changes in the zooplankton composition of the Atlantic inflow and, hence, the quantity of food for adult herring.”			

Almroth & Skogen, 2010.		"The assessment of eutrophication status according to the threshold values for summer CHL concentrations (direct effects) (Fig. 4a) indicates elevated levels in the river mouth areas in the southeastern North Sea. The assessment of eutrophication status according to the integration of the categorized assessment parameters (OSPAR 2005b) indicates that the entire southeastern part of the North Sea may be classified as a problem area."		
Bjorndal, 1989.			"The schooling behavior has permitted the development of very effective means of harvesting, in particular the purse seine. This means that with modern fish-finding equipment harvesting can be viable even at low stock levels."	
Clausen, 2007.	"However, growth rate and temperature strongly influence the formation of the first discernible increment (Høie *et al.*, 1997; Folkvord *et al.*, 2000; Pavlov *et al.*, 2000; Fox *et al.*, 2004). Folkvord *et al*. (2004) found no increase in size of sagittae from herring larvae			

	reared at 4°C up to 30 d, whereas herring reared at 12°C showed sagittal growth after 9 d.”			
Corten, 2000.	“Main food item *Calanus finmarchicus* is sensitive to temperature changes.”			“Main food item *Calanus finmarchicus* is sensitive to temperature changes.”
Corten, 2001a.	“So far it has been very difficult to link observed changes in herring to specific climate variations due to three different reasons: 1. It is difficult to isolate natural changes in fish stocks from man-induced effects; 2. Hydrographic variation in one area can be the combined effect of several independent processes, some of which are of climatic origin, and others which result from other causes (tidal and extra-terrestrial); 3. There is surprisingly little actual information on long-term hydrographic variation in the North Sea.” “Long-term changes in herring could be symptoms of variations in currents or other hydrographic		“A feature of these (herring) fisheries, and indeed of the herring fisheries in other parts of the world, has been the large and often sudden short- and long-term fluctuations and trends in their productivity, bringing periods of great prosperity, and ones of equally striking hardship to the fishing communities and industries engaged in them. In some cases, these fluctuations have been short-lived and sporadic, as in almost all marine fisheries, but in others they have been sufficiently large and sustained as to lead to the complete collapse of traditional fisheries. With the advent of modern fishing methods, the effects of fishing started to outweigh the natural changes in the stock.”	“Contrary to the northern North Sea, the southern North Sea receives only a limited input of Atlantic (or actually Celtic Sea) water. This is due to the restrictions posed by the narrow passage through the Strait of Dover. The inflow of Atlantic water into this area is strongly dependent upon the wind conditions over the English Channel and southern North Sea (Pingree and Griffiths 1980, Salomon and Bretton 1993).” “The Atlantic inflow is a major source of nutrients for the southern North Sea, and thereby will affect plankton production and feeding conditions for juvenile herring in this area.” “Since local winds will be influenced by the NAO (North Atlantic Oscillation), the NAO will affect the SEC (Shelf Edge

	parameters that have not yet been detected by hydrographic monitoring programmes. The observed changes in herring distribution, therefore, could be used to formulate new hypotheses about the existence of hydrographic changes that went unnoticed until now.”			Current) and thereby ultimately the Atlantic inflow into the North Sea. This might affect nutrient inflow.”
Corten, 2001b.	“If the recent climatic trend towards higher winter temperatures continues, the anomalous distribution of herring in 1988±1990 could become the normal pattern in future years.” “Data show that temperatures in the deep parts of Skagerrak have risen consistently over the last 50 years, which means that winter temperatures on the North Sea plateau must also have increased over this period.” “The northern distribution of herring in 1988±1990 coincided with high winter/spring temperatures, and low abundances of C. finmarchicus. Each of these two parameters could be the cause of the			“The herring will have encountered a scarcity of food on their normal feeding areas, and this food shortage may have stimulated them to extend their feeding migration northward into areas where C. finmarchicus was still abundant.”

	northern distribution of the herring." "The fish requires a specific temperature regime during the year to control its physiological processes. One of these processes is gonad development. Too high a water temperature may accelerate gonad development and result in maturation before the normal spawning time."			
Corten, 2013.	"During its subsequent meeting (ICES, 2007), the group concluded that the poor recruitment in North Sea herring was probably related to an increase of water temperature at the spawning sites in the central and northern North Sea, which could have affected frontal development and thereby food supply for the larvae."		"After a period of heavy exploitation in the 1950s and early 1960s, the southern and central populations were severely reduced and some of their spawning grounds were completely abandoned."	
Dickey-Collas et al., 2010.			"The collapse pattern demonstrates that North Sea herring exhibit the "basin effect" (MacCall, 1990): at low abundance, the population retracted to core spawning areas, whereas the peripheral areas were	

			recolonized during recovery.”	
Edwards et al., 2002.	“We suggest that these anomalous ocean climate conditions have far reaching consequences on the ecology of the North Sea and are arguably the principal cause of conspicuous ecosystem shifts rather than trends in atmospheric oscillations or anthropogenic perturbations.” “Corten (1990) and Corten & van de Kamp (1992) suggested that most of the observed changes in the pelagic fish stocks in the North Sea (particularly the dramatic decline of herring in the late 1970s) could be explained by a reduction of Atlantic water and changes to the circulation of the North Sea during this period.” “It is still open to question as to whether the biological changes are associated with a temperature-mediated response, circulatory changes within the North Sea, chemically driven changes via oceanic influxes or a combination of many factors.			

	Furthermore, we conclude that while the volume of oceanic water entering the North Sea is of considerable ecological importance, the original source of this water, from processes farther afield, maybe equally or more so.”			
Edwards et al., 2006.	“A pronounced decrease in sub-Arctic zooplankton and an increase in warm-temperate species also occurred during this period, suggesting a shift in the North Sea to a warm-temperate ecosystem. Recent work by Edwards and Richardson (2004) has also shown that climate warming has influenced the phenology of plankton, with the earlier seasonal appearance of dinoflagellates significantly correlated with SST. There has clearly been an increase in the percentage of exceptional bloom frequencies over the last 10 years in this area (west of Norway), with the last 6 years all above 10% exceptional bloom frequency and with the post-9Os distribution of Dinophysis spp. and C. furca	“The most prominent feature in the interannual bloom frequencies over the last four decades was the anomalously high values recorded in the late 1980s in the northern and central North Sea areas. In particular, recent large HAB blooms appear to be associated with warm temperatures coupled with the general decrease in salinity in the Norwegian Coastal Current. The long-term decreasing trend in salinity is probably caused by the increase in precipitation and substantial increase in runoff associated with positive values of the NAO. These changes are also likely to have enhanced the nutrient export to marine waters from terrestrial sources, which may have further enhanced the formation of phytoplankton blooms in the Skagerrak and in Norwegian coastal waters.”		

	showing increased abundance in this area." "there is no evidence of increasing bloom formation in the central and southern North Sea during the last decade. According to our results, Prorocentrum spp. has increased most markedly over the last decade in the German Bight and in Danish coastal waters (Fig. 3). This is in accordance with geographical areas that show the warmest summer temperatures in the North Sea."			
Fässler et al., 2011.	"In this study, we show empirically that there has been an increase in the mortality rate of newly hatched herring larvae since 2000, as hypothesized by Payne et al. (2009). We also show that the trends in mean daily mortality rate of larvae, estimated here over approximately the first 30 days of life, correlate with the increasing trend in component biomass and with the temperature in the northern North Sea from 1972 to 2008."			

	“It is not surprising that the Downs component shows a different trend in mortality and temperature from the three northern components (see Figs 3 and 5). The oceanographic and environmental conditions are very different in the southern North Sea (Berx and Hughes, 2009; Hjøllo et al., 2009; Ro ¨ckmann et al., 2011). Hjøllo et al. (2009) suggest that the environmental conditions in the north are more dependent on the oceanic influence and controlled by basin scale climatic patterns such as the North Atlantic Oscillation (NAO) than is the southern North Sea.” “Groger et al. (2010) suggested that the NAO and the Atlantic Multidecadal Oscillation (AMO; a smoothed temperature signal) greatly influenced the recruitment of the whole North Sea herring stock. As the temperature is linked to the AMO and NAO, this study suggests a link between basin scale environmental variability and mortality of larvae from the three			

	northern components but less with Downs.”			
Gröger et al., 2009.	“Taken together, this implies to us that abundances of eggs and small larvae are mainly determined by adult herring biomass, whereas the abundance of post yolk-sac larvae is mainly determined by environmental factors linked to climate. We reach the same conclusion when we focus on the most recent decline of 2001–2006, which cannot be explained by high fishing mortality.” “Such time-lags could develop from a combination of delayed development of ocean features, such as ocean currents and properties of the water mass (e.g. temperature and salinity), in response to NAO- and AMO-related physical forcing, or sequenced ecological processes involving food-chain effects. Adult herring are expected to be less vulnerable to changes in their environment than early life stages due to avoidance behaviour.”		“Evidence for density-dependence (i.e. a reduced frequency of good year classes) at low stock sizes strongly implies the need to avoid overfishing.”	“Cannibalism provides a potential mechanism for a density-dependent effect at high levels of SSB. However, it appears to operate only in years when adult herring have extended residence in shallow water, which is not generally the case. We speculate that climate variability causes interannual changes in prey availability and therefore the need for adult herring to resort to cannibalism in any one year. Directed field research is necessary to understand better the apparent ephemeral role of cannibalism in North Sea herring.” “The sensitivity of first-feeding larvae to prey availability and quality led to Cushing’s (1969, 1995) match–mismatch hypothesis, which posits that when the spring bloom is poorly matched with the relatively fixed spawning time of fish, poor survival will lead to a weak year class.”

Herdson, & Priede, 2010.			"Since a severe population crash in the stock in the 1970s, limits were imposed on the harvest levels of this species in an attempt to rebuild the stock. Since then the biomass has shown in an increase. Current estimates suggest that only 10% of the stock is being exploited and there are no reports of over-fishing occurring."	
Hufnagl & Peck, 2011.	"Water temperature was the main driver with the survival of (early) autumn-spawned larvae increasing with decreasing water temperature: a total of <10% successful simulations happened at mean annual temperatures ≥11°C."			
Kellnreitner, 2012.	"Corten (1986) assumed that low recruitment of North Sea herring during the late 1970s was caused by unusual hydrological conditions which caused a disruption of the transport of herring larvae to their nursery grounds. He supposed that most of the larvae were thus bound to areas with unfavorable conditions, such as low food supply."	"The increase of abundances of jellyfish in marine ecosystems all over the world is currently a matter of concern (Attrill et al. 2007; Lynam et al. 2006; Pauly et al. 2009; Richardson et al. 2009) and there have been numerous discussions on the causes and consequences of jellyfish blooms (Bilio and Niermann 2004; Oguz et al. 2008; Parsons and Lalli 2002; Purcell 2005; Purcell et al. 2007).		"Although environmental variables structuring recruitment variability are not yet satisfyingly understood, there is some consensus on bottlenecks in early life stages - such as suitable zooplankton prey availability at the point of first feeding (Cushing 1975, Pederson et al. 1990, Fossum 1996) and in the first year of life (Norcross et al. 2001) - where recruitment strength is

	"The increase of abundances of jellyfish in marine ecosystems all over the world is currently a matter of concern (Attrill et al. 2007; Lynam et al. 2006; Pauly et al. 2009; Richardson et al. 2009) and there have been numerous discussions on the causes and consequences of jellyfish blooms (Bilio and Niermann 2004; Oguz et al. 2008; Parsons and Lalli 2002; Purcell 2005; Purcell et al. 2007)." "Almost simultaneous reports from the Baltic Sea (Javidpour et al. 2006), North Sea (Boersma et al. 2007), Wadden Sea (Faasse and Bayha 2006) and Skagerrak and Kattegat (Hansson 2006; Oliveira 2007; Tendal et al. 2007) indicate that this invasion may have been unrecognized for several years (Faasse and Bayha 2006)." "The consequences for the ecosystems invaded by M. leidyi have been controversially discussed. This jellyfish is held responsible for diminishing zooplankton abundance and diversity in invaded habitats	Almost simultaneous reports from the Baltic Sea (Javidpour et al. 2006), North Sea (Boersma et al. 2007), Wadden Sea (Faasse and Bayha 2006) and Skagerrak and Kattegat (Hansson 2006; Oliveira 2007; Tendal et al. 2007) indicate that this invasion may have been unrecognized for several years (Faasse and Bayha 2006). The consequences for the ecosystems invaded by M. leidyi have been controversially discussed. This jellyfish is held responsible for diminishing zooplankton abundance and diversity in invaded habitats (Riisgård et al. 2011; Roohi et al. 2008; Shiganova 1998). M. leidyi can have an augmenting effect on phytoplankton abundance by grazing on zooplankton in its native habitats (Deason and Smayda 1982) and may exert similar influence in invaded habitats (Riisgård et al. 2007, Shiganova et al. 2004a, b). After a massive bloom in the Black Sea in 1989 M. leidyi was held responsible for the coinciding collapse of pelagic fish populations by predation on eggs and larvae and competition for		determined (Axenrot and Hansson 2003, Nash and Dickey-Collas 2005). Food limitation can also result from competition of multiple predators for a common resource. Lynam et al. (2005) concluded that competition by jelly fish might have a negative impact on herring recruitment in the North Sea." "We analysed feeding interactions between Mnemiopsis leidyi and juvenile herring Clupea harengus in the Wadden Sea. Abundance, diet overlap, prey selectivity and stable isotope composition (15N, 13C) of both species were assessed from June to September 2010. High abundance of C. harengus was found in June and July (2.3±1.4 ind.m-3) followed by a steep decline from August to September (0.1±0.1 ind.m-3), coinciding with a dramatic increase in M. leidyi abundance (10.3±8.2 ind.m-3 during September). These two species showed a high overlap in their respective diets (copepods,

	(Riisgård et al. 2011; Roohi et al. 2008; Shiganova 1998). M. leidyi can have an augmenting effect on phytoplankton abundance by grazing on zooplankton in its native habitats (Deason and Smayda 1982) and may exert similar influence in invaded habitats (Riisgård et al. 2007, Shiganova et al. 2004a, b). After a massive bloom in the Black Sea in 1989 M. leidyi was held responsible for the coinciding collapse of pelagic fish populations by predation on eggs and larvae and competition for zooplankton food (Shiganova et al. 2001; Shiganova and Bulgakova 2000; Vinogradov et al. 1996). Vinogradov et al. (1996) calculated the amount of zooplankton consumed by M. leidyi and the most important zooplanktivorous fish stocks. They concluded that M. leidyi consumed large amounts of the zooplankton biomass and that together with fish, it is likely that they consume the complete daily zooplankton production. They hypothesized the collapse of the fish stock as a result of the competition between fish and the	zooplankton food (Shiganova et al. 2001; Shiganova and Bulgakova 2000; Vinogradov et al. 1996). Vinogradov et al. (1996) calculated the amount of zooplankton consumed by M. leidyi and the most important zooplanktivorous fish stocks. They concluded that M. leidyi consumed large amounts of the zooplankton biomass and that together with fish, it is likely that they consume the complete daily zooplankton production. They hypothesized the collapse of the fish stock as a result of the competition between fish and the ctenophores. These hypotheses have been controversially discussed and more recent publications state that it is overfishing and a regime shift in the 1980s what played a prominent role in this decay (Bilio and Niermann 2004; Gucu 2002).” “The most reliable comparisons of dietary overlap are those obtained by sampling specimens both at the same location and time. The main results of this study suggest low potential of competition in the Wadden Sea area due to the low temporal overlap of the		meroplankton) during the study period. Furthermore, we assessed the potential of competition between M. leidyi and C. harengus in a mesocosm experiment. Results indicated that intraspecific competition in C. harengus seemed to be greater than interspecies competition with M. leidyi. Due to their temporarily high diet overlap, competition between these two species could occur should their common food resource be limited. Healthy stocks of planktivorous fish might therefore increase the resistance of a system against zooplanktivorous invaders such as M. leidyi, which need to be taken into consideration in fisheries management decisions.” “After a massive bloom in the Black Sea in 1989 M. leidyi was held responsible for the coinciding collapse of pelagic fish populations by predation on eggs and larvae and competition for zooplankton food (Shiganova et al. 2001; Shiganova and

	ctenophores. These hypotheses have been 77 controversially discussed and more recent publications state that it is overfishing and a regime shift in the 1980s what played a prominent role in this decay (Bilio and Niermann 2004; Gucu 2002). The most reliable comparisons of dietary overlap are those obtained by sampling specimens both at the same location and time. The main results of this study suggest low potential of competition in the Wadden Sea area due to the low temporal overlap of the occurrence of M. leidyi and C. harengus. In recent years population development of M. leidyi in the Wadden Sea seemed to be similar to the situation in the Sea of Azov, where M. leidyi was unable to survive cold winters. The most important conditions for the development of M. leidyi are temperature and food availability (Kremer 1994; Oguz et al. 2008). found a significant correlation between spring temperatures and M. leidyi abundance in Narragansett Bay, USA. In the northern Wadden Sea	occurrence of M. leidyi and C. harengus.”		Bulgakova 2000; Vinogradov et al. 1996). Vinogradov et al. (1996) calculated the amount of zooplankton consumed by M. leidyi and the most important zooplanktivorous fish stocks. They concluded that M. leidyi consumed large amounts of the zooplankton biomass and that together with fish, it is likely that they consume the complete daily zooplankton production. They hypothesized the collapse of the fish stock as a result of the competition between fish and the ctenophores. These hypotheses have been 77 controversially discussed and more recent publications state that it is overfishing and a regime shift in the 1980s what played a prominent role in this decay (Bilio and Niermann 2004; Gucu 2002).” “The most reliable comparisons of dietary overlap are those obtained by sampling specimens both at the same location and time. The main results of this study suggest low potential of competition in the Wadden Sea area due to the low temporal

	the winter 2009/10 was exceptionally cold, with temperatures below 0°C and drift ice temporally covering the bight. In 2010 the first individuals of M. leidyi appeared in June, whereas in 2008, after a mild winter, first individuals were observed already in January (Fischer, 2008)."			overlap of the occurrence of M. leidyi and C. harengus."
Lindegren et al., 2011.				"In the Bothnian Sea, recruitment and growth of herring are most strongly influenced by community composition and the size distribution of zooplankton prey. In the case of Bothnian Sea herring, the incorporation of zooplankton dynamics in stock assessments is an obvious first step in improving recruitment predictions and providing ecologically sound reference points and thresholds for management."
Lynam et al., 2004.	"The mechanisms linking the climatic changes to interannual jellyfish population variation could be indirect, resulting in improved availability of prey to the growing jellyfish, either by altering the timing of the spring			

	bloom to synchronize with the period of rapid ephyral growth or by increasing the abundance of zooplankton or ichthyoplankton prey to juvenile medusae (Ba˚mstedt et al. 2001; Edwards et al. 2002; Platt et al. 2003). Therefore, there could be an effect of jellyfish on fisheries either through top-down (medusae prey on fish eggs and larvae) or bottom-up processes (medusae reduce zooplankton abundance, including copepods, thus limiting fish populations).” “If North Sea fish stocks are presently in a perilous state. A boom in medusae could exacerbate the situation and might hinder the recovery of fish stocks, even following the cessation of fishing.”			
Lynam et al., 2005.	“At a regional level, part of the interannual variability has been linked to changes in the climate as quantified by the North Atlantic Oscillation Index (NAOI). both the abundance of medusae and herring, and their distributions, appear to be linked to climatic variation.”		“A reduction in the spawning stock biomass of herring may release jellyfish from competition for prey with herring and exacerbate any impact by jellyfish on herring survival. It has been suggested that the overexploitation of fish stocks could increase prey	“A significant negative relationship ($p < 0.05$) between the survival of herring to Age0 and the abundance of the scyphozoan Aurelia aurita implies that this jellyfish might adversely impact the North Sea herring population. This concurrence heightens the

			availability and release jellyfish from competitively imposed restrictions on population abundance, which may exacerbate any detrimental effect.”	potential for competition as well as predation. Competition for food between jellyfish and adult finfish has also been shown, with dietary similarities of 73 and 50% respectively for Pacific herring and medusae of Aurelia labiata and Cyanea capillata. The main period of A. aurita and C. capillata medusa abundance in the North Sea is during the early summer (May to August), and by September/October these species become scarce in the plankton (Russell 1970). Indirect impact via competitive removal of food by medusae during the summer might also result in low prey availability for herring hatchlings in the autumn, and thus poor larval survival.”
Möllmann et al., 2008.	“In conclusion, our results demonstrate the linkage between climate-induced zooplankton and fish-regime changes, and how overfishing amplified and stabilized the climate-induced changes.”		“Regime shifts and trophic cascades generally involve collapses of important exploited fish stocks. Recent investigations have demonstrated that ecosystem changes are also induced by human exploitation, both through direct effects on the target	

			species and through indirect influences on ecosystem structure and function. In conclusion, our results demonstrate the linkage between climate-induced zooplankton and fish-regime changes, and how overfishing amplified and stabilized the climate-induced changes.”	
Ottersen et al., 2001.	“The NAO appears to be a good proxy for winter SST and wind strength in the North Sea. The most obvious and probably best-documented influence of the NAO on marine and terrestrial ecosystems is through temperature. This is particularly evident in north-western Europe where the NAO and temperature are closely related, with high winter and spring temperatures during years of high NAO index and vice versa.” “As a result of warming during winter-spring in the past three to four decades, possibly related to increasingly positive NAO index values, the length of the active growing season for terrestrial plants has increased in the			

	northern part of the northern hemisphere (Myneni et al. 1997), and particularly in Europe (Menzel and Fabian 1999). Similarly, the length of the growing season of phytoplankton in the North Sea has increased in parallel with the warming of SST associated with the NAO. The increase in temperature and alteration in the winter circulation pattern observed during the last decades of predominantly positive NAO index values have resulted in unfavourable conditions for the population of the copepod *Calanus finmarchicus*, leading to a significant decrease in the abundance of the species." "Temperature acts on almost every biological step leading to recruitment: adult growth (Brander 1995), adult maturity (Tyler 1995), timing of spawning (Hutchings and Myers 1994; Kjesbu 1994), egg viability (Flett et al. 1996), timing of food availability (Ellertsen et al. 1989; Nakken 1994) and larval growth and mortality (Pepin 1990; Otterlei et al. 1999)."			

Overzee & Rijnsdorp, 2015.			"Fishery closures during the spawning season are commonplace. Spawning closures have been put into place to protect spawning populations in order to enhance the reproductive output of spawning fish and hence improve the number of recruits in the exploited stock (e.g. European spiny lobster, Pacific halibut, cod, herring and haddock; Table 1, #5–10). However, none of the latter studies provide compelling evidence to demonstrate that spawning closures are in fact achieving their stated objectives." "The chance of catching the older (and larger) age classes may be higher during the spawning period as they gather on the spawning grounds, which are often more confined in space than the feeding grounds." "The selective removal of older age classes during the spawning period will enhance the truncation of	

			the age and size structure (Lambert 1990; Marteinsdottir and Thorarinsson 1998; Wright and Trippel 2009), diminishing the proportion of big old fecund fish (Boff) that produce more (Green 2008; Kjesbu 2009; Trippel et al. 2005) and larger (Kennedy et al. 2007; Kjesbu 1989; Raventos and Planes 2008) eggs per unit body weight than smaller females. Larger eggs are thought to have a survival advantage at the beginning of their life as they result in larger hatchlings which are physiologically more likely to survive." "The selective removal of older, more experienced fish by a spawner fishery may disrupt spawning migrations when inexperienced recruits can no longer learn from experienced fish. Furthermore, spawning disturbance may cause a forced delay in fertilization which again may negatively	

			affect the reproductive output. It has been shown that when females are unable to shed their ovulated eggs, the quality of the eggs deteriorate and the fertilization rate declines, a process called overripening. However, this problem is more prominent among other species since overripening occurs after multiple days among herring while other species experience overripening after a couple of hours." "The benefits of a spawning closure are highest when the body condition or adult catchability during the spawning period is higher than during the non-spawning period (during over-exploitation). If the spawning stock is at a very low level, fishing during the spawning period is expected to increase the risk of stock collapse due to depensation. When a stock is at a level where recruitment increases with	

			stock size, density-dependent processes will be weak and a reduction in the number and quality of the eggs or their fertilisation probability is expected to lead to a decline in recruitment. When a stock is at the level where an increase in egg production has no effect on recruitment, fishing during the spawning period is expected to have no effect on recruitment.”	
Paerl, 1997.		“Growing urban, industrial, and agricultural AD and GW inputs to coastal and offshore waters may be linked to a purported expansion of harmful algal blooms.” “Coastal and estuarine environments are heavily influenced by new N, supplied either naturally by weathering of minerals, decomposition, lightning, and geothermal emissions or anthropogenically. Anthropogenic sources include urban and rural wastewater, nonpoint source agricultural (i.e. fertilizers, animal waste,		

		sediments), atmospheric deposition of fossil fuel and other combustion products (NOx, DON: dissolved organic N) and agricultural emissions (NH3, DON), and N-enriched groundwater. In response to growing exogenous N inputs, new production is often enhanced, leading to eutrophication (Nixon 1995), increased frequencies and magnitudes of phytoplankton blooms, including harmful (toxic, hypoxia- and anoxia- inducing, and food-web-altering) taxa." "Urbanized and industrialized regions (North America, Europe, China, Japan) generally exhibit Fe-enriched rainfall (Church et al. 1984, 1991; Duce et al. 1991; Duce and Tindale 1991; Zhuang et al. 1995). Emissions from these regions have long-range impacts on Fe loading in coastal and offshore waters (Duce and Tindale 1991; Jickells 1995) and may be of considerable importance in the regulation of growth and bloom potential among near shore and pelagic HAB and non-HAB taxa."		
Payne et al., 2013.	"Temperature increases in the North Sea have been widely			"There is a suggestion that changes have occurred in the

	reported and shown to be associated with increased larval mortality, though this study does not support the hypothesis.”			UK shelf seas with the latest reduction in abundance of tintinnids (loricate ciliates) occurring from 2003 onward which might affect herring. Changes in the food supply therefore appear to be a likely candidate-mechanism.”
Payne, 2009.	“Alternatively, changes in the physical environment may also have contributed to, or indeed been the major driving force behind, the recent reduced larval survival. Significant hydrographic changes, including an increase in bottom-water temperature, have been observed near the main herring spawning areas in recent years.”		“Our analysis suggests that the sequence of poor recruitment cannot be attributed to the fishery, and instead is more likely determined during the larval overwintering period. There are several candidate mechanisms that may be responsible for these reduced rates of survival. Although the proximate causes of the current sequence of poor recruitment in North Sea herring are uncertain, it appears that the ultimate cause most probably lies with changes in the North Sea environment, and not overfishing.”	“The event has been associated with changes in the prey of herring larvae, in particular with the decrease of small copepods such as *Paracalanus* spp. and *Pseudocalanus* spp. that were typically very abundant in autumn (PL, unpublished data).”
Peperzak, 2003.	“The global change in climate between 1990 and 2100 leads to a projected rise in temperature of	“The projected effect of climate change for the year 2100 in the coastal zone of The Netherlands, a 4 °C temperature rise and		

	1.4–5.8 °C with a 90% probability interval of 1.7–4.9 °C. The projected change in climate will also lead to alterations in the geographic distribution and intensity of precipitation. Global climate change expressed as an increase of the summer temperature maximum by 4°C in 2100, in combination with water column stratification, led to a doubling of growth rates of potentially harmful dinoflagellates and raphidophytes. This means that the risk of HABs by these species increases considerably.”	increased salinity stratification, on the growth rates of six harmful and two non-harmful phytoplankton species was investigated in batch laboratory cultures.” “Even at present, the river Rhine delivers pulses of fresh water into the Dutch coastal zone of the North Sea, leading to intermittent salinity stratification in an area extending 30–40 km offshore and 100 km along the coast towards the north. It has been shown that stratification in this region is conducive to blooms of P. globosa and D. acuminata.” “In the 2100 scenario the surface growth rates of the non-harmful species Rhodomona ssp.and S. costatum did not differ much from present mixed conditions. On the other hand, the 2100 surface growth rates of the dinoflagellates P. micans and P. minimum and the raphidophytes C. antiqua and F. japonica doubled compared to the present mixed conditions.”		
Polte et al., 2013.				“A potential mismatch of that critical period with the

				availability of suitable food is considered as the major bottleneck of herring ontogenesis as well as that of many other pelagic fish species.”
Portner & Knust, 2007.	“We show in the eelpout, Zoarces viviparus, a bioindicator fish species for environmental monitoring from North and Baltic Seas (Helcom), that thermally limited oxygen delivery closely matches environmental temperatures beyond which growth performance and abundance decrease. Decrements in aerobic performance in warming seas will thus be the first process to cause extinction or relocation to cooler waters. The reduction in aerobic scope is caused by limited capacity of circulatory and ventilatory systems to match oxygen demand. Such a constraint affects all higher functions (muscular activity, behavior, growth, and reproduction) and might thereby shape the long-term fate of species. Aerobic scope becomes minimal beyond low or high critical temperatures.”			

	"During the past 40 years, water temperatures in the German Bight increased by 1.13°C (at Helgoland Roads). Cold winters with sea surface temperatures (SSTs) around –1°C had occurred about once every 10 years up to 1944 but were experienced only once since 1960 (11).Models predict further SST increments for the next 90 to 100 years, by about 1.6° to 3.0°C in the northern and even by 3.0° to 3.9°C in the shallower southern North Sea(12),accompanied by rising sea levels(13 to 68 cm by 2050) and an increasing frequency of storm events (13)."			
Purcell & Arai, 2001.				"Within a species, feeding rates on ichthyoplankton increase with medusa size, as shown for Aurelia aurita. Most pelagic coelenterates consume primarily zooplankton, and would be expected to compete with zooplanktivorous fish such as anchovies, herring and sardines. When over fishing includes those fish species, there could be significant unconsumed zooplankton, and pelagic coelenterate populations might expand."

Purcell, 2005.	"Linkages to climate variation suggest that jellyfish abundance could rise and fall with ocean basinwide climate oscillations (El Niño Southern Oscillation, North Atlantic Oscillation, North Pacific Decadal Oscillation). Global warming could result in expanded temporal and spatial distributions and larger populations of jellyfish and ctenophores. Jellyfish and ctenophores are important consumers of ichthyoplankton and zooplankton, and therefore are both predators and potential competitors of fish. For most temperate species, warm temperatures lead to large numbers of jellyfish and ctenophores, and increased asexual reproduction in scyphozoans and hydrozoans. Sexual reproduction also increases at warm temperatures. Size-specific egg production of Mnemiopsis leidyi was significantly greater at warm temperatures. In temperate species tested, the numbers of medusae produced, the proportions of new medusae			

	relative to new polyps, and the speed of production were greatest at the warmest temperatures tested."			
Reid & Edwards, 2001.	"In climate studies, change through time may not be reflected in the form of a progressive trend, but in series of years (not necessarily continuous) that have a similar and unusual character; years in between are of average character. This phenomenon is known as 'clustering'." "A major change has occurred in the North Sea eco-system circa 1988 that has affected all trophic levels from phytoplankton to fish and birds. Sea surface temperatures since this time have largely remained above average as a direct response to an exceptionally long and high NAO index. Part of this change may be a consequence of global warming. The period has also been characterised by the incursion and development of species of plankton normally found in more southerly latitudes.			

	While the coincident timing of all these events does not prove a relationship, the large- scale nature of the changes suggests that they are part of a regional and possibly Adantic wide climatic change." "An opposite scenario occurred in the period 1978-82 when influx of upper layer oceanic water appears to have been at a minimum. Temperatures at this time were below normal and the plankton present indicates some incursion of cold oceanic water, possibly at intermediate depths. Reduced biomass of zooplankton occurred at this time and the size of the total stocks of North Sea fish appears to have been at a minimum with stocks of herring declining to 50,000 tonnes from an estimated 6 million tonnes in the early 1950s. There is thus increasing evidence for the importance of environmental regulation of many aspects of fish dynamics."			
Reid et al., 1999.	"Lab: preference for 26-32 ppt, can resist salinities as low as 5 ppt for brief periods; at < 10oC a			

	preference for > 29 ppt; at > 10oC no salinity preference seen. Field: present in 16-32 ppt; highest abundance at 30-32 ppt. Older juveniles generally avoid brackish conditions. *<u>Juveniles:</u>* Preference for higher salinities with increasing age. *<u>Adults:</u>* Enter bays and estuaries, but 28 ppt is lower limit of occurrence. Spawn at high salinities, ranging from 31.9 - 33.0 ppt; never brackish water.”			
Richardson et al., 2009.	“Global warming is known to contribute to jellyfish blooms which can have severe consequences to the local ecosystem, especially near the coast.”	“Eutrophication is known to contribute to jellyfish blooms which can have severe consequences to the local ecosystem, especially near the coast.”	“Overfishing is known to contribute to jellyfish blooms which can have severe consequences to the local ecosystem, especially near the coast.”	“An increase in jellyfish reduces the amount of food in the water column, making waters unsuitable for fish to feed.”
Rijke Waddenzee, 2015.	“Trend Stable or decreasing. Available information on drivers Probable causes: changes in the North Sea hydrography, and shift in the dominant food items. Abundance of herring varies as a result of natural variability in recruitment and human exploitation. Most stocks in the Northeast Atlantic have been overexploited, resulting in low abundance during the 1970s. By 2010, recovery to numbers close to the pre-collapse state.”		“Trend Stable or decreasing. Available information on drivers Probable causes: changes in the North Sea hydrography, and shift in the dominant food items. Abundance of herring varies as a result of natural variability in recruitment and human exploitation. Most stocks in the Northeast Atlantic have been overexploited, resulting in low abundance during the	“Trend Stable or decreasing. Available information on drivers Probable causes: changes in the North Sea hydrography, and shift in the dominant food items. Abundance of herring varies as a result of natural variability in recruitment and human exploitation. Most stocks in the Northeast Atlantic have been overexploited, resulting in low abundance during the 1970s. By 2010,

			1970s. By 2010, recovery to numbers close to the pre-collapse state.”	recovery to numbers close to the pre-collapse state.”
Rijnsdorp et al., 2009.	“Temperature, because of its pervasive effect on organisms, is important in all regions. Stratification (resulting from the interplay between temperature and windforcing) will also be an important factor in all regions, owing to the effect of stratification on the vertical structure of marine ecosystems and on bottom-up processes.” “Changes in wind strength and direction not only influence mixing and water circulation in the open ocean, but also affect the strength of upwelling within shelf and coastal regions.” “Species can only tolerate a specific range of environmental conditions that, among other factors, places constraints upon their range of distribution. The sensitivity of larval stages to climate change may be further increased, because of their small body size, which will make them less capable of selecting and migrating towards a suitable	“Although mass mortalities during summer in relation to harmful algal blooms (Yin *et al*., 1999; Heil *et al*., 2001) have been reported elsewhere, no records are known for the Northeast Atlantic.”	“Commercial exploitation greatly affects the abundance and distribution of fish and may interact with the effects of climate change. A major implication is that fishery-induced impoverishment of stock structure (reduced and fewer ages and smaller sizes) can increase the sensitivity of a previously “robust” stock to climate change.”	“Changes in plankton have been linked to changes in climate.”

	habitat, and because of their reasonably high (mass-specific) metabolic rates and lower energy reserves." "It is worth noting that responses at higher levels of organization (population, community, and ecosystem) to climate change are ultimately driven via differences in physiological responses that affect trophodynamic relationships. For example, physiological responses to a change in temperature can differ between primary, secondary, and tertiary consumers, thereby influencing trophic coupling (Freitas *et al*., 2007) via changes in productivity or phenological shifts and match–mismatch dynamics (Cushing, 1990). Behavioural changes can have unexpected consequences. For example, because of an increase in temperature, fish swimming speed increases (Peck *et al*., 2006). In addition, fish can behave differently in response to oncoming fishing gear making them more (or less) vulnerable to capture."			

	"Finally, at longer temporal scales, climate-driven changes in temperature can modify the phenology of annual migrations to feeding and/or spawning grounds, as already observed (Carscadden *et al*., 1997; Sims *et al*., 2004), and predicted (Huse and Ellingsen, 2008), for temperate marine species." "We expect that climate change will have a major effect on the distribution and abundance of fish through its influence on recruitment." "Within shelf areas, increased warming will result in earlier water mass stratification (if not balanced by increased wind-mixing), which will affect the timing of the spring bloom and the level and composition of primary production." "Climate-related distribution shifts may affect the protective capabilities of closed-areas, because species or life stages may shift outside the boundaries of the protected area and hence become vulnerable to fishing."			

	"Populations living at the border of the distribution range are expected to live close to the limits of their range of physiological tolerance, so will be more vulnerable to changes in abiotic conditions than populations living in the centre of the distribution area." "With regard to the hypothesis about invasive species (H6), there is strong evidence that increasing connectivity between geographically distinct areas may result in major changes in ecosystems."			
Sims et al., 2004.	"Sea temperatures have risen in many regions over the past two decades, and recent predictions indicate a 0·5–4·0 °C increase in North Atlantic sea-surface temperatures over the next century."			
Sinclair & Tramblay, 1984.				"Metamorphosis is seasonally restricted and coincides approximately with the productive period of the year."
Skogen et al., 2004.		"At the second national conference on the protection of the North Sea (London; 1987), all countries around the North Sea		

		agreed that inorganic N and phosphorous (P) inputs to coastal areas should be reduced by 50% of the 1985 concentrations for those areas where nutrients cause, or are likely to cause, pollution. This decision was based on the fact that the loads in many European rivers were extremely high, an increasing frequency of harmful algal blooms seemed to be occurring, and in some areas significant O_2 reductions were occasionally observed in the bottom water.” “In the North Sea, the highest modeled production is along the Southern North Sea coast with an annual production of more than 200g C/M2/year. This is more that 3 times the values in the central and Northern parts of the North Sea.” “Even if more than 90% of the nutrient input to the North Sea originates from oceanic waters, also the contribution from rivers plays an important role. This influence is of especially importance to the coastal zone of the Southern		

		North Sea were about 75% of the freshwater-borne nutrients discharges are found. Model experiments indicate that natural interannual variations might be larger than the total contribution from the rivers."		
Tulp et al., 2008.	"Shallow waters along the North Sea coast provide nursery areas for juveniles of commercially exploited species and natural habitat for resident species and seasonal visitors. The areas have gone through major changes in the last decades due to climate change and human activities such as fishing and eutrophication and changes in abundance of apex predators." "In addition to its natural dynamics, environmental characteristics in the coastal areas have changed considerably in the past decades. Long-term data series have shown that water temperature has increased (van Aken, 2003), a phenomenon that has been observed at North Sea scale as well (Becker and Pauly, 1996)."	"Shallow waters along the North Sea coast provide nursery areas for juveniles of commercially exploited species and natural habitat for resident species and seasonal visitors. The areas have gone through major changes in the last decades due to climate change and human activities such as fishing and eutrophication and changes in abundance of apex predators." "Nutrient loads showed a peak in the seventies of the last century and decreased subsequently (Van Raaphorst and De Jonge, 2004)."	"Shallow waters along the North Sea coast provide nursery areas for juveniles of commercially exploited species and natural habitat for resident species and seasonal visitors. The areas have gone through major changes in the last decades due to climate change and human activities such as fishing and eutrophication and changes in abundance of apex predators."	

Vuorinen et al., 2014.	"Several climate models, both global and regional, indicate an increase in the runoff of the northern latitudes due to proceeding climate change. Results suggest a critical shift in the S range 5-7, which is a threshold for both freshwater and marine species distributions and diversity. Consequences could include a shift in distribution area of marine benthic foundation species and some 40-50 other species associated with these foundation species."			
Weijerman et al., 2005.	"Several researchers have reported sudden (from one year to the next) changes around the late 1970s and late 1980s. Reid et al. (2001b) also reported a possible third shift in 1998. These apparent shifts have been linked with climate–ocean variability such as the large-scale salinity anomaly in 1978 (Dickson et al. 1988), severe winters with low temperatures and high storm frequencies (Beukema 1990), and a drastic reduction of the Atlantic inflow in the late 1970s (Svendsen & Magnusson 1992), as well as with anthropogenic			

	factors such as eutrophication and fisheries (OJaveer 1996). the NAO has a strong influence on ecological dynamics and that it causes diverse responses in ecological processes, ranging from the timing of reproduction to spatial distribution of biological communities." "It appears possible that ocean climate conditions have had far-reaching consequences on the ecology of the North Sea, but at present it is not possible to say what the primary cause(s) of these conspicuous ecosystem shifts were. Lindeboom (in press) hypothesizes that there may be a combination of factors, a complex interaction between ocean, climate, anthropogenic perturbations and atmospheric oscillations, each having a varying degree of importance."			