Deliverable 1.2
Process knowledge from existing data

PAradigm for Novel Dynamic Oceanic Resource Assessments

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Deliverable D 1.2

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[1] PU: Public, PP: Restricted to other programme participants (including the Commission Services), RE: Restricted to a group specified by the consortium (including the Commission Services), CO: Confidential, only for members of the consortium (including the Commission Services)

PANDORA Project

The Blue Growth of European fisheries is at risk due to over-exploitation, unforeseen changes in stock productivity, loss of markets for capture fisheries due to aquaculture, future trade agreements opening European markets to external fleets, and fluctuations in the price of oil and other business costs. All of these risks need to be considered when providing advice needed to sustainably maximize profits for the diverse array of fisheries operating in European waters and to help safeguard the benefits this sector provides to the social coherence of local, coastal communities.

PANDORA aims to:

1. Create more realistic assessments and projections of changes in fisheries resources (30 stocks) by utilizing new biological knowledge (spatial patterns, environmental drivers, food-web interactions and density-dependence) including, for the first time, proprietary data sampled by pelagic fishers.

2. Advice on how to secure long-term sustainability of EU fish stocks (maximum sustainable/”pretty good” and economic yields) and elucidate tradeoffs between profitability and number of jobs in their (mixed demersal, mixed pelagic and single species) fisheries fleets. Provide recommendations on how to stabilize the long-term profitability of European fisheries.

3. Develop a public, internet-based resource tool box (PANDORAs Box of Tools), including assessment modelling and stock projections code, economic models, and region- and species-specific decision support tools; increase ownership and contribution opportunities of the industry to the fish stock assessment process through involvement in data sampling and training in data collection, processing and ecosystem-based fisheries management.

The project will create new knowledge (via industry-led collection, laboratory and field work, and theoretical simulations), new collaborative networks (industry, scientists and advisory bodies) and new mechanisms (training courses and management tools) to ensure relevance, utility and impact.

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Document history

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01	1.0	Initial version, Øyvind Fiksen
02	14th Sept	First collection of contributions

03	25th Sept	All parts collected, first complete draft
04	10th Oct	Revision 1
05	29th Oct	Revision 2

1 Contents

List of symbols and abbreviations

Please put here all abbreviations used in this deliverable

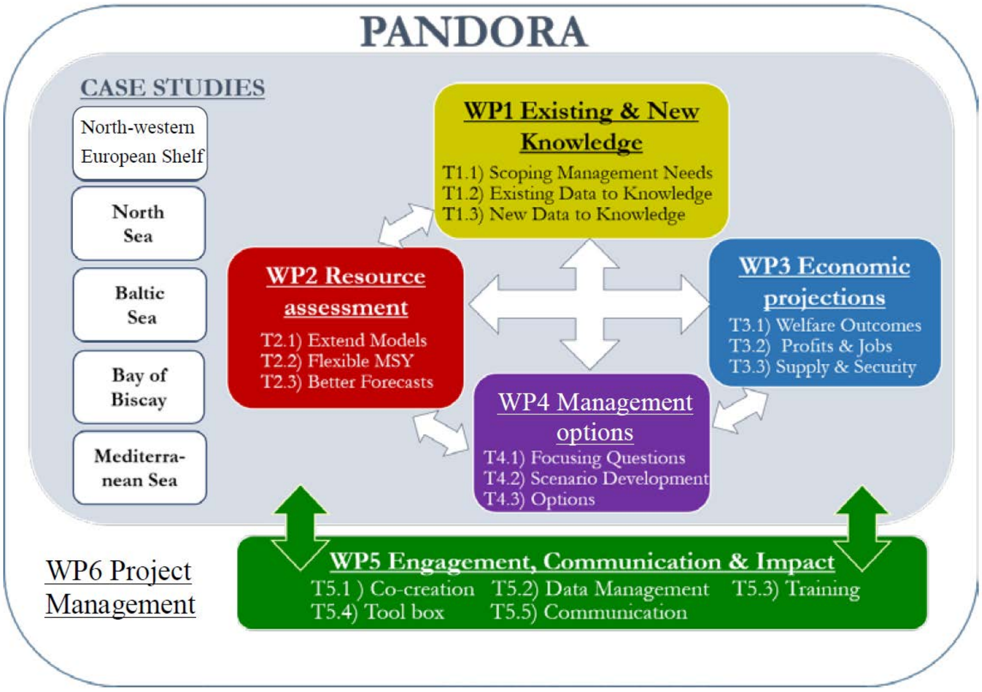
DBEM	Dynamic Bioclimate Envelop Model	EwE	
DoA	Description of Action	ICES	

NAO	
RCP	Regional Concentration Pathway
SDM	Species Distribution Model
SMS	
SSB	
SS-DEB	
B_{lim}	
WP	Work Package

2 Executive summary

2.1 Introduction

Across European waters, dramatic differences exist in the biology, ecology and status of fish stocks, as well as the amount and quality of data available for their assessment. PANDORA is designed to provide new biological knowledge on fish and their ecosystems, integrate that knowledge to build more robust tools to assess the future status of fish stocks, and improve science-based advice to fisheries management for maximizing the long-term, sustainable exploitation and Blue Growth of Europe's fisheries resources. PANDORA addresses the most urgent needs of fisheries management and its various fleets in each of five Case Study areas to provide a step change in Europe's ability to support productive fisheries, boost employment and profits in the sector and promote European food security.



2.2 Defining the Challenge

In PANDORA, the first step is to map the manement needs, mine the existing knowledge base and to generate some new data and knowledge. This is specified in the description of Work Package 1: *'**WP1: Existing and new biological knowledge** (WP lead Jane Behrens, DTU Aqua) will provide the baseline causal knowledge needed to improve existing stock assessment and especially for predictive stock projections. The species- and case-specific provision of e.g. vital rates, changes in species distributions, interactions with other species and/or experienced climate changes affecting e.g. growth potential will be based on a scoping exercise, **scoping regional management needs** (Task 1.1) to identify critical knowledge gaps in relation to existing assessments and new resources. For each case study regions separately, PANDORA will **create process-knowledge from existing data** (Task 1.2). Collation of data will be output driven (as identified in Task 1.1). The **generation of new data and knowledge** (Task 1.3) has high priority in PANDORA, and comprises three different activities: (i) fisheries self-sampling, (ii) targeted experiment and data collection, and (iii) expanding the theoretical basis of fisheries ecology.'*

In this report, we deliver causal, basis knowledge of selected fish stocks in European waters: *'For each Case Study region separately, PANDORA will collate existing information from laboratory studies and field observations on environmental preference and tolerance, growth rates and spatial distribution and abundance of selected fishery species based on T1.1.*

Collation of data is output-driven (as identified in the initial workshops, Task 1.1) and focused on information needed for projections into WP2 through WP4. The scoping exercise in T1.1 mapped the needs perceived by some stakeholders and regional assessors and managers of fish stocks in European Seas. We follow up on the responses from managers and stakeholders, and review which of the identified needs can be filled from existing knowledge, which can be addressed by PANDORA, and which must be dealt with in future activities.

Each region and complex of species have their own specific challenges, and the questionnaire from Task 1.1 only sampled some issues in fisheries management. Therefore, we review the state of each region separately, and focus on some selected species and topics of relevance to PANDORA.

We review spatial structure, food-web interactions, density-dependence, and how how environmental drivers influence growth, natural mortality, reproduction and distribution of selected fish stocks in the regions covered by PANDORA.

2.3 Approach

Creating process knowledge from existing data
The findings in Task 1.1 (*Deliverable 1.1. Scoping of regional management needs*) is a starting point for the work presented in this report. There we used survey questionnaires distributed among different stake-holder groups to extract the main message and requests from managers and stakeholders. The main activity is to review the literature and databases to dig out and contextualize studies to the management setting. We discuss the remaining issues, and how process knowledge and existing data may can be improved by planned activities in PANDORA.

What do we know already – area by area?

This report contains a detailed review of state-of-the-art expert knowledge for a number of species. The review of information is organized region by region, including a mix of core scientific publication and various reports and material from organizations and meetings. We list current existing relevant databases and where they are stored partly within the main text and partly in more detailed appendixes (for the North Sea).

These species are covered in each region:

1) North Sea: Cod, herring, haddock, saithe, whiting and flatfishes (plaice and sole).
2) The Baltic Sea : Cod
3) The Bay of Biscay: Seabream and various skates
4) The Mediterranean Sea: European hake (*Merluccius merluccius*), Red Mullet (*Mullus barbatus*), Deepwater pink shrimp (*Parapeneus longirostris*), Albacore (*Thunnus alalunga*), Atlantic bluefin tuna (*Thunnus thynnus*).

2.4 Contribution to the project

This report contains information collected in Task 1.2, an overview of existion knowledge and more detailed plans for what to do within PANDORA, area by area. The work builds on T1.1 and provide a basis for WP 2 and WP 4, and T1.3 in WP1 (Fig 2.1).

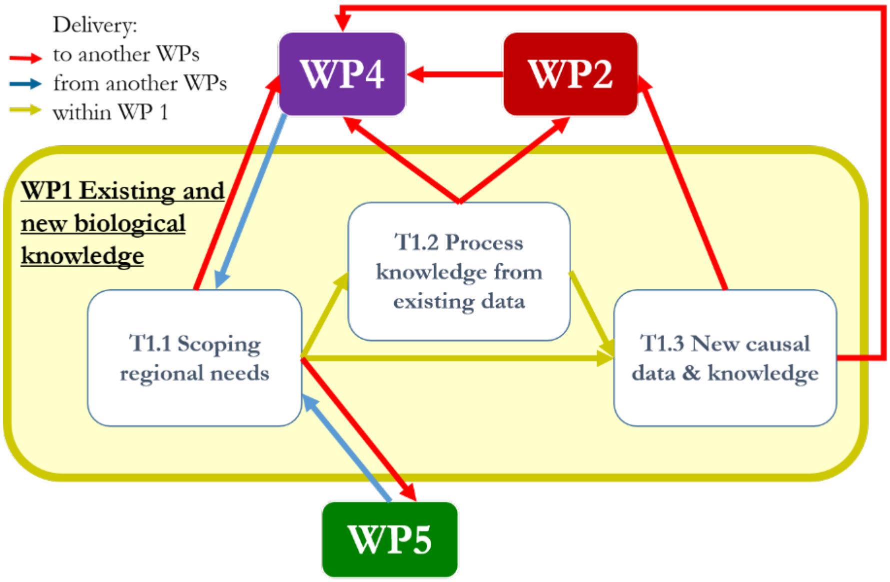


Fig. 2. 1. Flows of information and data to, from and within WP1.

2.5 Summary of existing knowledge from each region

2.5.1 The North Sea

Recruitment: All stocks, but to a lesser degree haddock, show a substructure within the mature stock (cod, herring, whiting) or exchange with adjacent populations (saithe, herring), likely to influence recruitment dynamics. In addition, varying spatial dynamics and a heterogenous distribution of spawner biomass play a role in shaping stock-recruitment pattern. Several environmental influences ranging from bottom up to top down processes were linked to critical stages in the life cycle of each stock in past research. Bottom up effects are most likely exerted through temperature, hydrodynamic processes as well as suitable feeding conditions (e.g. zooplankton) affecting development, growth and mortality of early life stages. The recent regime shift(s) in the North Sea ecosystem reflected by a general warming and a change in the composition of lower trophic levels are likely to influence recruitment of the reviewed stocks. As the North Sea is strongly dependent on the overall dynamics in the Northeast Atlantic (e.g. Inflow of Atlantic water), all stocks seem to be shaped to some degree by processes having their origin outside the North Sea, reflected by links to large scale atmospheric/oceanographic pattern (e.g NAO). Density-dependent processes are likely to play a role through cannibalism (cod, whiting, herring) and/or competition over available resources (food, habitat) experienced within (saithe) and between year classes (haddock) in the juvenile stage. Predation of immature life stages is relevant for all stocks and all life stages, but with considerable inter-annual variation related to the abundance as well as spatial overlap of predators.

Environment and early life stages: A holistic approach incorporating both bottom-up and top-down drivers and working beyond defined stock boundaries is crucial to understand fish stock dynamics within the North Sea ecosystem. Some data gaps have been identified. To accurately understand which effect parental effects exert on recruitment, knowledge of quality of eggs and larvae is crucial. So far SSB only takes into account differences in quantity and mean weight of spawners with age. Further data on the reproductive potential by age/length would be beneficial as e.g., an earlier maturation and therefore larger SSB must not lead to a larger of amount recruits surviving to higher ages (like observed for cod). Additionally, getting a better idea on the abundance of gadoid larvae/earlier recruitment stages, similarly to herring, might help to gain insight into the processes affecting the stocks before recruitment compared to standard scientific surveys.

Multispecies modelling: There exists a wealth of multi species and ecosystem models in the North Sea area that are able to inform on consequences of species interactions for fisheries management. In the North Sea mainly three models are currently used to estimate natural mortalities and to perform analyses on the impacts of management decisions: The stochastic multi species model SMS , Ecopath with Ecosim and the LeMans model.

Spatial structure: Despite this, aspects of their spatial distribution, stock identification and rates of mixing (both within and across stocks) remain uncertain. For example, cod in the North Sea, including ICES Divisions 4.a, 4.b, 4.c, 7.d and subdivision 3.a20, is currently assessed as a single stock unit.

2.5.2 The Baltic Sea

The Baltic Sea is constantly changing, because it is semi-enclosed and the exchanges of oxygen-rich, high saline deep water has to pass narrow and shallow straits to the entrance area to the Baltic Sea. Furthermore, eutrophication as well as changing riverine fresh-water input contribute to the environmental conditions in the Baltic, which are both variable but also show a trend towards lower salinity and higher temperature. The main drivers of the observed ecosystem changes vary somewhat between sub-regions, but they all include the increasing temperature and decreasing salinity (Figure 4.2.a).

The fish distribution has changed considerably during the past decades. The Eastern Baltic cod, in parallel with the decrease in its stock size, contracted its distribution to the southern areas since the mid-1980s. The sprat stock on the other hand, increased mostly in the northern areas of the Baltic Proper.

A recent reversal has occurred in the ontogenetic development of feeding level over body length, resulting in present feeding levels of these small cod, that indicate severe growth limitation and increased starvation-related mortality.

Reduced consumption rates of cod in relation to sprat and benthic crustaceans go hand in hand with a worsening of cod condition. Therefore, it can be assumed that the mentioned species represent a main biotic driver (in terms of prey items) especially during fish fattening in fall-winter season, influencing the physiological state of all cod size groups

The eastern Baltic cod stock carries the parasitic liver worm, *Contraceacum osculatum*. Especially the fish of 35 cm or larger are heavily infected, and a high worm burden suggestively decrease the health status of the individual fish.

2.5.3 Bay of Biscay

The Bay of Biscay case study focusses on one species of teleost fish, the blackspot sea bream (*Pagellus bogaraveo*) and the assemblage of skates (Rajidae). The blackspot seabream used to be a major species in the landings from the Bay of Biscay up to the early 1980s. Several marine fish stocks have strongly declined during the 20th Century as a consequence of overfishing, including several. In the past two decades management measures aiming at halting such declines and restoring skates stocks to higher levels have been introduced. Overall, spawning occurs over the offshore shelf and/or at the shelf break. Current spawning areas might be mostly in the Cantabrian Sea (where larvae were found in recent ichthyoplankton surveys) and to the West of Brittany. At the current low stock level, abundance and therefore spawning in more northern areas, e.g. the Celtic Sea and Western Channel might be insignificant.

The two main skate species reported in recent landings from the Bay of Biscay are the Cuckoo ray *Leucoraja naevus* and the Thornback ray *Raja clavata* (ICES, 2018). Data on all skates stocks are mostly insufficient for stock assessment purposes because until 2009 landings were not reported by species but as "skates and rays". There are no published studies on nurseries and spawning areas of skates in the Bay of Biscay.

2.5.4 The Mediterranean Sea

The Mediterranena Sea is a regional sea in which most ecological and environmental processes are spatially structured. This is also the case for harvested fishes, including their nursery areas, key retention and feeding areas. We review the status of five species in the Mediterranean Sea, 3 demersal species and 2 pelagic species: European hake (*Merluccius merluccius*), Red Mullet (*Mullus barbatus*), Deepwater pink shrimp (*Parapeneus longirostris*), Albacore (*Thunnus alalunga*), Atlantic bluefin tuna (*Thunnus thynnus*). For each of them, we present the basic biological status and distribution, some catch statistics and an assessment of the current management regime.

Genetic studies have shown that a clear genetic difference exists between the Atlantic and the Mediterranean hake, and recent evidence suggest a more complex popuations structure and transboundary populations over the current managent areas. Since 2009, fishing mortality were considered to be outside optimal levels. As a result, a national multi-annual management plan targeting fisheries exploiting the hake stock has been put in place since 2014.

Red mullet is one of the most important species for Mediterranean coastal fisheries. The results of the EU project STOCKMED found three main stock units in the region: Western basin-Ionian Sea, Adriatic-Aegean Sea, Levantine Sea. Most of the assessed stocks are overfished, with a few exceptions. Red mullet in the Agean Sea is exploited by bottom trawlers and various artisanal fisheries using gillnets. The Greek bottom trawl fishery captures more than 100 commercial species, with red mullet one of the most important targets. All assessment models predict that the Aegean red mullet stock is currently being fished below Fmsy, and fishing mortality shows a declining trend.

The most recent assessments of Deepwater pink shrimp indicate overfishing, with a spawning biomass fluctuating without a clear trend. A multiannual management plan for bottom trawl fisheries exploiting demersal stocks in the Strait of Sicily applies the precautionary approach to fisheries management, ensuring that exploitation levels of European hake (*Merluccius merluccius*) and deep-water rose shrimp are at MSY by 2020 at the latest.

For the tuna species, population assessment are still based on data poor methods using catch statistics and production models. The status of the stocks are highly uncertain with respect to both fishing mortality and biomass. One way to improve the assessment is to develop abundance indices that are independent of fisheries data. A new abundance index based on icthyoplankton surveys are now developed annually in the Western Mediterranean.

3 List of Annexes

Annex 1 Review on environmental effects on recruitment dynamics of commercially important North Sea stocks.

- Annex.1.1 Recruitment of North Sea cod
- Annex.1.2 Recruitment of North Sea autumn-spawning herring
- Annex.1.3 Recruitment of North Sea haddock
- Annex.1.4 Recruitment of North Sea saithe
- Annex.1.5 Recruitment of North Sea whiting

Annex 2. Review on stock structure of North Sea cod and plaice.

Annex 3. Review of available knowledge on North Sea food web interactions relevant for stock assessments and fisheries management.

4 Status and planned activities within each region

4.1 The North Sea

4.1.1 The regional scoping of management needs

The survey on regional management needs from T1.1 revealed four main topics for the North Sea that seem to be relevant for stakeholders:

1. Several stocks experience currently a low productivity and climate change impacts are among the main hypothesis for this observation. A low productivity in recent years has been especially observed for North Sea cod, haddock and other gadoids, but also herring. North Sea cod became very rare in the southern part of the North Sea what may be the impact of climate change.

2. Density dependent effects may impact various parameters (growth, maturity, recruitment, cannibalism etc.). Due to the substantial recovery of the plaice stock, such effects have been mainly discussed for North Sea flatfish (e.g., plaice and sole) in recent years but are generally important and may be taken into account in reference point determinations after their existence has been proofed.

3. Spatial structure often in combination with stock structure has been mentioned as important issue for various stocks (e.g., cod, whiting, plaice, sole, rays and skates). In general, an adequate stock definition is a prerequisite for any assessment. The stock structure of North Sea cod is especially under debate and the development of the cod population in different regions of the North Sea needs to be explained.

4. Species interactions in the North Sea food web have been mentioned as potential explanation of observed stock dynamics. Knowledge on natural mortality levels and changes over time is beneficial according to the opinion of stakeholders.

Based on the stakeholder feedback under T1.1 and the work proposed by Pandora partners, the available knowledge, data sets but also knowledge and data gaps have been reviewed for the following topics:

1. Knowledge on the recruitment dynamics of gadoids and herring in the North Sea (including climate change and density dependent effects) (TI)

2. Climate change impacts on the distribution of North Sea stocks and predicted shifts in distribution (UHAM)

3. Density dependent effects with focus on North Sea flatfish (Wageningen)

4. Stock/Spatial structure of North Sea cod and Plaice (CEFAS)

5. Available knowledge on species interactions with focus on commercially important fish species (TI and DTU)

In the following chapters for each topic a summary of the review is provided together with an overview on available data sets available in Pandora as well as identified knowledge and data gaps. Full reviews further details can be found in **Annexes 1-3**. A final chapter succinctly describes further work during Pandora to make progress on the main gaps in knowledge and data identified.

4.1.2 Recruitment dynamics in cod, herring, haddock, saithe, whiting

Fish stocks have always been subject to fluctuations that are understood to result from effects of the marine environment acting on the growth and mortality of early life stages. This is termed the “Recruitment-problem” and many hypothesis have been put forward explaining the observed variability ranging from favourable/unfavourable drift, timing and quantity of available prey, density-dependence as well as the effects of predation on early life stages. Despite the effort invested in this field, environmental drivers are rarely included in the assessment and management of fish stocks. This is, in part, attributed to limited observations and the ability to test hypotheses in the marine environment. Additionally, the shear multitude of effects acting simultaneously on various temporal and spatial scales and the inability of models to cope with all of these scales and effects lead to spurious correlations or even the breakdown of statistical relationships previously thought to be robust. Learning from these failures, common ground now exists that recruitment research should be based on a conceptual framework with a priori hypothesises, rather than a pure exploratory analysis, as well as the use of robust statistical methods (e.g. Myers 1998, Haltuch & Punt 2011, Subbey et al. 2014, Haltuch et al. 2019). The increasing availability of data as well as new computational methods demand a fresh start in addressing the recruitment-problem. For the North Sea, many commercially important stocks are believed to be influenced by environmental drivers, especially the recent warming, with strong effects on the fisheries. Therefore, understanding the drivers of fish stock fluctuations for the North Sea and incorporation into assessment can help improve science-based advice for the sustainable management of stocks. Consequently, this work within PANDORA aims to review current work on important commercial stocks (cod, herring, haddock, whiting, saithe) in the North Sea and identify potential drivers of recruitment. This is a prerequisite for further analyses in the course of PANDORA before identified drivers can tried to be incorporated into stock-recruitment relationships by means of conventional and new statistical methods.

As a basis for further research, environmental influences on life stages, recruitment and stock dynamics of commercially important North Sea stocks (cod, herring, haddock, saithe, whiting) have been reviewed. The aim was to identify bottlenecks and knowledge gaps for each species. The focus was on peer-reviewed literature as well as reports from ICES, from ICES conference meeting and expert groups using a set of meaningful key words. See **Annex 1.1-5** for further info and a list of key words used.

4.1.2.1 Summary of reviews of recruitment dynamics

All stocks, but to a lesser degree haddock, show a substructure within the mature stock (cod, herring, whiting) or exchange with adjacent populations (saithe, herring), likely to influence recruitment dynamics. In addition, varying spatial dynamics and a heterogenous distribution of spawner biomass play a role in shaping stock-recruitment pattern. Several environmental influences ranging from bottom up to top down processes were linked to critical stages in the life cycle of each stock in past research. Bottom up effects are most likely exerted through temperature, hydrodynamic processes as well as suitable feeding conditions (e.g. zooplankton) affecting development, growth and mortality of early life stages. The recent regime shift(s) in the North Sea ecosystem reflected by a general warming and a change in the composition of lower trophic levels are likely to influence recruitment of the reviewed stocks. As the North Sea is strongly dependent on the overall dynamics in the Northeast Atlantic (e.g. Inflow of Atlantic water), all stocks seem to be shaped to some degree by processes having their origin outside the North Sea, reflected by links to large scale atmospheric/oceanographic pattern (e.g NAO). Density-dependent processes are likely to play a role through cannibalism (cod, whiting, herring) and/or competition over available resources (food, habitat) experienced within (saithe) and between year classes (haddock) in the juvenile stage. Predation of immature life stages is relevant for all stocks and all life stages, but with considerable inter-annual variation related to the abundance as well as spatial overlap of predators. See **Annex 1** for further details.

4.1.2.2 Cod

Research on cod early life stages and the influence of environmental factors is extensive and there exists a large literature linking effects of various processes to recruitment. The most prominent processes comprise the change in spatial dynamics of North Sea cod (Hedger et al. 2004), the heterogeneous stock structure (Holmes et al. 2014, ICES 2015a), the effects of a warming North Sea (Nicolas et al. 2014, Núñez-Riboni et al. 2019), changes in the transport and/or retention processes of either early life stages (Huserbråten et al. 2018) or their food (Munk et al. 1999, Beaugrand et al. 2003) as well as predation pressure exerted during egg, larvae and juvenile phase (e.g. Daan et al. 1985, Pálsson 1994, Kempf et al. 2013). A large number of studies have focused on the effects of temperature, as it is strongly influences the growth and survival of cod early life stages both directly and indirectly with warming in the North Sea considered to be negative (Akimova et al. 2016, Sguotti et al. 2019). This is most likely attributed to a combination of the direct effects of temperatureon rates of growth and mortality and indirect effects of temperature on the availability of prey (zooplankton) and/or Atlantic water inflow. The role of match-mismatch dynamics between cod early life stages and their prey is believed to be one of the main processes causing recruitment bottlenecks (Cushing 1984, Beaugrand et al. 2003, Beaugrand & Kirby 2010). Predation pressure by clupeids (Speirs et al. 2010, Minto & Worm 2012) and grey gurnard (Floeter et al. 2005, Kempf et al. 2009, 2013) also received attention in the recent years (e.g. see Akimova et al. 2019). However, which of these processes dominate to shape recruitment dynamics of North Sea cod is poorly resolved and interactions and/or masking effects of different environmental drivers make it difficult to pinpoint real causal relationships. See **Annex 1.1** for further detail.

4.1.2.3 Herring

The autumn spawning herring in the North Sea represents a stock with a complex life cycle due to its separation into different spawning components, highly migratory life stages as well as mixing with other stocks (Corten 2002, Bierman et al. 2010, Dickey-Collas et al. 2010). Environmental influences on subsequent recruitment act already on the adult stage, possibly through suitable feeding conditions (Damme et al. 2009, dos Santos Schmidt et al. 2017). The bottleneck in recruitment in recent years is understood to be determined during the over-winter period as larvae grow and develop into juveniles (Nash & Dickey-Collas 2005, Payne et al. 2009, 2013). Due to the multitude of effects acting within this period, comprising drift, temperature, feeding conditions and predation/cannibalism, several equally plausible hypotheses have been formulated to explain the current recruitment failure in herring (Corten 2013). Additionally, it is likely that multiple factors interact with different effects on the stock components (e.g. Downs vs. Orkney-Shetland). See **Annex 1.2** for further detail.

4.1.2.4 Haddock

Haddock recruitment shows the most interannual variation among the gadoid stocks in the North Sea. The overall recruitment pattern is strongly driven by density-dependent processes acting in the younger year classes through inter-cohort competition (Jones 1983, Cook & Armstrong 1984, 1986). A very strong year class in one year results in low recruitment for the following 2 to 5 years. However, what causes these exceptional high year classes is not fully understood. Links between environmental drivers and recruitment are scarce for North Sea haddock and most information comes from literature on the western Atlantic stocks (e.g. Polacheck et al. 1992, Werner et al. 2001, Lough et al. 2006). In the NW Atlantic, bottom-up processes are thought to be critical for recruitment with food availability in relation to bloom dynamics playing a crucial role for both spawners and early life stages (Friedland et al. 2008, 2015, Leaf & Friedland 2014). On Georges Bank, hydrodynamic processes seem to have a significant impact either directly through beneficial/adverse drift of early life stages or transport of suitable food (Smith & Morse 1985, Werner et al. 2001, Lough et al. 2006). In the North Sea, enrichment processes in relation to frontal zones, gyres and inflow of Atlantic water could be important. Temperature also seems to shape recruitment dynamics in haddock, however the direction of the overall temperature effect is not clear (Dippner 1997, Ottersen et al. 2013, Linderholm et al. 2014) and might be attributed to Atlantic water inflow as most of the life cycle takes place in the area influenced by northern Atlantic inflow into the North Sea (Saville 1959, Hedger et al. 2004). See **Annex 1.3** for further detail.

4.1.2.5 Saithe

Saithe is a highly migratory species with its life cycle extending far beyond the North Sea (Bjørke & Saetre 1994, Homrum et al. 2013, Behrmann et al. 2015). Mixing of spawners as well as recruits with the adjacent Barent Sea stock can, therefore, bias the perception of the stock-recruitment relationship within the North Sea. As most of the life stages thrive within the North Atlantic current system (Norwegian coastal current, North Sea inflow) effects of wind, current pattern and temperature are likely to be related to recruitment. Juvenile saithe spend a long time in their coastal nursery habitat with feeding conditions and predation pressure exerting possible effects on recruitment. Pinpointing one particular environmental driver to recruitment of saithe, however, might pose considerable challenge as recruits enter the scientific survey as well as commerical catches in the North Sea late (at age 3) and might therefore experience a magnitude of different influences. Large-scale indices such as the North Atlantic Subpolar Gyre (SPG) or the North Atlantic Oscillation (NAO) integrate dynamics over larger areas and might, therefore, correlate well with saithe recruitment, as they do for other stocks (Steingrund & Hátún 2008, Zimmermann et al. 2019). These indices, however, obscure process understanding needed to improve stock-recruitment relationships. The challenge lies in finding mechanistic links (or at least promising proxies), which incorporate the complex stock structure of saithe and connecting ecosystem knowledge beyond the conventional stock boundaries. Trophic interactions such as the link with feeding migrations of herring and blue whiting (Jakobsen 1978, Homrum et al. 2013), as well as competition with hake for Norway pout (Cormon et al. 2014, 2016) pose another pitfall as they are highly dynamic in time and space. In conclusion highly migratory species such as saithe require more “ecosystem-thinking” and spatial dynamics are likely more important to take into account. See **Annex 1.4** for further detail.

4.1.2.6 Whiting

Of the commercially important gadoids in the North Sea, whiting displays a more stable recruitment pattern, compared to cod and haddock, although with a slight downward trend. The ability to cope with varying environmental conditions could explain the more stable recruitment of this species. The extended spawning season inherent in whiting (Daan et al. 1990, Sundby et al. 2017) also smooths over episodic adverse effects (e.g. low prey availability at the onset of the season), but this attribute also makes it more challenging to pinpoint one environmental factor or process responsible for a particular year class dynamic. Indication of a positive relationship between recruitment and temperature (Svendsen & Magnusson 1992, Zheng et al. 2001, Cook & Heath 2005), a wide feeding niche and less reliance (than cod) on the boreal copepod *Calanus finmarchius* in the diet (Last 1978, Shaw et al. 2008) may make whiting less suceptable than cod to having poor year class success due to warmer temperatures and decreased *C. finmarchicus* abundance associated with the North Sea regime shift. Additionally, the unique behaviour hiding under jellyfish umbrellas comes in handy with the North Sea predicted to become more gelatinous in the future (Attrill et al. 2007). See **Annex 1.5** for further details.

Available data sets for further use

To analyse environmental influences on stocks and their recruitment following datasets are available for the North Sea:

Table 4.1: Information on of available datasets/ data portals that can be used in environmental-mediated stock-recruitment relationships

Dataset/Data portal	**Description**	**Class**	**Scale**	**Extent**	**Variables (examples)**	**Type of data**	**Format**	**Availability**	**URL** (last checked on 2019-09-04)
Fisheries related data:									
ICES Database of Trawl Surveys (DATRAS)	Database of trawl survey data coordinated by ICES expert groups	Biological	Local	Spatial, Temporal	Raw or processed data from various surveys (e.g. IBTS, BTS)	In situ observations	CSV	Free	https://ices.dk/marine-data/data-portals/Pages/DATRAS.aspx
ICES stock assessment output	Results of the ICES assessment	Biological	Local	Temporal	Time series of stock data (recruitment, SSB)	Stock assessment/advice	XML	Free	http://standardgraphs.ices.dk/stockList.aspx
Maps of spawning grounds for North Sea (KINO project)	Compilation of survey and literature data on spawning grounds of North Sea fish (Sundby et al. 2017)	Biological	Local	Spatial	Spawning grounds for various North Sea fish (e.g. cod)	Synthesis of literature/observations	Various: e.g. KML, shp, GeoTiff	Free	http://maps.imr.no/geoserver/web/ (in Norwegian)
Environmental data:									
NOAA Earth System Research Laboratory, physical sciences devision (ESRL)	Data portal of various available datasets in climate and ocean research	Physical	Global, Local	Spatial, Temporal	Various e.g.: SST, SSH, Wind, Chl-a	Reanalysis, Atmospheric/Ocean model output, remote sensing, Climate Indices	Various: netCDF, txt (for Climate Indices)	Free	https://www.esrl.noaa.gov/psd/data/

Dataset/Data portal	**Description**	**Class**	**Scale**	**Extent**	**Variables (examples)**	**Type of data**	**Format**	**Availability**	**URL** (last checked on 2019-09-04)
NOAA National Weather Service/ Climate prediction centre	Data portal of various time series of large-scale climate Indices/Teleconnection patterns	Physical	Global	Temporal	Various e.g.: NAO, AMO, SCAND	Climate Indices/Teleconnection pattern	txt	Free	https://www.cpc.ncep.noaa.gov/data/teledoc/telecontents.shtml
Copernicus Marine environment Monitoring Service (CMEMS)	Data portal of various datasets in climate and ocean research provided by Mercator Ocean (EU)	Physical, Biological	Global, Local	Spatial, Temporal	Various e.g.: SST, SSH, Wind, Chl-a, Ocean Colour	In situ observations, Reanalysis, Atmospheric/Ocean model output, remote sensing	netCDF	Free, Registration required	http://marine.copernicus.eu/
European Centre for Medium-Range Weather Forecasts (ECMWF)	Data portal of various datasets provided by the research institute ECMWF (EU)	Physical	Global	Spatial, Temporal	Various e.g.: SST, SSH, Currents, Wind	Reanalysis, Atmospheric/Ocean model output, Forecasts	Various: netCDF, GRIB	Free or Data request	https://www.ecmwf.int/en/forecasts/datasets
Climate data store (CDS)	Data portal providing climate data (part of the Copernicus project and ECMWF)	Physical	Global	Spatial, Temporal	Various e.g.: SSH, Currents, Wind	Reanalysis, Atmospheric/Ocean model output, Forecasts	Various	Free, Registration required	https://cds.climate.copernicus.eu/cdsapp#!/home

Dataset/Data portal	**Description**	**Class**	**Scale**	**Extent**	**Variables (examples)**	**Type of data**	**Format**	**Availability**	**URL** (last checked on 2019-09-04)
Integrated Climate Data Center – ICDC (Uni Hamburg)	Data portal of various datasets/links to datasets provided by the Centre for Earth System Research and Sustainability (CEN)	Physical/ Biological	Global, Local	Spatial, Temporal	SST, salinity, SSH, Ocean colour	Reanalysis, Atmospheric/Ocean model output, remote sensing, Climate Indices	Various	Free or Data request	https://icdc.cen.uni-hamburg.de/1/daten.html
AHOI-dataset	Adjusted Hydrography Optimal Interpolation model to produce monthly gridded in situ hydrography provided by the Thuenen Institute of Sea Fisheries	Physical	Local	Spatial, Temporal	Temperature, Salinity	Interpolation of in situ observations	netCDF	Free	https://www.thuenen.de/de/sf/projekte/ahoi-ein-physikalisch-statistisches-hydrographie-modell-fuer-fischerei-und-oekologiestudien/
GlobColour	Data portal of Ocean Colour products provided by the European Space agency (ESA)	Biological	Global	Spatial, Temporal	Ocean colour products of different sensors: SeaWIFs, MERIS, MODIS, Merged products	Remote Sensing	netCDF	Free	http://hermes.acri.fr/
European Marine Observation and Data Network (EMODnet)	Data portal of datasets on bathymetry, habitats, geology,	Physical/ Biological	Global	Spatial, Temporal	Bathymetry, Substrate type, Seabed habitats, Human activities,	Various aggregated and processed datasets	Various	Free	http://www.emodnet.eu/portals

Dataset/Data portal	**Description**	**Class**	**Scale**	**Extent**	**Variables (examples)**	**Type of data**	**Format**	**Availability**	**URL** (last checked on 2019-09-04)
	physics, chemistry, marine species and species traits from all European regional seas provided by the EU				Various observations of biological and physical properties				
Continuous zooplankton recorder (CPR) data	Long-term monitoring of the marine plankton composition provided by Marine Biological Association (MBA)	Biological	Local	Spatial, temporal	Abundance of various zooplankter (e.g. *Calanus finmarchicus*)	In situ observations	CSV	Data request	https://www.cprsurvey.org/

4.1.3 Knowledge and data gaps in North Sea stocks

Based on the review, the following knowledge and data gaps have been identified in general and for each stock separately:

4.1.3.1 Conclusion relevant for all five stocks analysed

Although research on environmental influences on early life stages is extensive for some of the species (cod, herring), this is not the case for stocks of other species (haddock, saithe, whiting). The general tendency of linking environmental variables to the stocks is either to focus on particular processes or links to large-scale oceanographic or atmospheric indices, which have the advantage of condensing numerous environmental processes into one index. However, the use of the latter makes it harder to understand the particular mechanisms driving the stock. There is the need to consider spatial and temporal characteristics of the stocks and, potentially, also non-stationarity. In conclusion, a holistic approach incorporating both bottom-up and top-down drivers and working beyond defined stock boundaries is crucial to understand fish stock dynamics within the North Sea ecosystem.

4.1.3.2 Cod

Many environmental influences on cod early life stages in the North Sea are known, but the effects on recruitment dynamics are less clear. This comprises effects of differences in spawner composition, hydrodynamic processes related to drift and frontal zones as well as processes in the bottom habitat during the juvenile stage. As many processes are interlinked it is hard to identify real causal interactions. Correlative recruitment studies look either on local abiotic indices or large scale indices. However, mechanisms that exert their effect on cod recruitment within the North Sea might have their origin elsewhere (e.g. Atlantic water inflow and *C. finmarchicus*), which requires one to look beyond the boundaries of the stock's distribution.

4.1.3.3 Herring

Herring is one of the best researched fish stocks in terms of knowledge about its life cycle and scientific survey effort. However still, many hypotheses are discussed for what determines recruitment in recent years. One way to gain further insight is to look again at some of the known or hypothesised mechanistic relationships and try to incorporate these into a statistical framework taking into account the unique spatial and temporal characteristics of the substocks. Additional tailoring of local environmental variables to match the spatial and temporal scales of each life stage is needed.

4.1.3.4 Haddock

The greatest problem in understanding haddock recruitment across stocks is the occurrence of these large recruitment spikes. These spikes become lower and lower over the last decades and the processes behind this observation have not been resolved yet. Based on the understanding of other haddock stocks these likely happen if several favourable effects co-occur. Therefore looking at several environmental drivers and their combined (additive or non-linear) effect, might help in finding possible explanations.

4.1.3.5 Saithe

Most research of saithe focuses on older life stages, their migratory behaviour and general life cycle with a paucity of studies on early life stages and their sensitivity to environmental effects. As the life cycle of saithe in the North Sea in part follows the theory of a "migration triangle" research in the early life stages (eggs and larvae, juveniles) might help in gaining insight which phase might be the "recruitment-bottleneck". Stock mixing, being the case particularly in the North Sea, however might make it hard to track these effects. As mentioned earlier understanding spatial effects are of paramount importance and need to be taken into account even beyond stock boundaries.

4.1.3.6 Whiting

Whiting recruitment shows a positive correlative effect to temperature, but if the positive effect is due to increased feeding conditions for various life stages, transport, temperature effects on growth and spawning potential, changes in predator fields, competitive advantage over cod or attributed to increased jellyfish abundance is not resolved. Additionally, most of the correlative relationships were done with time series until the late 1990s and information if the proposed relationship hold true with increasing time series length is therefore missing. There is also a paucity of studies examining the effects of transport on early life stages of whiting. The ubiquitous distribution of spawning grounds over the North Sea and the extended spawning season, however, poses a challenge for a systematic investigation. The same is true for a link of recruitment with environmental variables as effects on life stages are integrated over a longer time, which might cancel each other out. In summary, which particular environmental variables drives recruitment in North Sea whiting is still poorly understood.

4.1.3.7 Data gaps related to life cycle characteristics of the stocks

Additionally some data gaps have been identified. To accurately understand which effect parental effects exert on recruitment, knowledge of quality of eggs and larvae is crucial. So far SSB only takes into account differences in quantity and mean weight of spawners with age. Further data on the reproductive potential by age/length would be beneficial as e.g., an earlier maturation and therefore larger SSB must not lead to a larger of amount recruits surviving to higher ages (like observed for cod). Additionally, getting a better idea on the abundance of gadoid larvae/earlier recruitment stages, similarly to herring, might help to gain insight into the processes affecting the stocks before recruitment to the standard scientific surveys. Other issues concern the availability of detailed assessment output per age class, as mostly aggregated indices (e.g., SSB) are publicly available. The ICES transparent assessment framework (TAF) may imrove the situation in the near future. To understand how trophic relations change over time/space in the North Sea a regular stomach sampling program needs to be implemented (see also 4.1.7 in this chapter) to better quantify and monitor top-down impacts on early life stages of commercially important fish species.

4.1.4 Climate change impacts on the distribution of North Sea stocks and predicted shifts in distribution

Considerable research has been conducted documenting historical changes in North Sea fish stocks due to climate variability and ongoing climate change, and to provide robust projections of future climate change impacts. The North Sea is, arguably, one of the best-studied LMEs with respect to climate change impacts. The regions poses a unique situation for examining the effects of CC on fish stocks because of its: i) unique mixture of cold- and warm-water fishes at the edges of their lower and upper latitudinal limits, respectively, ii) existence of long-term (>100 years) spatially disaggregated data on commercial catches of trawlers. These data have been used to explore drivers of changes in the distribution and size-composition of catches of plaice, cod and many other species (Engelhard et al. 2011, 2014), and iii) the wealth of IBTS and other survey data at ICES contributing data to many highly-cited papers documenting historical shifts in the community of North Sea fishes. These papers and their results have been thoroughly discussed in two recent climate change reports on fish and fisheries in the North Sea: 1) The North Sea Region Climate Change Assessment (Pinnegar et al. 2016) and the FAO Technical Paper 627 (Peck and Pinnegar 2018). The ICES DATRAS was used in a recent analysis of distributional shifts (ICES WKFishDish) where 18 of 21 Atlantic and North Sea fish stocks displayed shifts in distribution, 11 of which were considered „large“ (ICES 2016). That report was unable to attribute the shifts in distribution to climate but listed climate among a variety of other potential drivers.

Alarming, long-term trends have been reported in the productivity of the North Sea. A global-scale projection of the impacts of climate (warming) as well as fishing suggested up to a 30% decline in the productivity of the North Sea ecosystem had occurred from the 1930's to 2010 which was attributed to warming (Free et al. 2019). Such declines (both globally and in the North Sea) are projected to continue due to the trophic amplification of reductions in primary production driven by increased stratification (e.g. Lotze et al. 2019) and due to the continued shift in the distribution of cold-water (boreal) fish fauna further poleward (outside the North Sea).

4.1.4.1 ***Summary of Review***

New (unpublished) projections of changes in distribution of a variety of fish species (including cod, herring, saithe, whiting and haddock) are available from the EU H2020 CERES project. Unlike global analyses, these projections are based on regionally downscaled physical-biogeochemical models linked to Species Distribution Models (SDMs). These efforts have examined > 50 species of finfish and invertebrates. These projections suggest that future warming will cause a net loss of suitable North Sea habitat for 11 of the commercially most important species. A few species appear to shift to the south (mackerel, hake and saithe; shaded light grey in the Table 4.2) but this is, in fact, due to a constriction of their habitat to their southern-most range within the North Sea model domain. The distribution of all other species is projected to shift to higher latitudes along isotherms. This includes expansion of temperate geographical ranges such as European anchovy, European sardine and sole (shaded dark grey in the table) and shifts of suitable habitats of other, boreal species poleward outside the model domain in the North Sea. Note, these results are an indication of the reduction in suitable habitat for each species and the potential shift in the centre of their distribution and changes are more pronounced under the "business as usual" RCP 8.5 compared to the RCP 4.5.

Maps of habitat suitability and time series of changes in abundance at different fishing levels were included in CERES Deliverable Report 2.3 that has been made available on PANDORA's internal communications platform (TeamWork site). The SDM maps show both present day habitat suitability and change in habitat suitability by mid- (2040 to 2050). The SS-DEB results are continuous time series of abundance at different levels of fishing (0, 0.8 MSY, 1.1 SY) from 1990 to 2099. Both SDM and SS-DEB projections were made at RCP 4.5 and RCP 8.5. The SDM work captured uncertainty in terms of both future environmental change (both scenario and global climate model) and biology (structural differences in the 3 SDMs). An example of the results for mid-century projections of changes in distribution for 11 North Sea species is provided (Table 4.2)

Table 4.2: Table summarising key SDM finding for a subset of species. For each RCP the table give the change in habitat suitability for the North Sea (in percentage) and the latitudinal shift (in kilometres). The standard deviation is given within parenthesis for each value. This work was presented in CERES deliverable report 2.3.

	RCP 4.5		RCP 8.5	
Species	**Habitat suitability (%)**	**Latitudinal shift (km and direction)**	**Habitat suitability (%)**	**Latitudinal shift (km and direction)**
Atl. Cod	-19 ± 2	1.14 ± 26 North	-29 ± 3.4	3.17 ± 60 North
Atl. Herring	-3.6 ± 7.6	19.5 ± 49 North	-11 ± 8	31.7 ± 65 North
Atl. Mackerel	21 ± 47	19.9 ± 47 South	33 ± 49	47 ± 94 South
Eur. Hake	20 ± 44	29.2 ± 120 South	42 ± 93	47.4 ± 180 South
Eur. Sardine	94 ± 290	15.3 ± 68 North	250 ± 850	10.1 ± 120 North
Eur. Plaice	1.6 ± 14	32.2 ± 62 North	-4.7 ± 18	56.2 ± 94 North
Haddock	-5.1 ± 17	14.1 ± 36 North	-13 ± 21	24.2 ± 54 North
Saithe	-28 ± 37	31 ± 120 South	-36 ± 41	55.1 ± 210 South
Sole	26 ± 32	37.3 ± 60 North	47 ± 82	65.6 ± 110 North
Whiting	1.2 ± 17	21 ± 56 North	-6 ± 11	37.5 ± 86 North
Eur. Anchovy	36 ± 94	34 ± 110 North	62 ± 160	23.5 ± 94 North

4.1.4.2 *Available Data Sets for Future Use*

There are three different types of data sets available to help improve projections of climate change impacts on North Sea fish stocks. First, a large dataset has been compiled that includes data from published and grey literature from both laboratory (e.g. biology, physiology) and field (distribution, growth) studies on key North Sea species. A gap analysis was performed on the laboratory studies. Laboratory studies examined the effect of temperature, salinity, oxygen, pH and their interaction on metabolism, growth, mortality and reproduction. In total, 37 species yielded 344 datasets from experiments that met the inclusion criteria (see Catalan et al. 2019). That list included 9 species important to North Sea pelagic or demersal fisheries. In order of available data sets, these species included: i) Atlantic herring, ii) plaice, iii) sole, iv) Atlantic cod, v) haddock, vi) sprat, vii) sardine, viii) anchovy, and ix) squid (*Loligo vulgaris*). Few to no data (that met the criteria for inclusion) were available for saithe or whiting. The data are within excel tables available to PANDORA on the internal communications platform (TeamWork).

Second, long-term time series data are available on commercial catches of key species. Field data include those publicly available from ICES areas e.g. (DATRAS, Eggs and Larval Surveys from ICES Dataportal, or Cefas such as DAPSTOM (Pinnegar 2014). Many of these data are available online for inferring changes in field distributions or production in relation to CC, and some have been deeply analyzed within this context (Rijnsdorp et al. 2010). For example, the ICES dataportal has 16 time-series of 11 key species. Results of the most recent exploration of these distribution data from DATRAS (ICES 2016) were previously mentioned.

Third, the results of new climate projection modelling of North Sea fishes are available through the EU CERES project. The first and second data sources help one disentangle various natural (e.g.

trophodynamic) and anthropogenic (climate change and fishing) drivers by better understanding processes behind changes in historical productivitiy of North Sea fish stocks. The third source of data provides the most up-to-date projections of shifts in abundance and distribution using, arguably, the best available modelling tools groundtruthed to extensive field data (see Table 4.3).

Table 4.3. Available data (historical and future projections) for North Sea fishes available from the H2020 CERES project.

Model	Species	Time Period	RCPs	Contact
Historical (observed) Changes				
GAMMs	Plaice	1902-2016	NA	Cefas / CERES
GAMs	152 species (winter), 140 species (summer)	1983 (1992)-2013	NA	DTU / CERES
individual-based evolutionary model (INLA)	Plaice	1988-2017	NA	WMR / CERES
Future Projections				
SS-DBEM, 0.5° grid	Cod, haddock, saithe, hake, sole, plaice, herring, mackerel	2000-2999	4.5, 8.5	PML / CERES
INLA	Plaice	2018-2030 (quarterly)	4.5, 8.5	WMR / CERES
SDM(s)	Cod, haddock, whiting, saithe, hake, sole, plaice(s), herring, sardine, anchovy, mackerel (plus 41 other species	1997-2016; 2050-2070	4.5, 8.5	Cefas / CERES

4.1.5 Knowledge and Data Gaps for climate change scenarios

There are at least three important knowledge gaps which represent current challenges for the global scientific community performing climate change projections on living marine resources. A recent review comparing the amount of empirical (laboratory) data available for the 13 most valuable marine fisheries targets across all European regional seas. In that review, the NE Atlantic and North Sea ranked first in terms of the number of independent data sets published on the effects of abiotic factors on the growth, survival and physiology of commercially important fish (Catalan et al. 2019). The vast majority of that work, however, was on the effect of temperature on embryos with very little work on other life stages or other abiotic factors. On the other hand a vast amount of literature exists indicating temperature effects on commercially important fish stocks (e.g., recruitment, species distribution). However, this literature is mostly correlative studies (see also for recruitment under 4.1.1) without a clear understanding of the exact, underlying process(es)causing a shift in distribution and/or productivity. Knowledge from both types of sudies needs to be combined in the future to get a better mechanistic understanding and also to groundtruth modelling studies with real-world observations.

Second, methods employed to project the effects of climate change normally do not include indirect effects such as changes in trophodynamic structure and function. For example, food web interactions can dampen or amplify the effect of climate change on single species. For example, positive effects of climate change were projected for European anchovy in the Bay of Biscay using a coupled lower trophic level, full-life-cycle DEB-IBM. Positive effects of climate (projected increases in anchovy stock productivity) stemmed from both warmer temperatures and increased zooplankton production in the future. There are other, very recent examples of where end-to-end models such as 'Atlantis' have been used in the Barents/Norwegian Seas (cod, herring, capelin) and Baltic Sea (cod, herring, sprat) to make climate projections on stock productivity that integrate both indirect and direct processes. Therefore, Pandora will need to take into account these indirect effects when creating scenarios of climate change in WP2-WP4. The ability to use more holistic approaches when making projections of climate change impacts will be challenged by the same gaps in knowledge and data reported in North Sea reviews on recruitment, density-dependence and food web dynamics.

Third, direct tests of climate projections are now possible. A sufficient amount of time has passed since projections of climate impacts have been made that these should now be revisited with empiricle data. For example, Drinkwater (2005) raised awareness of the potential negative impacts of climate-driven warming on cod in the southern North Sea (and Irish Sea) after comparing trends in recruitment versus bottom-water temperatures experienced during spawning across 22 stocks through 1998. He suggested that a 2° to 3°C warming would lead to a stock collapse of cod in the southern North Sea that has now been observed.

4.1.6 Density dependent effects with focus on North Sea flatfish

The prevailing view in fisheries science is that density dependence, and consequently population regulation, occurs exclusively in the earliest life-history stages. This is reflected in the widespread practice in fisheries stock assessment of using non-linear stock-recruitment functions to relate Spawning Stock Biomass (SSB) to the number of recruits (often one year old individuals), combined with a linear model for the development of the older population. Despite this, there is ample evidence for density-dependent growth and weight-at-age in older and larger individuals. A recent study (Zimmerman et al. 2018) examined 115 harvested stocks and found that in 26% of stocks growth correlated negatively to SSB, while 69% of stocks exhibited a significant negative relationship between stock size and weight at age. Which of these (growth or weight at age) is the better criterion remains subject of discussion (ICES 2019), but the message is clear that density dependent growth in post-recruit stages is a common phenomenon in fish stocks.

Conceptual models show that in stocks with density- or food-dependent individual growth, mortality of small fish can actually strongly enhance harvestable fish production, because it reduces the food limitation that slows down individual growth (de Roos et al. 2007, van Kooten et al. 2007). This leads to the hypothesis that density-dependent individual growth may facilitate higher sustainable catches, as compensatory growth of the remaining individuals leads to higher biomass production under harvesting. This is also the general expectation of fishermen: including density-dependent growth in assessments will lead to a larger quota, because compensatory stock growth is stronger. Models similar to those used in determining reference points for fished stocks, however, generally show a reduction in MSY with increasing strength of density-dependence (van Gemert et al. 2018). An important question we study in PANDORA is to what extent this result depends on the assumptions made in these models. In particular, we test how these results change when using a more mechanistic model of fish physiology and ecology. A manuscript studying the effects of adding density-dependence in growth to a model using density-dependent recruitment is about to be submitted (Croll, van Kooten & De Roos, *in prep*). The main work on the topic will be conducted under Task 1.3.

In response to strongly decreased fishing intensity, the spawning stock biomass of the North Sea plaice population has quadrupled in the last 15 years, while individual growth has decreased to the extent that 6-year-old individuals currently are the same size as 3-year-olds were before recovery. North Sea plaice is also a well-studied species: we have reliable stock age and weight distribution estimates going back to the 1950's. This presents a perfect case study for the appearance and consequences of density-dependent individual growth in an exploited stock, and an excellent scenario to compare with model outcomes. The aim of this work is to use plaice to extract general lessons, facilitating fisheries management which can deal with the potential consequences of post-recruitment density dependence. Another addition to this work is the stakeholder perspective. There is a large discrepancy between scientists convinced that the stock is at a historic high while, at the same time, fishermen report that they are unable to find enough plaice to fill their quota.

4.1.6.1 Relevant data sets on flatfish in the North Sea

Wageningen Marine Research carries out a number of bottom fish surveys annually. The Beam Trawl Survey uses a beam trawl gear to survey North Sea plaice and Sole, each August/September since 1985. Because the gear is similar to a commercial beam trawl net, this survey targets mostly mature (age 3+ fish). The Sole Net Survey uses a finer mesh gear to estimate specifically juvenile plaice and sole. It is considered an adequate sampling for age groups 1-4. The Demersal Fish Survey (DFS) is a coastal survey using a fine mesh gear to specifically estimate the abundance of young of the year and one-year-old plaice and sole. Both surveys run annually in September/October since 1970. The Dutch International Bottom Trawl Survey uses an otter trawl gear, mainly to sample roundfish. However, it also catches larger plaice. The timing of this survey (January/February) is just around the spawning period of plaice, when reliable information on maturity and spawning status can be obtained.

Wageningen Marine Research also samples the fish landed at Dutch auctions. These are sampled year-round, since the 1950's. All these surveys and market sampling measure individual lengths of all sole and plaice caught, and a length-stratified subsample is subsequently weighed and aged. There are also considerable, long-term data on North Sea-wide length frequency and abundance of plaice since 1909 compiled by Cefas for the CERES project.

These data sources together (plus those available through ICES), allow for a very thorough study of North Sea plaice population dynamics, especially combined with the mechanistic models based on individual energetics that are being developed.

4.1.6.2 Knowledge gaps in our understanding of density dependence

Density-dependent individual growth has clearly shown to be a common phenomenon in harvested fish populations. In the last decades, great progress has been made in understanding the dynamics of size-structured populations and communities with density-dependent individual life history (de Roos & Persson, 2013; Andersen 2019). However, uptake of this new work into operational fisheries management has been slow. In Pandora we aim to facilitate this uptake by highlighting specifically how and under which conditions it requires a change in the current fisheries management paradigm, to ensure successful future management. The main work on this topic will be carried out under Task 1.3.

4.1.7 Stock/Spatial structure of North Sea cod and Plaice

Gaining knowledge about the spatial and stock structure of a commercially important fish species is a fundamental step in the assessment and management process (Hunter et al. 2004, Neat et al. 2014, ICES 2015a). Such knowledge feeds into estimates of abundance, recruitment and spawning stock biomass (SSB), sheds light on essential fish habitats and migratory highways, and allows catch/landings allocations to be increasingly more reflective of the underlying dynamics of the resource.

In the North Sea, the spatial and stock structure of Atlantic cod and European plaice has received considerable research effort (e.g. Hunter *et al.*, 2004; Kell *et al.*, 2004; Wright *et al.*, 2018, 2006; Neat and Righton, 2007; van Keeken *et al.*, 2007; Engelhard *et al.*, 2011, 2014, Ulrich *et al.*, 2013, 2017; Neat *et al.*, 2014). Despite this, aspects of their spatial distribution, stock identification and rates of mixing (both within and across stocks) remain uncertain. For example, cod in the North Sea, including ICES Divisions 4.a, 4.b, 4.c, 7.d and subdivision 3.a20, is currently assessed as a single stock unit. Recent examination, most notably during the 2015 Benchmark Workshop on North Sea Stocks (WKNSEA; ICES, 2015), however, highlighted that cod stock structure is an area of large uncertainty and concluded that 'strong evidence from several studies shows that the North Sea cod population structure is complex, and at least two distinct stocks could be confidently assumed for the assessment area'. Additionally, recent developments, for instance the 2019 North Sea cod assessment estimating an SSB below B_{lim} (an indicator of reduced reproductive capacity; ICES, 2019a) and the outburst of plaice biomass in the southern and central North Sea (ICES 2014, 2019b), have fuelled calls for further work.

Here, we review existing knowledge concerning stock structure in these two demersal fish species and highlight data gaps or research needs. Throughout the review, we draw on several information sources, ranging from genetics to tagging studies, to demonstrate how our understanding of stock structure in the North Sea has changed and how the rate of mixing can vary at differing spatial scales. We will briefly discuss the age structure of both stocks and summarise existing information on growth, maturity and recruitment. This latter part will be by no means an exhaustive review, primarily because these topics are covered elsewhere (e.g., see **Annex 1** for recruitment), but it will provide some building blocks for future work. Furthermore, by discussing the role that temperature plays in the individual-level processes of growth, maturation and recruitment, we strive to place stock structure and spatial distribution in the context of a changing environment (Peck & Pinnegar 2018). For more details see **Annex 2**.

4.1.7.1 Available datasets for further use in PANDORA

Table 4.4. Datasets available for further use in PANDORA, Cod, plaice and zooplankton.

Data	Species	Time	N	Location
Mark-recovery (release & recapture locations)	Atlantic cod (*Gadus morhua*)	1962 - 2015	7,296 Fish	Cefas tagged fish database*
Mark-recovery (release & recapture locations)	European plaice (*Pleuronectes platessa*)	1957 - 2005	18,951 Fish	Cefas tagged fish database*
IPCC simulations (HadGEM2-ES model output)	-	1900 – 2090	-	https://cera-www.dkrz.de/WDCC/ui/cerasearch/

CPR database	Mix of small (n = 40) and large (n = 75) zooplankton species	1958 - 2019	55,396 samples	https://www.cprsurvey.org/†

*The Cefas tag database is not currently freely available online (see Burt *et al.* (2006) for details). Access via request (contact Gary Burt at gary.burt@cefas.co.uk or Nicola Hampton at nicola.hampton@cefas.co.uk).

†The Continuous Plankton Recorder (CPR) database is available upon request (contact David Johns at djoh@MBA.ac.uk).

4.1.7.2 Knowledge and data gaps in spatial structure

Atlantic cod. The North Sea cod stock is currently assessed as a single functional unit (ICES 2019a). Regardless, multiple information sources, including results from genetic (e.g. Nielsen *et al.*, 2009; Poulsen *et al.*, 2011; Heath *et al.*, 2014; Wright *et al.*, 2018) and tagging (e.g. Neat and Righton, 2007; Righton *et al.*, 2007; Nedreaas *et al.*, 2008; Neat *et al.*, 2014) studies, as well as trends in landings and catch data (Holmes et al. 2014, ICES 2019a), support the idea of two distinct stocks. One of these stocks occurs in the deep waters of the northern North Sea, centred on the Viking Bank in 4.a. The second inhabits the much shallower central (4.b) and southern (4.c) North Sea, extending southeast into the eastern English Channel (7.d). Our knowledge about the level of mixing, both between and within these two stocks, has risen in recent years. For instance, the genetic work of Wright *et al.* (2018) demonstrates that juvenile cod in the northern stock disperse towards and settle in the western Skagerrak (3.a20), before making return migrations prior to spawning. Moreover, tagging efforts in the south yield little evidence that cod in these regions disperse northwards, instead remaining within the geographical limits of 4.b for the duration of deployment (Neat & Righton 2007, Neat et al. 2014). Despite such advances, there is a clear need for further work on stock mixing, especially in different quarters and across life stages (as recommended in the 2015 WKNSEA benchmark report; ICES, 2015). As detailed in **Annex 2**, this topic has received some attention, for example in the tagging work of Righton *et al.* (2007), however questions remain unanswered regarding spatio-temporal trends and how they vary with age. Using the same data sources as Righton *et al.* (2007), we plan to analyse Cefas' tagged fish database, which currently represents an untapped resource that includes over 7000 individual fish and dates back to the early 1960s (Burt et al. 2006). In addition to gaining new knowledge on cod stock structure, spatial distribution and the extent of mixing, any findings will also contribute to the two-stock hypothesis debate.

Temperature also plays a key role in the individual-level processes of North Sea cod. For example, growth (Blanchard et al. 2005, Righton et al. 2010), maturity (Wright et al. 2011) and recruitment (O'Brien et al. 2000) have all been linked directly to changes in temperature. Due to this, there is clear need for research that scales up these processes to explore what effect any future changes in temperature might have on stock dynamics and stock recovery rates. Within Pandora, we plan to revisit the match/mismatch hypothesis (Cushing 1990), using the experimental work of Kjesbu *et al.* (2010) to investigate how the date of spawning in North Sea cod may respond to forecasted temperature scenarios (IPCC simulations). This work will take the form of an individual-based maturation model, where the rate of maturation is modelled as a function of temperature and body size in each ICES Division (4.a, 4.b and 4.c). The outputs will be compared with the Continuous Plankton Recorded (CPR) database, thus allowing us to identify any mismatches between the predicted onset of spawning and the timing of production in the North Sea.

European plaice. As in cod, North Sea plaice in ICES Divisions 4.a, 4.b, 4.c and subdivision 3.a20 is currently assessed as a single stock (ICES 2019b). The addition of 3.a20 is a recent one (occurring in 2015; ICES, 2015a, 2015b) and is mainly a consequence of the work of Ulrich *et al.* (2013) who showed that North Sea plaice regularly move into the Skagerrak during the feeding season. Unlike in cod, ICES Division 7.d is not currently considered to be part of the North Sea plaice stock (ICES 2019b). That said, previous work has shown that plaice do move in and out of the eastern English Channel during the spawning season (Bolle et al. 2005, ICES 2010a). Thus, the assessment now assigns 50% of landings and estimated discards in 7.d during quarter 1 to the North Sea stock (ICES 2010b).

Based on current knowledge, a clear gap surrounds the topic of population sub-structuring in North Sea plaice. From both a genetic and tagging perspective, we know quite a lot about the difference between plaice in the North Sea (e.g. Hunter *et al.*, 2004; Bolle *et al.*, 2005), Irish Sea (e.g. Dunn and Pawson, 2002; Was *et al.*, 2010) and the Skagerrak (e.g. Ulrich *et al.*, 2013, 2017), but very little about the degree of mixing that occurs at regional or local scales. Individual studies do exist, for example the tagging work of Hunter *et al.* (2004) and Griffiths *et al.* (2018), that provide important information on the long-term movement patterns and behaviour, however electronic tagging only provides a small window into the spatial distribution of the stock. Previous work demonstrates that the North Sea plaice stock has shifted northwards in response to warming (Dulvy et al. 2008, Engelhard et al. 2011) and has experienced a large population outburst in recent years (ICES 2019b). Within the WP1 North Sea case study we plan to utilise Cefas' tagged fish database (Burt et al. 2006) to further investigate the movement patterns of North Sea plaice. The data includes just under 19,000 individual fish (both adults and juveniles) dating back to the early 1950s. As in cod, this resource is currently untapped, and we expect that any knowledge gained will help contribute to the hypothesis of a climate driven re-distribution of the stock.

Continuing on from the above, there is a clear need for regional and local scale genetics work. In cod, the use of SNPs and microsatellite DNA has greatly advanced our understanding of stock structure and spatial dynamics within the North Sea stock unit (e.g. Heath *et al.*, 2014; Wright *et al.*, 2018). In plaice, genetic work has occurred at the broad scale, for example in European waters (Hoarau et al. 2002, 2004, 2005, Was et al. 2010, Watts et al. 2010) and in transitional waters between the North Sea and the Baltic Sea (Ulrich et al. 2013, 2017), but is lacking at the sub-stock level. In line with this research need, Gary Carvalho and his research team at the University of Bangor will conduct an in-depth review of available genetic information on population structuring in exploited species. This work will include possible pipelines for the implementation of genetic data in the general framework for resources assessment and will be presented as part of the 30-month 1.3 WP1 deliverable.

4.1.8 Available knowledge on North Sea food web interactions relevant for stock assessments and fisheries management.

The North Sea has a complex food-web which leads to many trade-offs in the yield of fisheries due to complex predator-prey dynamics and competition compared to simpler food-webs (e.g., Baltic foodweb). If managers decide to adopt a multispecies/ecosystem-based management approach, this will be very challenging as politicians often try to avoid making decisions on trade-offs between species or fisheries of different countries (e.g., Kempf et al. 2016, Rindorf et al. 2018). So far, management of fish stocks in the North Sea is still focused on single--species assessments although natural mortality estimates are taken from the stochastic multi-species stock assessment model SMS (Lewy and Vinther 2004). The availability of SMS and the use of its outputs in single stock assessment models of commercially important fish stocks (WGNSSK 2018, HAWG 2018) provides an excellent opportunity for testing how food web interactions influence stock assessment.

This review work is meant to illustrate current work in the North Sea area on modelling predation mortality as input for stock assessments and forecasting stock dynamics and management implications. It aims to highlight the most important implications of available knowledge for fisheries management and to identify knowledge gaps. In this work, the focus is on the interactions between important commercially exploited fish stocks in the area and does not attempt to provide a full food-web description. For further details see **Annex 3**.

4.1.8.1 *Summary from the review on the North Sea food web models*

There exists a wealth of multi species and ecosystem models in the North Sea area that are able to inform on consequences of species interactions for fisheries management. In the North Sea, mainly three models are currently used to estimate natural mortalities and to perform analyses on the impacts of management decisions: The stochastic multi species model SMS , Ecopath with Ecosim (Christensen and Walters 2004) and the LeMans model (Thorpe et al. 2015, 2016, 2017).

The most important input to parameterize food web models is stomach data. Most of the available modelling approaches use the so called “Years of the Stomach” as the main source of information on species interactions in the North Sea. Observed relative stomach contents (weight-based) are available from five years (1981, 1985, 1986, 1987 and 1991) of North Sea wide stomach sampling exercises (Anon 1988, Daan, 1989, Hislop et al. 1997) coordinated by the ICES. Another valuable source for diet information is Dapstom (Pinnegar 2014). DAPSTOM (integrated database and portal for fish stomach records) is an ongoing initiative (supported by Defra and the EU) to digitise and make available fish stomach content records spanning the past 100 years. However, the database does not include as many parameters as the ICES database (i.e. no relative share by weight) and the samples are not from a coordinated sampling program in space and time leading potentially to difficulties when using the data to parameterize food web models (spatial mis-matches in data and model domain).

The North Sea SMS model has a clear focus on higher trophic levels and commercially important fish species (WGSAM 2017). It includes the main species interacting with commercially important fish stocks through predation. All other prey organisms eaten by predators in the model are represented as so called “Other Food” assuming a constant in time biomass pool. In the keyrun with EwE a wider range of species/functional groups is included (WGSAM 2015). Compared to SMS, the EwE keyrun includes e.g., functional groups like Spurdog, different ray and skate species, monkfish, several flatfish species and crustaceans like Nephrops and brown shrimp. In addition, as full ecosystem model it also covers lower tropic level plankton and benthic functional groups down to primary producers. However, while EwE covers more species interactions, the populations are less detailed than in SMS. The LeMans model covers such as SMS interactions between commercially important fish species, however, also bycatch species like witch, turbot and anglerfish are included. A total of 21 fish species is represented in 32 equal length classes of 5 cm (Thorpe et al. 2019).

Based on the ICES advice on multi species considerations (ICES 2013), published literature (e.g., Mackinson et al. 2009, Kempf et al. 2016, Thorpe et al. 2017 and 2019) and results from projects (i.e. EU project MYFISH; http://www.myfishproject.eu) conclusions can be made on the main impacts of species interactions on management relevant questions in the North Sea area:

- *Potential target multispecies F_{MSY} depends on the management objectives* and SSB constraints used. There is no single maximum sustainable yield solution in a multispecies context, and policy choices will have to be made. These results are common for all three main multi species applied in the North Sea area (SMS, EwE, LeMans). An analysis of trade-offs caused by species interactions can inform on the possible consequences of various policy decisions. To decide on trade-offs, however, is often avoided by politicans making any implementation of a multi species approach difficult.
- Yield of *virtually all species were affected by the abundance of cod and saithe* in model simulations with SMS. They are the main predator fish species in the SMS North Sea configuration. Changing management target fishing mortality (target F) for cod and saithe therefore influenced the yield of all other stocks.
- *Indirect predation effects may be also important in the complex North Sea food web .* For example, a lower F on cod increases cod biomass, which can lead to a decrease in SSB and yield for whiting and haddock (direct predation effect), which in turn can lead to an increase in SSB and yield e.g., for herring, sandeel, Norway pout, and sprat. The increase in SSB for these prey species is caused in simulations with the model SMS due to the reduction in predation pressure from whiting and haddock, which more than compensates the increase in direct predation from a larger cod stock (indirect effect).
- *Due to predation, it is no longer guaranteed that all stocks can be maintained above precautionary single-species biomass reference points* simultaneously. A new approach may be needed to define what precautionary means in a multispecies context.
- *Target fishing mortalities leading to close-to-maximum average yield* (F_{MSY}) in a multispecies context can be derived similar to F_{MSY} ranges calculated by ICES in a single species context and implemented in the EU plan for mixed fisheries in the North Sea. Management based on Nash equilibria, however, turned out to be superior over these ranges in simulations with the LeMans model (Thorpe and De Oliveira 2019).
- It happens that *multi species F_{MSY} is higher than the agreed single-species F_{MSY} values* because of density dependent effects like cannibalism or competition. Also a reduction of predators increases the yield from more productive prey species. This highlights the previous point that the target multi species F_{MSY} depends on defining agreed constraints and acceptable risk levels for all species involved.
- Due to a successful reduction in fishing, *natural mortality is an increasingly important source of mortality in the North Sea*. This means that the stock dynamics are increasingly more influenced by natural processes. At the same time, improving estimates of consumption of fish by top predators, such as seals and cetaceans, is important, particularly when these predator populations are expected to increase further.

4.1.8.2 Available data sets for further use in Pandora

Table 4.5. Available dagasets for further use in Pandora –stomach data.

Data set	**Description**	**Source**
ICES stomach database	Stomach contents from the years of the stomach and latest internationally coordinated stomach sampling	**http://www.ices.dk/marine-data/data-portals/Pages/Fish-stomach.aspx**
DAPSTOM (integrated database and portal for fish stomach records)	Frequency of occurrence of prey for 188 predator species from 100 years (not only North Sea)	**https://www.cefas.co.uk/cefas-data-hub/fish-stomach-records/**

WGSAM Keyruns	Detailed output from keyruns reviewed by WGSAM	https://www.ices.dk/community/groups/Pages/WGSAM.aspx

4.1.8.3 Knowledge and data gaps in multispecies assessment models

The various models available in the North Sea area have been used for various strategic analyses on fisheries management options. As one of the few examples worldwide, natural mortality estimates from the stochastic multi species model SMS are used as input to single species ICES assessments for commercially important fish stocks. However, forecasting capabilities have so far not been used for tactical advice on quotas and only to a minor extent for management plan evaluations that are still mainly conducted with single species management strategy evaluations (MSEs). Approaches are also missing that are able to predict the impact of management options for mixed fisheries in detail taking into account biological interactions in short- to medium term projections for tactical advice on quotas. Next to biological interactions also technical interactions in mixed fisheries are highly relevant for North Sea demersal fisheries.

The bottleneck for a successful application of multi species assessments and forecasts are stomach data. The last internationally coordinated stomach sampling program in the North Sea is from 1991. An international coordination for a new stomach sampling program is missing substantially preventing multi species models becoming a serious alternative to single species approaches. The lack of a time series of data does not only hinder analyses of processes behind dynamics in species interactions, it is also a main argument against using multi species approaches for advice due to a perception of too large uncertainties and potential bias. A coordinated stomach sampling program inside the data collection framework is needed based on already existing best practice guidelines on how to sample and analyse stomach data in a cost effective way.

Processes acting on the egg and larval phase are not directly implemented and only captured via stock recruitment relationships in the main multi species models used in the North Sea area. Therefore, an improvement in our understanding the dynamics determining stock recruitment relationships will also be beneficial for the available multi species models. A review of processes influencing recruitment can be found under 4.1.1 and in **Annex 1**.

The lack of uptake of multi species management options can among other reasons be found in a general mistrust in complex multi species and ecosystem models. To some extent this mistrust could be elevated by more rigorous skill assessments. Best practice guidelines on what needs to be included in such a skill assessment would be beneficial.

4.1.9 Activities in PANDORA to fill the gaps (or needs) – The North Sea

Based on the reviews further work will be conducted in Pandora to fill some of the main gaps. In the following the work on each topic is described in short.

4.1.9.1 Knowledge on the recruitment dynamics of gadoids and herring in the North Sea (including climate change and density dependent effects)

The strategy in Pandora to assess how information on environmental effects could help to improve the management of commercially important North Sea stocks under altered productivity regimes comprises four steps to utilize the information from the extensive review in the course of the project:

i. Based on the reviews it is possible to identify spatial and temporal interactions with likely environmental drivers.
ii. As the next step, available environmental data are tailored towards temporal (e.g. spawning time) and spatial scales (e.g. spawning grounds) to derive meaningful environmental indices, representing the environmental conditions experienced during vulnerable life stages (or proxies for that).
iii. Stock- and recruitment time series will be combined with tailored environmental indices by means of conventional and advanced (e.g. machine learning/causal modelling) statistical methods to improve predictive power and inform scenarios in WP2 and WP3.
iv. Implement improved stock recruitment relationships in the FLBEIA modelling framework to allow for more realistic predictions of future stock productivity under e.g., climate change.

4.1.9.2 Climate change impacts on the distribution of North Sea stocks and predicted shifts in distribution

The knowledge on the potential severity of shifts in distribution and productivity due to climate change (ongoing and projected) will be used throughout Pandora to target efforts on sensitive stocks / species to i) integrate knowledge on shifts in distribution into ICES advice products (e.g. ecosystem overviews accompanying single-species advice), ii) inform the scenario development in WP2 to WP4, iii) help to get a better understaning of processes behind spatial stock structure and density-dependent effects, and IV) guide recommendations for necessary changes in reference points (e.g., biomass limits and targets for stocks moving into or out of management areas) and future management.

4.1.9.3 Density dependent effects with focus on North Sea flatfish

During Pandora further work will be conducted on the topic. A manuscript documenting the recent plaice recovery, the appearance of size-dependent growth in the stock and the effects this has had on the current management and exploitation will be produced. This is a collaboration with the University of Amsterdam. A further manuscript will be produced studying the addition of density-dependent individual growth in a model with a mechanistic implementation of a stock-recruitment relationship (through food- or condition-dependent reproduction). Also this is a collaboration with the University of Amsterdam. In addition, a brief written report will be produced outlining the different perceptions of the North Sea plaice stock by scientists (stock is very large) and fishermen (unable to find enough fish to take their quota) as main stakeholders.

4.1.9.4 Stock structure of North Sea cod and plaice

North Sea cod: As detailed in the review under 4.1.5 and **Annex 3**, stock mixing has received some attention, for example in the tagging work of Righton *et al.* (2007), however questions remain unanswered regarding spatio-temporal trends and how they vary with age. Using the same data sources as Righton *et al.* (2007), we plan to analyse Cefas' tagged fish database, which currently represents an untapped resource that includes over 7000 individual fish and dates back to the early 1960s (Burt et al. 2006). In addition to gaining new knowledge on cod stock structure, spatial distribution and the extent of mixing, any findings will also contribute to the two-stock hypothesis debate.

Temperature also plays a key role in the individual-level processes of North Sea cod. For example, growth (Blanchard et al. 2005, Righton et al. 2010), maturity (Wright et al. 2011) and recruitment (O'Brien et al. 2000) have all been linked directly to changes in temperature. Due to this, there is clear need for research that scales up these processes to explore what effect any future changes in temperature might have on stock dynamics and stock recovery rates. Within Pandora, we plan to revisit the match/mismatch hypothesis (Cushing 1990), using the experimental work of Kjesbu *et al.* (2010) to investigate how the date of spawning in North Sea cod may respond to forecasted temperature scenarios (IPCC simulations). This work will take the form of an individual-based maturation model, where the rate of maturation is modelled as a function of temperature and body size in each ICES Division (4.a, 4.b and 4.c). The outputs will be compared with the Continuous Plankton Recorded (CPR) database, thus allowing us to identify any mismatches between the predicted onset of spawning and the timing of production in the North Sea.

North Sea plaice: Within the WP1 North Sea case study we plan to utilise Cefas' tagged fish database (Burt et al. 2006) to further investigate the movement patterns of North Sea plaice. The data includes just under 19,000 individual fish (both adults and juveniles) dating back to the early 1950s. As in cod, this resource is currently untapped, and we expect that any knowledge gained will help contribute to the hypothesis of a climate driven re-distribution of the stock. There is a clear need for regional and local scale genetic work. In plaice, genetic work has occurred at the broad scale, for example in European waters (Hoarau et al. 2002, 2004, 2005, Was et al. 2010, Watts et al. 2010) and in transitional waters between the North Sea and the Baltic Sea (Ulrich et al. 2013, 2017), but is lacking at the sub-stock level. In line with this research need, Gary Carvalho and his research team at the University of Bangor will conduct an in-depth review of available genetic information on population structuring in exploited species. This work will include possible pipelines for the implementation of genetic data in the general framework for resources assessment and will be presented as part of the 30-month 1.3 WP1 deliverable.

*4.1.9.5 **Available knowledge on North Sea food web interactions relevant for stock assessments and fisheries management.***

As outlined in the review in 4.1.7 and **Annex 3**, models combining multi species and mixed fisheries interactions for tactical short-term forecast and MSE simulations are so far missing. During Pandora the output from the multi species SMS will be utilized to identify the main dynamics between predator and prey stocks in the North Sea food web. This dynamic will be captured by simple relationships and implemented in the mixed fisheries bio-economic model FLBEIA to allow improved short-term predictions, but also MSE simulations for the evaluation of management plans.

To tackle the lack of more recent stomach data, Pandora will develop a strategy on how to sample and analyse stomach data in a cost effective way based on knowledge from other projects such as FISHPI2. Pandora will engage with important stakeholders as regional DCF groups and ICES WGSAM to come up with a strategy for regular stomach sampling in the North Sea and other areas.

Together with ICES WGSAM and ICES WGIPEM (both groups are central in ICES to develop multi species and ecosystem models for management purposes), Pandora will develop a general guide to conduct skill assessments to increase the trust in more complex models. These more complex models can be used to gauge the performance of (and potentially provide inputs to) traditional single-species assessment models and can be used in management strategy evaluations.

4.2 Eastern Baltic Sea

Existing knowledge relevant to the needs – Eastern Baltic Sea

4.2.1 Abiotic factors in the Baltic Sea

The ecosystem changes in the Baltic Sea are synthesized by the ICES WGIAB (2008 and subsequent reports) in Integrated Ecosystem Assessments (IEA) conducted for seven sub-regions of the Baltic Sea: i) the Sound (ÖS), ii) the Central Baltic Sea (CBS), encompassing the three deep basins, Bornholm Basin, Gdansk Deep and Gotland Basin; iii) the Gulf of Riga (GoR), iv) the Gulf of Finland (GoF), v) the Bothnian Sea (BoS), vi) the Bothnian Bay (BOB) and a coastal site in the southwestern Baltic Sea (COAST). The updated IEA (ICES WGIAB, 2015) corroborated the correlation between temperature and salinity, and included 2014 values for the abiotic factors being tracked.

The main drivers of the observed ecosystem changes vary somewhat between sub-regions, but they all include the increasing temperature and decreasing salinity (Figure 4.2.a). These are influenced by large-scale atmospheric processes illustrated by the Baltic Sea Index (BSI), a regional calibration of the North Atlantic Oscillation index (NAO) (Lehmann *et al.*, 2002). The change from a generally negative to a positive index for both BSI and NAO in the late eighties was associated with more frequent westerly winds, warmer winter and eventually a warmer climate over the area (Figure 4.2.a). Further, the absence of major inflow events has been hypothesized to be related to the high NAO period (Hänninen *et al.*, 2000). An indication of this is that only two major inflows to the Baltic Sea have been recorded during the high BSI-period since the late 1980s. Contrary to what occurred in surface waters, salinity in deeper waters has increased after the early 1990s to levels as high as in 1960s–1970s (Figure 4.2.a).

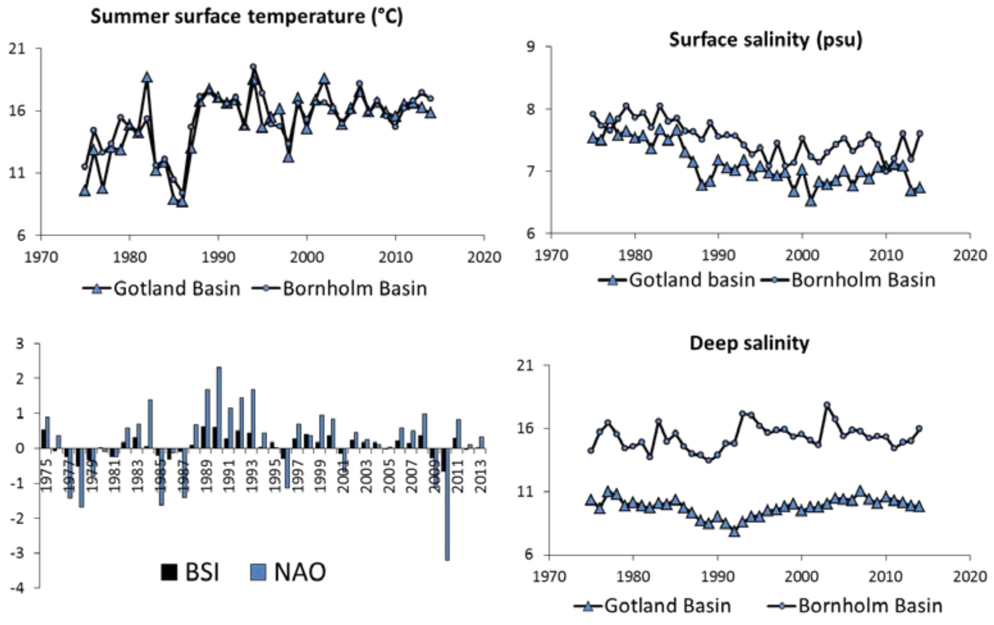


Figure 4.2.a. Time-series in summer surface temperature and surface salinity (top panels), BSI (Baltic Sea Index) and NAO (North Atlantic Oscillation index) and deep salinity (lower panel) in the Gotland Basin and Bornholm Basin.

In addition to temperature and salinity, fishing pressure was identified as an important driver for CBS and BoS. For the highly eutrophicated GoF, also nutrient loads were found to be an important driver. Trends in nutrient concentration and loading vary between the sub-regions; the concentrations of DIN and DIP decreases in ÖS and CBS, whereas in GoR and GoF DIP concentration is increasing because of internal loading. In contrast, in BoS and BoB DIN concentration is increasing, and in BoB and COAST the total DIP loading from run-off is also increasing. Although the long-term decrease in salinity is apparent in all sub-regions, the recent trends in salinity differ. In GoR, as in the CBS, salinity has increased since 2003, whereas in COAST salinity is continuing to decrease due to the increased freshwater input from runoff.

The suggested driving forces of the observed regime shift in all sub-regions, decreasing salinity and increasing temperature, are both consequences of climate change. However, it must be underlined that the population changes observed in several trophic levels (fish and plankton) in many areas are also the result of top-down regulation and trophic cascades (Casini *et al.*, 2008, 2009), emphasizing the role of fishing pressure on ecosystem changes.

Moreover, the reversal of abiotic factors back to the values as observed in the 1970s–1980s did not produce a parallel reversal of the biotic conditions, this likely confirming that currently the Baltic Sea is strongly controlled by other mechanisms, as for ex. trophic interactions (Casini *et al.*, 2009, 2010; Möllmann *et al.*, 2009).

Contaminant levels in general remain elevated, and the overall contamination status has been at the same level for the past two decades, but many potential contaminants are not monitored. Some of the main contaminants have been reduced (e.g. DDT, dioxins, and PCBs).
A particular feature of the Baltic Sea since the mid-1990s has been a drastic increase in the extent of anoxic and hypoxic areas, likely due to lack of strong water inflows from the North Sea and potentially increased biological oxygen consumption on seafloor (Figure 4.2.b).

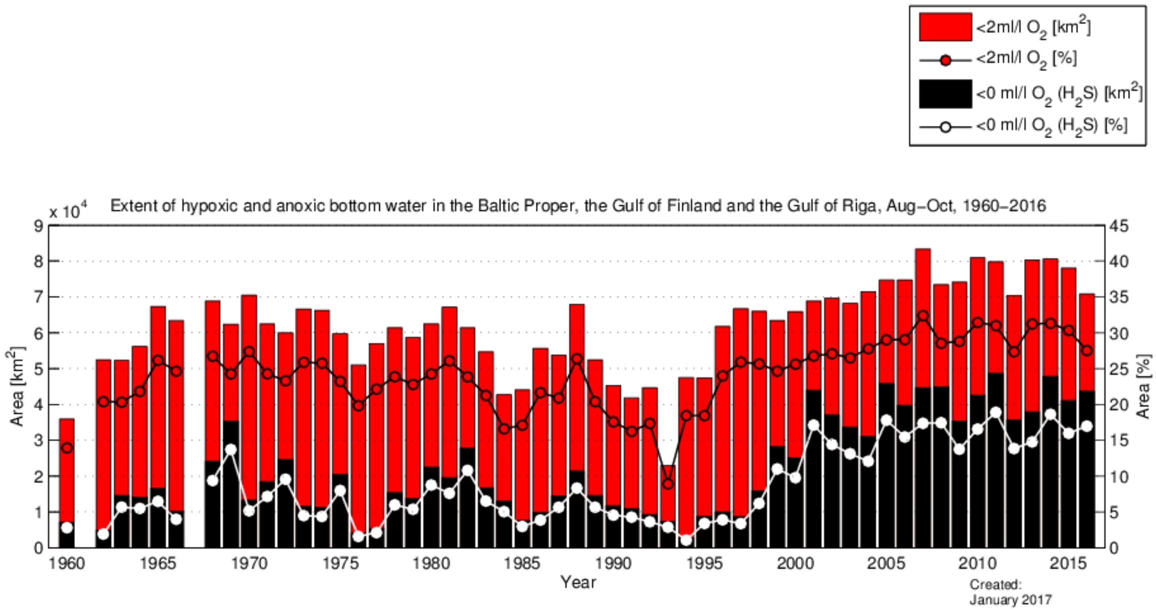


Figure 4.2.b. Time-series of anoxic and hypoxic seabed in the entire Baltic Proper. From the Swedish Meteorological and Hydrological Institute (SMHI) annual report.

In a changing environment, the status of individual fish populations and consequently the fishing possibilities can change rapidly, not always for reasons directly related to fisheries. In order to take the ecosystem context into account in the management process and achieve consensus concerning fishing possibilities among stakeholders, it is important that the status of various drivers influencing fish stocks, and their relative impacts are broadly understood.

An overview of the dynamics of the eastern Baltic cod, sprat and central Baltic herring SSB and recruitment together with the dynamics of drivers influencing the dynamics of biomass and recruitment is presented in Figure 4.2.c.

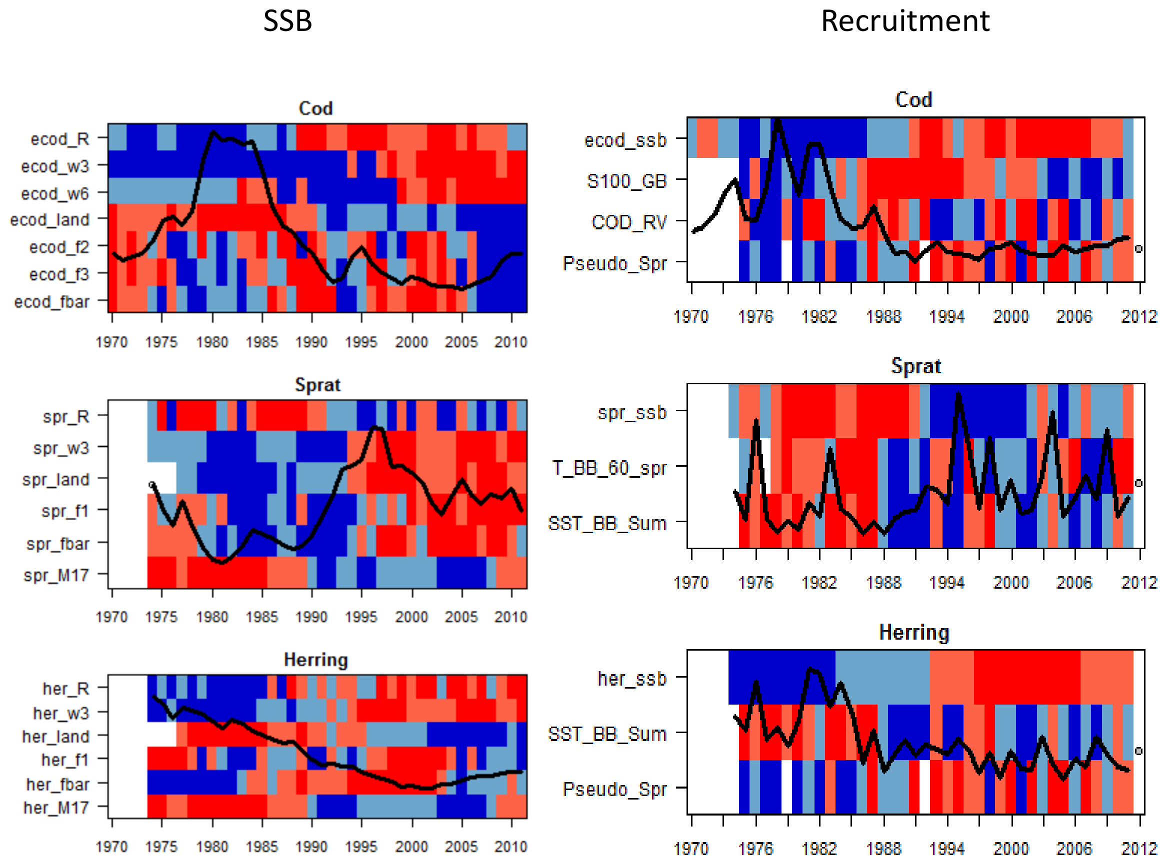


Figure 4.2.c. Temporal changes in indicators influencing the SSB and recruitment of the eastern Baltic cod, sprat and central Baltic herring. The colours refer to quartiles of the values observed in the time series, high values are marked with blue and low values with red colours, except for mortality where the colours are inversed. The lines show the trends in SSB and Recruitment of the stocks, the dots for recruitment in the final years show the values used in short-term forecast (R-recuitment; w-weight-at-age; land-landings, f-fishing mortality at age; M-natural mortality (average of ages 1–7); S100_GB- salinity at 100 m depth in Gotland Basin; COD_RV- cod reproductive volume, Pseudo_Spr- abundance of *Pseudocalanus* in spring; T-BB-60_spr- temperature at 60 m depth in spring in Bornholm Basin; SST_BB_Sum- Sea surface temperature in summer in Bornholm Basin).

Environmental conditions for Eastern Baltic cod recruitment of year-classes 2010–2011 were assessed by the ICES/HELCOM Working Group on Integrated Assessments of the Baltic Sea (ICES WGIAB, 2013). This assessment was made based on an indicator of the limiting abiotic conditions for cod egg survival, the reproductive volume, found to be the most encompassing indicator of the significant indicators of environmental conditions of cod recruitment (as assessed by models on SSB-recruitment residuals; WGIAB, 2013). The reference value of reproductive volume distinguishing positive from negative environmental influence on cod recruitment (Figure 4.2.d) was derived using the quantitative relationship between recruitment residuals and reproductive volume (WGIAB, 2013).

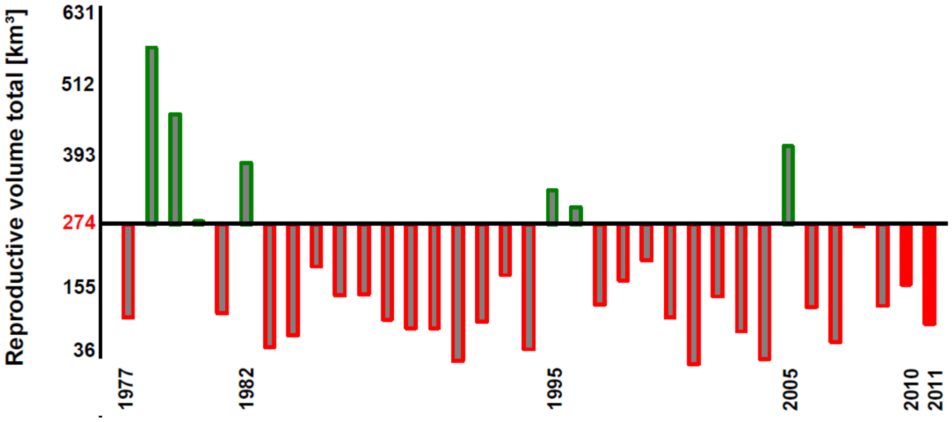


Figure 4.2.d. Time series of reproductive volume, consisting of water with more than 2 ml/l ogygen concentration and salinity>11, for Eastern Baltic cod (summed across the three deep basins in the Baltic Sea), assembled by WGIAB 2013. Relationships between each variable and residuals from cod recruitment (back shifted) vs. cod SSB were derived during WGIAB 2013, using linear models of first or second-order polynomials for year-classes 1977–2009. Bars indicate the values relative to the reference value of each variable (derived from the fitted relationships on cod recruitment residuals, as the point where there is no environmental effect on recruitment); green bars indicate beneficial environmental conditions and red bars poor conditions for cod egg survival. This shows the poor conditions for cod recruitment for the year-classes 2010–2011 (corresponding to recruitment of age 2 in 2012–2013).

4.2.2 Biotic factors in the Baltic Sea

4.2.2.1 Changes in commercial fishes' spatial distributions

Fish distribution has changed considerably during the past decades. The Eastern Baltic cod, in parallel with the decrease in its stock size, contracted its distribution to the southern areas since the mid-1980s. The sprat stock on the other hand, increased mostly in the northern areas of the Baltic Proper (Figure 4.2.e), which has been interpreted as a spatial predation release effect (Casini *et al.*, 2011). As a consequence of the spatial relocation of the sprat stock to more northern areas, the growth of sprat decreased mostly in these areas (Figure 4.2.f), indicating a spatial density-dependent effect (Casini *et al.*, 2011). These results show the importance of spatial analyses to deepen the knowledge on Baltic resources. The current low spatial overlap between predator (cod) and prey (sprat), at least in some seasons, implies changes in the strength of the predator-prey relationship from the 1970s–1980s. Moreover, the reallocation of the sprat population in the northern Baltic proper implies a spatial differentiation in the strength of intra-specific and inter-specific competition among clupeids.

Evidence highlighting the importance of coastal shallow waters as major nursery and feeding grounds for pre-mature young cod and to some extent mature individuals keeps increasing during very recent years. Standardized Baltic International Trawl Surveys (BITS) cover mostly deeper waters (>15m water depth) and thus possibly misestimate abundances of species inhabiting coastal areas.

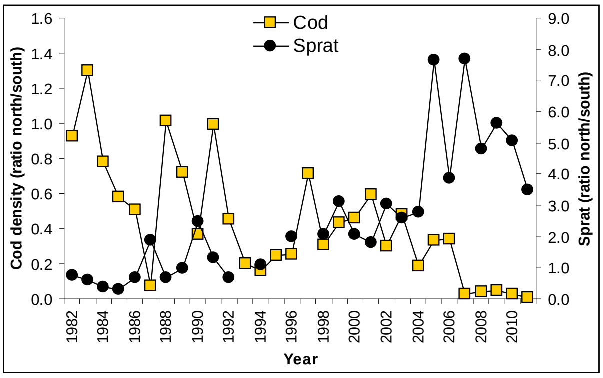


Figure 4.2.e. Ratio between sprat stock in northern Baltic Proper (SDs 27–29) and southern areas (SDs 25–26) as calculated by acoustic surveys, and ratio between cod stock in the northern Baltic Proper (SDs 27–28) and southern areas (SDs 25–26) from bottom trawl surveys. Modified from Casini *et al.* (2011).

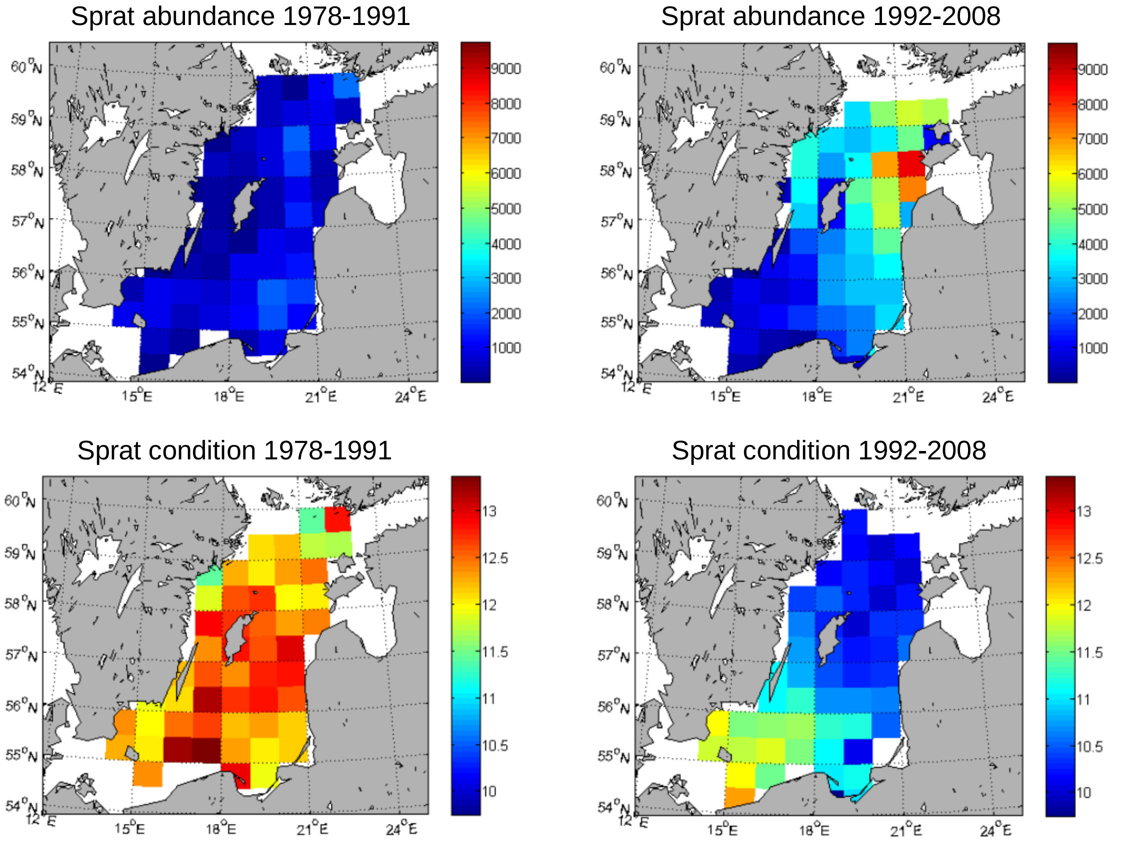


Figure 4.2.f. Spatial patterns in mean sprat abundance and clupeid condition in 1984–1991 and 1992–2008, from autumn acoustic survey. Only years with at least 10 individuals per rectangle were used in the condition calculation. From Casini *et al.* (2011).

4.2.2.2 Cod feeding and growth/condition

The work of ICES SGSPATIAL 2014 and WKSPATIAL 2015, 2016 (ICES, 2016) was focused on finalizing the stomach database from the data collated during the EU stomach tender running between 2012–2014 (Huwer *et al.*, 2014). Five decades of stomach content data allowed detailed insight into the long-term development of consumption, diet composition, and the resulting somatic growth of *Gadus morhua* (Atlantic cod) in the Eastern Baltic Sea. Post-settlement, pre-spawning cod feed almost exclusively on benthic prey. A recent reversal has occurred in the ontogenetic development of feeding level over body length, resulting in present feeding levels of these small cod, that indicate severe growth limitation and increased starvation-related mortality. Young cod manifest the low growth rate and high mortality rate in a reduction in size-at-age and low population abundance. The low feeding levels most probably result from a decrease in benthic prey availability due to increased hypoxic areas. Our study emphasizes that under the current environmental regime environmental forcing likely dominates the changes in consumption and growth rates of Atlantic cod in the Baltic Sea by reducing the availability of benthic prey. This food reduction is amplified by accumulation of cod of smaller size competing for the scarce benthic resources. Only the fishes with feeding levels well above average will survive, though growing slowly (Figure 4.2.g.). These results suggest that the relation between consumption rate, somatic growth and population density, as well as its consequences for species interactions and ecosystem functioning, are environmentally mediated and hence not stable under environmental change.

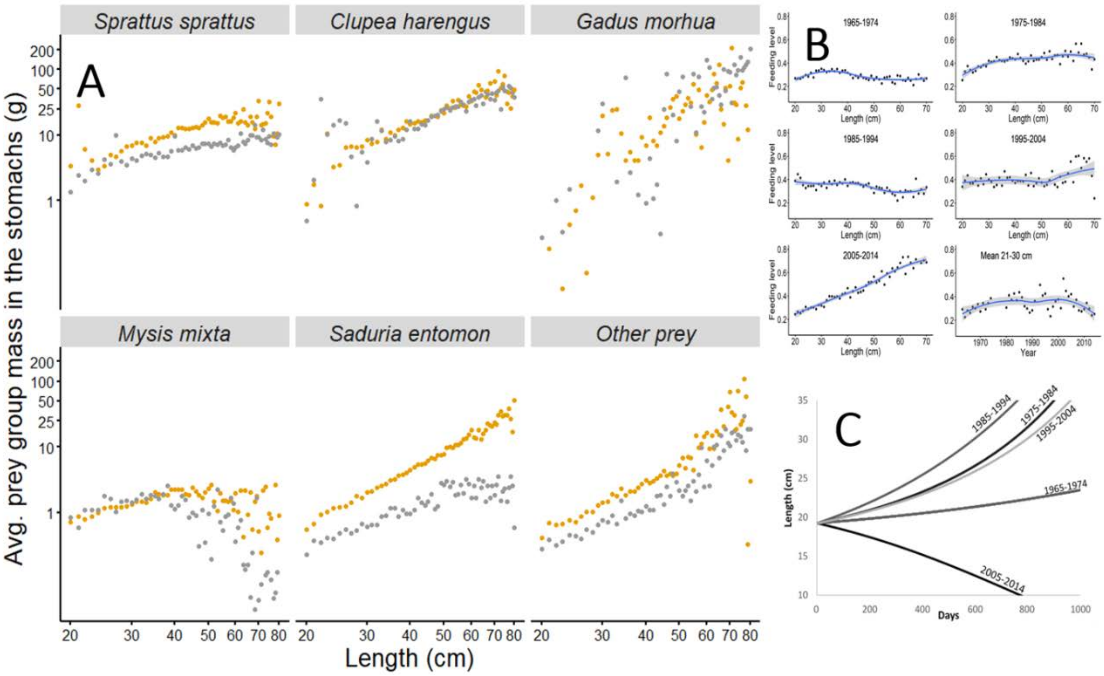


Figure 4.2.g. A Diet composition in *Gadus morhua* stomachs by mass before 1988 (orange) and after 1994 (grey). The transition period between ecological regimes from 1988 to 1993 (Moellmann et al. 2009) is left out. B Feeding levels of *G. morhua* by length during the past five decades. LOESS-based smoothed trends are plotted in blue together with shadowed confidence limits. The lower right panel: feeding level over time for *G. morhua* of 21 - 30 cm total length. C Simulated average growth trajectories of Gadus morhua in the total length range 20-35 cm for the five decades covered by the stomach sampling programme. (Neuenfeldt et al. in prep.)

4.2.2.3 Baltic cod body condition has declined the in last decades. Why?

Investigating the factors regulating fish condition is crucial in ecology and the management of exploited fish populations (Eero et al. 2015). The body condition of cod (*Gadus morhua*) in the Baltic Sea has dramatically decreased during the past two decades, with large implications for the fishery relying on this resource. We characterized the changes in the Baltic cod condition during the past 40 year. Moreover, we statistically investigated the potential drivers of the Baltic cod condition during the past 40 years using newly compiled fishery-independent biological data and hydrological observations (Casini *et al*., 2016).

The results showed that cod condition increased between mid-1970s to early 1990s, followed by a drop until the late 2010s. After that the condition stabilized at low levels. The same pattern was observed for all the ICES subdivisions and all the length classes investigated (Figures 4.2.h).

The statistical analyses evidenced a combination of different factors operating before and after the ecological regime shift that occurred in the Baltic Sea in the early 1990s. The changes in cod condition related to feeding opportunities, driven either by density-dependence or food limitation, along the whole period investigated and to the fivefold increase in the extent of hypoxic areas in the most recent 20 years (Figures 4.2.i,j). Hypoxic areas can act on cod condition through different mechanisms related directly to species physiology (Plambech et al. 2013), or indirectly to behavior and trophic interactions (Figure 4.2.k). Our analyses found statistical evidence for an effect of the hypoxia-induced habitat compression on cod condition possibly operating via crowding and density-dependent processes (Casini *et al.*, 2016). These results furnish novel insights into the population dynamics of Baltic Sea cod that can aid the management of this currently threatened population.

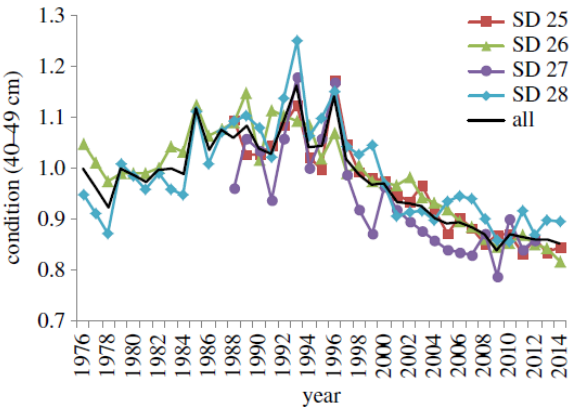


Figure 4.2.h. Temporal developments of mean cod condition in the different subdivisions (SDs) of the Central Baltic Sea for cod 40–49 cm. The black thick line is the average between the SDs. From Casini *et al.* 2016.

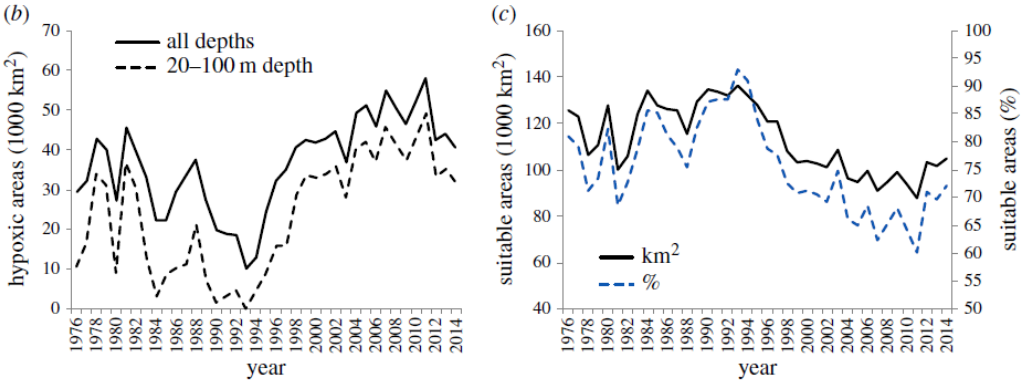


Figure 4.2.i. (b) time-series of total hypoxic areas (all depths), and hypoxic areas between 20–100 m depth, the latter used as predictors to explain cod condition in the GAMs; c) time series of suitable areas for cod (> 1 ml/l oxygen concentration) between 20–100 m depth, in absolute values and in percentage. The time-series refer to the Central Baltic Sea (SDs 25-28). From Casini *et al.* 2016.

Multiple studies were able to reveal a correspondence between the occurrence of grey seals and infestation levels of cod with the liver worm *Contracaeum osculatum*. Their life cycle includes crustaceans and several fish species as intermediate – and grey seal as final host. With the beginning of the 2010s infection levels increased drastically, resulting in a negative correlation between the amounts of worms found in cod livers and cod condition (lower HSI-values as well as corresponding decreased liver lipid contents). With less energy sored as fat in the liver, chances to withstand periods of food limitation decrease and fish mortality increases due to insufficient energy reserves not fulfilling metabolic needs (Horbowy et al., 2016).

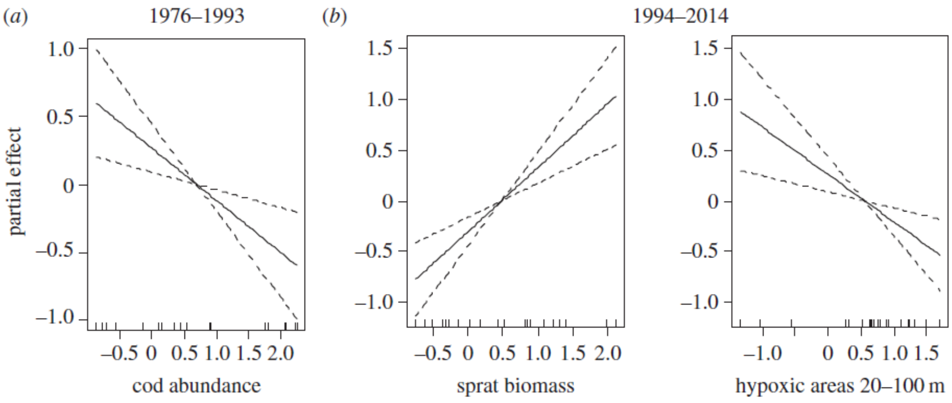


Figure 4.2.j. Results of the GAM (final model) for the two separated time periods (1976–1993 and 1994–2014). The partial effects of each predictor on cod condition are shown. From Casini *et al.* 2016.

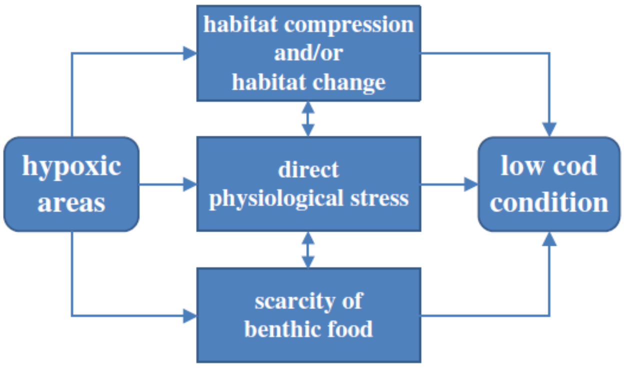


Figure 4.2.k. Schematic representation of the mechanisms potentially explaining the negative relationship between hypoxic areas and cod condition. From Casini *et al.* 2016.

4.2.2.4 Condition factor and feeding conditions in the Gotland Basin

The present available biological and fishery industry information reveal several changes in the structure and the biology of the cod stock in the Baltic. (i) Mean weight at age of cod decreasing since 2005. The decrease started earlier in the elder ages than the younger ones. (ii) There are observations from fishery that cod body condition in recent years has decreased. (iii) The deoxygenation and extension of hypoxic areas of Baltic Sea basins are increasing. This is to a large extent related to change of periodicity of major Baltic inflows. (iv) Cod stock in the Gotland basin remains very low although temporary increases were observed.

Based on these stock and ecosystem changes we tried to identify the main abiotic and biotic drivers that have led to the change in body condition of cod. As a test area we selected the Gotland basin, in which environmental and cod stock biological data have been collected since 1974. The results show that the temporal decrease in cod condition is mainly related to the extension of hypoxic area and oxygen saturation in water layers above the halocline. Extension of hypoxic area is also associated with change of cod diet. Since 1990's the share of benthic invertebrates and fishes has decreased significantly. The dominant species in the cod diet were clupeid fishes. Significant relation was found with herring abundance only, which has a more demersal distribution than sprat.

Fisheries industry indicated that cod body condition were quite sufficient in coastal areas (depths below 30 m) to compare with the deeper parts of the basin. We assume that this due to an expansion of invasive round goby in the coastal areas where total abundance has increased markedly since 2005 t Round goby is very easily accessible food item for cod in areas where the distribution is overlapping.

The main conclusions from the analyses are (i) The decrease of condition factor is determined by regime changes in the Eastern Baltic that depends from water exchange with North Sea; (ii) Main factors affecting condition factor from these analyses is hypoxia area and oxygen content; (iii) Although the sprat abundance is increasing the utilization of sprat may be insufficient due to prey and predator distribution (overlap) differences in time and space in the Gotland Basin; (iv) There were no stock density effects revealed on cod growth and condition.

4.2.2.5 Analyses of cod stomachs, biological and hydrological components

A study was conducted regarding recent (1999–2013) changes in cod physiological parameters of different size groups, which are related to food and maturation rates, and, to a certain extent, to an attempt to identify possible causes, factors and interactions that have formed the current environmental uncertainties and risks when assessing abundance, biomass of Eastern Baltic cod and prospects of this fishery type (Amosova et al. 2017). The results of our research in the ICES SD 26 confirm trends in growth and early maturation of the Eastern cod stock. Thus, at the present time the size composition of the cod stock is characterized by the dominance of small-sized fish, and the average length of 50% matured females decreased to 32 cm, males - up to 21 cm.

Energy and resources of liver provide generative processes. Even taking a decreasing gutted-weight at length into account, hepatosomatic indices (HSI) keep declining since the beginning of the 2000’s. Statistically significant HSI correlations between all parameters are found only in component 2, which characterizes the inter-annual variability of this index with a tendency to reduce its values. This fact is also proved by our analysis of cod energy level dynamics while studying the liver fat (% fat content in chemical composition – Figure 4.2.l). The organ liver represents next to its physiological importance an energy storage within gadoid fishes. Thus, decreasing HSI values and a shrinking liver fat content display an ongoing deterioration of cod condition in the study area.

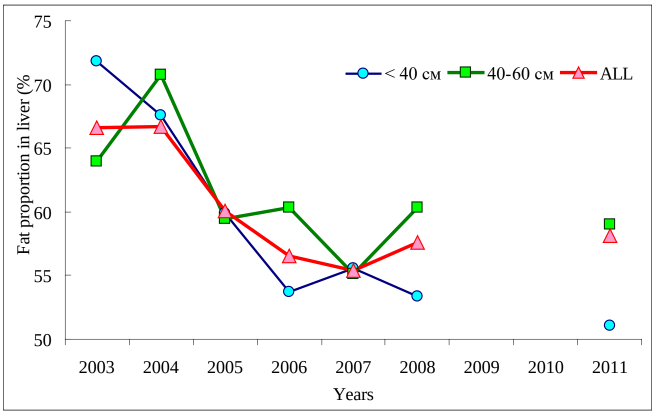


Figure 4.2.l Fat proportion in liver of different cod size groups (in %) based on chemical analysis (data obtained by L.I. Perova and M.L. Vinokur, technological direction of AtlantNIRO: Reports on the research work “Investigation of nutrition and biological value of commercial and non-commercial fishes of the Atlantic Ocean and the Baltic Sea based on the catches for the period of 2003–2011”).

The reduced consumption rate of sprat and benthic crustaceans goes hand in hand with the worsening of cod condition. Therefore, it can be assumed that mentioned species represent a main biotic driver (in terms of prey items) especially during fish fattening in fall-winter season, influencing the physiological state of all cod size groups

Changes in living conditions cause an adaptive response of cod, the biological essence of which is to preserve the species in the new environment. Based on the data presented, taking into account the results of the work showed that a size decrease of different species in aquatic systems is a universal or very general ecological response to warming, it can be concluded that the current increase in water temperature in the Baltic Sea, along with the expansion of waters with oxygen deficiency (in particular, through the influence of the latter factor in the narrowing of cod prey items spectrum) are the main abiotic drivers determining the structural changes in the population of Eastern Baltic cod in recent years.

4.2.2.6 Spatial distribution of cods liver worm, Contraceacum osculatum

Using a compilation of data available from sampling programmes and research projects, spatial trends of infestation with cods liver worm were made on cod sampled from a transect spanning the North Sea, Kattegat, the Sound, Kiel Bight and Mecklenburg Bay, Arkona Basin, and the western Bornholm Basin eastern Bornholm Basin, and south of Gotland. Both prevalence (percentage of cod infected) and abundance of infection (mean number of parasites per liver, including uninfected individuals) varied significantly between areas. More specifically, prevalence and abundance were highest in the three most easterly areas (i.e. eastern and western Bornholm Basin and south of Gotland, whereas parasite occurrence in general was low (or absent) in the more westerly and northwesterly areas (Sokolova et al. 2018) (Figure 4.2.m). Thus, the eastern Baltic cod stock primarily carries this parasite.

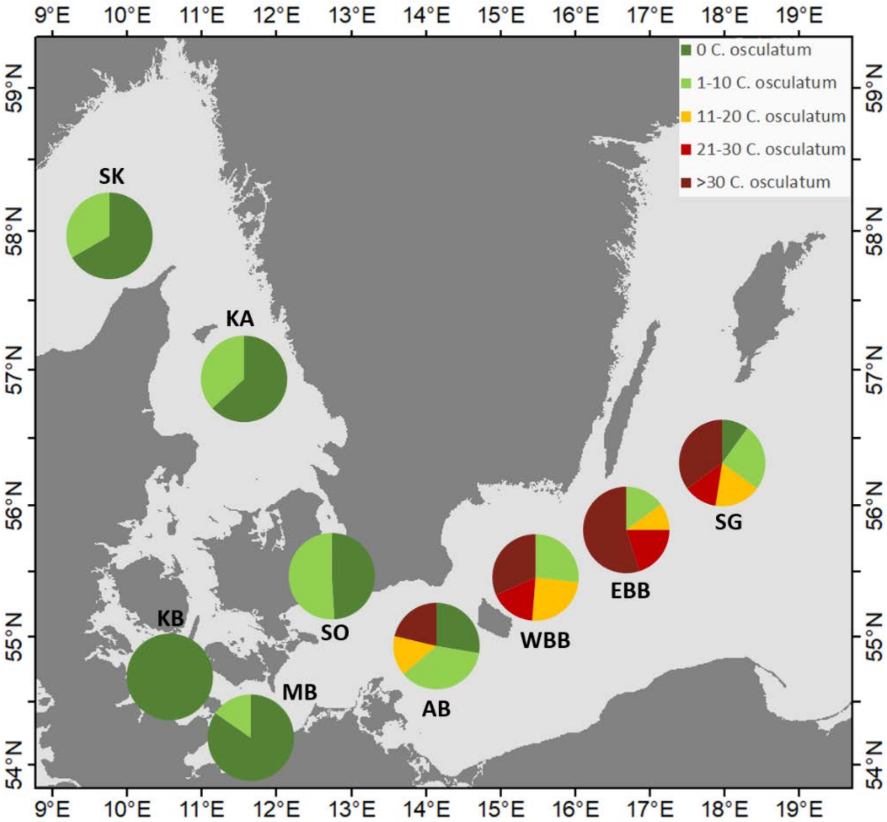


Figure 4.2.m. Abundance of infection (mean number of parasites per liver of cod including uninfected individuals) with liver worm C. osculatum in the nine study areas, Skagerrak (SK), Kattegat (KA), the Sound (SO), Kiel Bight (KB), Arkona Basin (AB), Western Bornholm Basin (WBB), Eastern Bornholm Basin (EBB) and south of Gotland (SG). From Sokolova et al. 2018.

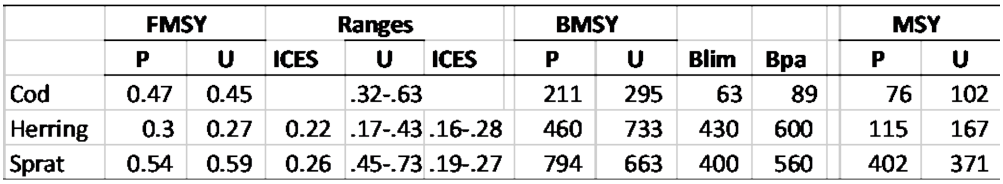
4.2.2.7 Multispecies, ecological-economic, and ecosystem models in the Baltic

Three papers have been published regarding Nash Equilibrium, a new management target to level off conflicts between interacting species. The Nash Equilibirum (NE) is defined as the multispecies state of fishing mortalities at which none of the species' yields can increase by changing the fishing effort. This is an optimum defined in general terms by John Nash (Nash, 1951), but not until now proposed as a management target in line with the MSY and ecosystem-based framework of the EU's common fishery policy (CFP).

A management strategy evaluation of NE was performed by Farcas and Rossberg (2016) comparing 9 other management options, including single-species MSY plans to achieve MSY from multiple (9-38) in silico stocks. Most plans outperformed (long-term yields) single-species management plans with pressure targets that were set without considering multispecies interactions. Nash equilibrium plans produced total yields comparable to plans aiming to maximize total harvested biomass, and were more robust to structural instability. They were concerned that implementation of the CFP, without "the systematic conservatism" of a NE, is in particular sensitive to structural instability. Expected yields are therefore comparably low, predicting the transition to MSY will lower rather than raise total long-term yields.

Norrström, Casini & Holmgren (2017) independently suggests NE as the multispecies MSY reference point. They analysed the NE for the cod, the herring and the sprat in the Baltic Sea main basin using an age-structured model capturing the ecological interactions between the species supported by ICES data. The study was also presented at WGSAM (ICES, 2017). Since the publication, an update has been made introducing density-dependent effects of herring and sprat on clupeid growth. The effect on the NE was higher yields on cod and herring, and lower yields on sprat (Table 4.6). This raised the B_{MSY} for herring above B_{pa}, which was already achieved for cod and sprat.

Table 4.6. Nash equilibrium reference points for herring and sprat according to Norrström *et al.* (2017), denoted P in the table. Updated values including density-dependence of clupeid growth is denoted U. For the update, also the F_{MSY} ranges are shown. ICES current single-species MSY, MSY ranges, B_{lim} and B_{pa} are shown for comparison. Yield and biomasses in thousand tonnes.



	FMSY		Ranges			BMSY				MSY	
	P	U	ICES	U	ICES	P	U	Blim	Bpa	P	U
Cod	0.47	0.45		.32-.63		211	295	63	89	76	102
Herring	0.3	0.27	0.22	.17-.43	.16-.28	460	733	430	600	115	167
Sprat	0.54	0.59	0.26	.45-.73	.19-.27	794	663	400	560	402	371

Nash equilibrium has now also been calculated for the North Sea by Thorpe, Jennings and Dolder (2017). They included 21 interacting species and took into account the existing mixed fisheries putting constraints on the set of Fs defining the NE. F-ranges for the NE were calculated, and the risk of stock collapse was analyzed across the range. The greatest collective long-term benefits from mixed multispecies fisheries will be achieved when F-PGY is close to or below F_{MSY} as defined at the Nash equilibrium.

In the Baltic Sea, the new approach of using ecological-economic optimization models for defining strategic as well as tactical management objectives was highly successful. This set-up takes into account species interactions, and the multiple ecological, economic or social needs of the fisheries. Such a broader management set-up, which tries to account for these multiple demands, has been advocated to abate the negative effects of fishing - both direct and indirect (Browman and Stergiou, 2004). Using optimization routines, the models are able to address and quantify different ecological and economic trade-offs (Voss et al. 2014 a, b). Such ecological-economic models of intermediate complexity (Nielsen et al., 2017) have also been used to address optimal spatial fisheries management (Voss et al., 2018), stochastic recruitment (Tahvonen et al., 2017), and alternative management targets, i.e. an ecologically constrained Maximum Economic Yield (eMEY; Voss et al., 2017).

A Baltic implementation of the spatially-explicit end-to-end Atlantis ecosystem model linked to two external models has been developed (Bossier et al., 2018), to explore the different pressures on the Baltic ecosystem. The HBM-ERGOM initializes the Atlantis model with high-resolution physical-chemical-biological and hydrodynamic information while the FISHRENT model analyses the fisheries economics of the output of commercial fish biomass for the Atlantis terminal projection year. The Baltic Atlantis model composes 29 sub-areas, 9 vertical layers and 30 biological functional groups. The balanced calibration provides realistic levels of biomass for, among others, known stock sizes of top predators and of key fish species. Furthermore, it gives realistic levels of phytoplankton biomass and shows reasonable diet compositions and geographical distribution patterns for the functional groups. By simulating several scenarios of nutrient load reductions on the ecosystem and testing sensitivity to different fishing pressures, the model has shown to be sensitive to those changes and capable of evaluating the impacts on different trophic levels, fish stocks, and fisheries associated with changed benthic oxygen conditions. The Baltic Atlantis forms hence an initial basis for strategic management evaluation suited for conducting medium to long term ecosystem assessments which are of importance for a number of pan-Baltic stakeholders in relation to anthropogenic pressures such as eutrophication, climate change and fishing pressure, as well as changed biological interactions between functional groups.

Activities in PANDORA to fill the gaps (or needs) – The Baltic Sea

4.2.3 Multispecies modelling as input for stock assessment

The changes in cod consumption and diet composition as well as the changes in the commercially important species' spatial distributions results in so far unseen dynamics in predation pressure on clupeids. These are currently accounted for in the assessments of herring in SD 25–27, 28.2, 29 and 32 and sprat SD 22-32 stocks by using SMS estimates of natural mortality up to 2012 (WKBALT 2013), and extrapolated using Eastern Baltic cod SSB index the year after.

Pandora will develop a new version of the Baltic multispecies model (SMS) that includes the latest analytical assessment method for Eastern Baltic cod. By including a large amount of so far unused stomach content data, the dependence of predator (cod) growth) on the prey abundances (herring and sprat as well as benthic food) will be investigated. A special focus here will be to understand, if lower fishing pressure on sprat will release more available prey for cod, counteracting the apparent density dependence observed for this stock in recent years. Since it is currently discussed to close certain areas with cod for sprat fisheries to improve cod condition, this question is highly management–relevant.

Furthermore, the new SMS runs will be benchmarked in WGSAM for application in WGFAS.

Updated ecological information will also be incorporated in single- and multispecies ecological - economic models. Optimal sets of fishing mortality will be determined for different political management objectives, including socio-economic aspects.

Recently a model for linking single stock assessment models has been developed at DTU-Aqua (Albertsen 2017). The model for linked stocks does not attempt to describe all ecosystem details or all details of the interaction between the selected stocks. A few links (correlations) are identified which describe the majority of the selected population's interaction. The model is designed to only require the existing standard data sources, which are already used in single stock assessments. The Pandora project will compare the results and performance of the simple linked stock model to a) the single stock assessments, and b) the newly developed Baltic multispecies model. The models will be compared via classical model diagnostics (e.g. residuals and retrospective patterns), and on their ability to predict (here observations are removed and the models predictions are compared to the actual observations). The relevant question is if the simple model for linked stocks can perform similarly (or close to similarly) to the full multispecies models, which demands more data and are more difficult to operate.

4.2.4 Data-poor assessment of round goby

Round goby has since its first introduction to the Baltic Sea spread and proliferated along the coastline, and now occurs in high abundance in several areas. PANDORA will develop a data-poor assessment of round goby, to provide information for a potential future advice on quota for this species.

4.2.5 Estimating total number of liver worm in cod

The only Baltic country that (since 2011) routinely (i.e. as part of their sampling program) has assessed individual cod livers for liver worm is Poland. These investigations are ideal to follow the status of liver worm in cod, but they are delicate, time-consuming and expensive, and cannot be carried out on-board the vessel. A different, more cost-efficient but also less precise way to assess nematode intensities in cod livers has been implemented during recent years on monitoring surveys in some Baltic Sea countries, the so-called ‘liver category’ method. The ‘liver category’ method assigns a category between 0 and 3, depending on the number of visible nematodes on the surface of the organ, with category 0, 1, 2 and 3 corresponding to counts of 0, 1-10, 11-20 and >20 nematodes, respectively. This method was initiated in the Baltic Sea in 2011 by Thomas Lang (Thünen Institute of Fisheries Ecology, Bremerhaven, Germany), and has since then been implemented in the German and Danish BITS (Baltic International Trawl Survey) cruises. Sweden is currently testing the method on their cruises. Notably however, the liver category assigned to the livers of Baltic cod is based on the number of worms visible on the liver surface. Most – in some cases all – nematodes often reside in the liver parenchyma, and are thus not visible on the liver surface. It is thus imperative to develop an estimation tool that can convert the assigned liver category to an estimated mean number of worms in the entire liver. PANDORA will develop such an estimation tool, including also effects of area and season.

4.3 Bay of Biscay

The Bay of Biscay case study focusses on one species of teleost fish, the blackspot sea bream (*Pagellus bogaraveo*) and the assemblage of skates (Rajidae). The blackspot seabream used to be a major species in the landings from the Bay of Biscay up to the early 1980s (Lorance, 2011). Several marine fish stocks have strongly declined during the 20th Century as a consequence of overfishing, amongst which several skates (Quéro and Cendrero, 1996; Dulvy et *al.*, 2014). In the past two decades management measures aiming at halting such declines and restoring skates stocks to higher levels have been introduced. In the Bay of Biscay, these include EU TACs for the blackspot seabream since 2003 and for the skate assemblage since 2009. Note that the modelling work on tuna, as mentioned in the application under Bay of Biscay, is passed on to the Mediterranean, where Bluefin tuna spawn.

Existing knowledge relevant to the needs – The Bay of Biscay

4.3.1 Blackspot seabream

Since the collapse in the early 1980s, the blackspot sea bream stock has only been exploited as a minor bycatch in the Bay of Biscay (ICES Subarea 8). Up to the mid-70s, more than 15 000 tonnes of blackspot sea bream were landed annually in Spanish and French ports. The history of the fishery collapse was described using time-series of landings since the 1900s (Lorance ,2011). The species was shown to be only able to sustain moderate fishing mortality because of its protandrous hermaphroditism, where a cohort comprise more than 50% of mature females from age 8 only, according to available growth and maturity data. In the Bay of Biscay, the fishing mortalities of the main demersal stocks (hake, anglerfish, sole) were in the range 0.2-0.5 from the 1980s to the 2000s. It was shown that a fishing mortality of 0.2 reduces the spawning stock biomass of females to less than 20% of unexploited levels. A population dynamics model assuming a stock-recruitment relationship fitted to landings explained the collapse with estimated fishing mortalities never exceeding 0.5.

Current landings are less than 1% of the historical catch level, and the stock remains at low level. Nevertheless, there are anecdotal reports of an increase in abundance, with aggregations of several tonnes being encountered by fishing vessels.

Pagellus bogaraveo is a male-first sex-changing species (protandric hermaphroditism). Sexing and staging the species is considered problematic because macroscopic scales are not validated with microscopic observations. The species is considered slow growing, a review of available growth curves ad length at age data was carried out by Lorance (2011). Like several authors from the 1960-1970s, Gueguen (1969) estimated age from scales. Recent length-at-age data are scarce but ICES defined a protocole for estimating age from otoliths (ICES, 2019b) and reported a maximum age of 20 years. The natural mortality was assumed to 0.2 by Lorance (2011) based upon the age of the oldest fish sampled and the empirical relationship $M=4.22/t_{max}$, (Hewitt and Hoenig, 2005).

4.3.1.1 Spatial distribution of juveniles

Juvenile blackspot seabream used to occur along the all Bay of Biscay coast, western Channel and South Ireland. Priol (1932) reported that the small fish known as "pirono" along the coast of Brittany was the juvenile of the blackspot seabream and fishing for pirono was one of the main entertainments at the coast during holidays. This author further reported that trawl catches of blackspot seabream came from smooth seafloors, as only those were practicable by trawls at the time; juveniles were found only on rocky seabeds. The occurrence of juveniles only on rocky areas should be considered as a reliable habitat preference, as coastal angling was spread everywhere. Recent data from the Azores, where coastal habitats were classified in 5 categories, showed that the highest catch rates of juvenile blackspot seabream are obtained by anglers in harbour habitats followed by beach, rock and cliff (Pinho, 2015). Therefore recent observations support a preference for hard grounds although catch on beach also exist.

Priol (1932) reported further abundant catch of juvenile blackspot seabream of 16 cm modal length at two sites along the coast of Southern Brittany as well as catch of young of the year of 3 cm or less in push nets in August and September. Although the level of the past abundance and landings of juvenile blackspot seabream was not quantified, Priol reported processing trials to canning small seabream like sardines. This suggests that large quantities were landed. Juvenile seabream were also used for bait for sea bass and conger fishing. Uses for bait, with targeted fishing and equipment to keep it alive, were also reported to exist until the 2010s in the Azores for live bait fishing for tuna and other species (Pinho, 2015).

In the English Channel, the species used to be abundant at the coast of the western English Channel and decreasing from the West to the East (Desbrosses, 1932). On the English coast, juveniles from 20 to 25 cm occurred along Cornwall and Devon and were fished from coastal angling (Desbrosses, 1932). Along the French coast of the Channel, juveniles were fished from spring to autumn along Northern Brittany up to the Normand-Breton Gulf. In some years, these juvenile were observed in the Eastern Channel up to Le Havre and Fécamp (close to longitude 0). During the same period juveniles were abundant at the French and Spanish coasts in most of the Bay of Biscay and larger fish were caught throughout the Bay of Biscay shelf by commercial fisheries.

In recent years, there are anecdotal records of occurrence of juvenile blackspot seabream in the Bay of Brest and the Bay of Douarnenez to the west of Brittany. The species occurs within the area of the Parc Naturel Marin d'Iroise (PNMI) and is mentioned in the management plan of this MPA (PNMI, 2010). In the 2000s, blackspot seabream smaller than 30 cm was occasionally sold on coastal retail markets. Marketing such small fish is now forbidden. On the Spanish coast, blackspot seabream occurs along the Cantabrian Sea coast. No publication or data at high resolution of occurrence or abundance has been found. Juveniles are also thought to occur along most of the Cantabrian sea coast, the distribution is expected to be patchy.

4.3.1.2 Distribution of spawning aggregations

There is no recent data on the distribution of spawning aggregation in the Eastern Bay of Biscay (ICES 8.a-b). Most probably, the blackspot seabream spawns over the shelf and upper continental slope and larvae are advected to coastal areas. Although some large fish occur sporadically at the coast, spawners do no aggregate in coastal areas. Observations from the Azores indicate that larvae are transported to the coast; juveniles live in coastal nurseries before migrating to offshore and deeper waters (Pinho, 2015). In this region, large adults are exploited on isolated seamounts and juveniles are only found at the coast of islands.

The only published account of eggs and larvae of the blackspot seabream in ICES divisions 8ab (continental shelf to the west of the French coast) reported on 12 larvae and 20 eggs sampled during ichthyoplankton surveys in front of the Gironde estuary from 1964 to 1966 (Arbault and Boutin, 1969). These authors did not report eggs and larvae elsewhere although their sampling covered all the Bay of Biscay, including the Cantabrian Sea (Division 8c). More recently, egg and larvae of the blackspot seabream were found in zooplankton samples collected in the central Cantabrian Sea at the longitude of about 5.7 °W in summer 2008 and in winter 2012 in Galician waters between longitude of 7.6 and 9.7 °West, i.e. to the West of ICES Division 8.c (Rodriguez et *al.*, 2011, 2015). Blackspot seabream larvae represented 0.4% of all fish larvae counted excluding the most abundant pelagic species (sardine, Mackerel and blue whiting).

Overall, spawning occurs over the offshore shelf and/or at the shelf break. Current spawning areas might be mostly in the Cantabrian Sea (where larvae were found in recent ichthyoplankton surveys) and to the West of Brittany. At the current low stock level, abundance and therefore spawning in more northern areas, e.g. the Celtic Sea and Western Channel might be insignificant.

4.3.1.3 Surveys

Although the stock area used to extend to the south and west of Ireland and the Irish Sea, blackspot seabream have not been caught in the Irish Ground Fish Survey (IGFS) in significant numbers. Numbers caught in the French EVHOE covering the southern Celtic Sea and Bay of Biscay and the Spanish DEMERSALE in the Cantabrian Sea (ICES Division 8a) are also very low with zero catch in the EVHOE survey in 2018, for example. However occasional large catch may occur in survey and a catch of 400 kg was made in the 2016 survey. Before the stock collapse, the species was caught in higher numbers. Two French surveys were carried out in 1973 and 1976. In these surveys, the species was then caught over most the Bay of Biscay shelf in 25% and 55 % of the hauls respectively in 1973 and 1976 (Quéro et *al.*, 1989; Figure 4.3.a). Since the start of the current EVHOE survey time-series in 1987, it has always been caught in less than 5% of the hauls, some years not at all. As a consequence, survey data are currently not informative about the year-to-year variations of the stock level but provide confirmation that the current stock abundance is low compared to historic levels. The species distribution in the two surveys from the 1970s is also of interest as the 1973 survey was carried out in November-December and the 1976 survey in May. In May the species was caught offshore and was absent at the coast while in November-December is occurred in coastal hauls and was rarer near the continental slope. This probably reflect the migration cycle where blackspot seabream arrives on the shelf in divisions 8ab in April-May, comes may inshore in summer and leave shelf areas in winter to overwintering along the continental slope and in the Cantabrian Sea (Desbrosses, 1932, Guéguen 1974).

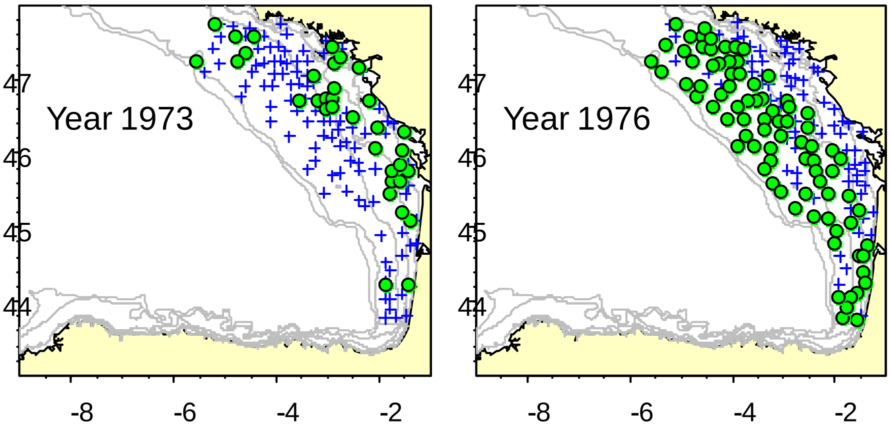


Figure 4.3.a. Occurrences of Red blackspot sea bream in surveys carried out in 1973 and 1976 and in the EVHOE survey in 2015 and 2016 (redrawn from ICES, 2019a)

4.3.1.4 Management

In 2003, the TAC for blackspot seabream in ICES subareas 6, 7 and 8 was set to 350 tonnes and then reduced to 130 tonnes in 2018. Whereas, the decline in landings in the 1970s-1980s reflected the stock collapse, landings in recent decades have been constrained by the TAC. Since TACs became constraining, the management at fisheries levels, have been aiming at preventing the targeting and incidental catch of blackspot seabream aggregations. For example, the Marine Stewardship Council (MSC) certification of the sardine fishery includes the ban of catching blackspot seabream since 2009 (Bureau Veritas, 2010).

4.3.2 Skates

The two main skate species reported in recent landings from the Bay of Biscay are the cuckoo ray *Leucoraja naevus* and the thornback ray *Raja clavata* (ICES, 2018). These two species make more than 90% of total landings of all skates from the Bay of Biscay. The former is a small bodies skates occurring of the offshore shelf. It is a bycatch of trawl fisheries. The latter is a larger bodied species, which occurs from coastal waters including estuaries and rocky shore to upper the slope continental slope. The thornback is also a bycatch of trawl fisheries and some targeting exists in coastal fisheries. Other species occurring in the Bay of Biscay are the blonde ray (*Raja brachyura)*, a coastal species rarely caught by more than 100 m depth, the undulate ray (*Raja undulata*) a costal species, rarely caught in waters deeper than 30 m in the Bay of Biscay, the small eyed ray (*Raja microocellata*) a coastal species locally present along the coast, the spotted ray (*Raja montagui)*, a small bodied species occurring from the coast to the slope, and two larger offshore species: the sandy ray (*Leucoraja circularis)* and the shagreen ray (*Leucoraja fullonica*). All these height species are reported in recent landings from the Bay of Biscay and are caught in the EVHOE survey, although some in very small numbers. Lastly, like in other areas worldwide, populations of large elasmobranch declined during the 20th century (Quéro & Cendrero, 1996; Dulvy et *al.*, 2014). The skates species involved in this decline in the Bay of Biscay include at least, the white skate (*Rostroraja alba*), the blue skate (*Dipturus batis*) and the flapper skate (*Dipturus intermedius*). At the North east Atlantic scale all available data suggest that these three species are at a low or very low level in recent decades compared to historical level. Their past abundance in the Bay of Biscay is poorly known, but they contributed significantly to landings in the 1950s to 1970s (Letaconnoux, 1948; Du Buit, 1974).

In addition to published studies, biological data, including length distributions, sex ratio, maturity ogives have been collected in projects carried out in the 2010s, mainly two projects studied skates populations in the Bay of Biscay RECOAM and raieBECA. PANDORA is not aware of published results of these projects, reports are in French and data are not publicly available. In recent years more data and spatial dististribution and length distribution have been collected in on-board observtion. Age composition of the catches is not known and there is no length-at-age data for the Bay of Biscay. Except in recent years, length compositions are also limited to survey data. The spatial distribution of species is known from the EVHOE survey.

The biology and life history traits relevant to stock assessment of the lesser abundant species is poorly known. For example, a search for *Leucoraja circularis* and *L. fullonica* in Web of Science (consulted on 11.09.2019) returned 13 articles. These articles were on taxonomy and occurrence records (7 articles), barcoding or molecular identification (3), length-weight relationships (1), heavy metals (1) and multispecies modelling (1). There are no estimates of the length-at-maturity (50% maturity) of these two species and to carry out population modelling using production models, using a production model we inferred the intrinsic growth rate from the maximum length of these species using published relationships (Le Quesne and Jennings, 2012).

4.3.2.1 Migration and population connectivity

There is no published study on nurseries and spawning areas of skates in the Bay of Biscay. Tagging have been carried out in RECOAM and raieBECA projects and these suggested migrations distance in the order of 100 km (Anon., 2014; Stéphan et *al.*, 2014) but results remained in grey literature. The population structure and genetic diversity was studied in the thornback ray and suggested little or no genetic differentiation over the European Atlantic shelf (Chevolot, 2006). A simulation study using migration distances relatively consistent with observed tagging-recapture data, showed that there are more demographic populations (i.e. stock units) that genetic populations (Marandel et *al.*, 2018). Depending on the simulated migration scenario the population of the Bay of Biscay was either independent or demographically connected to one adjacent population and it was no or slightly genetically differentiated from other thornback ray from the European Atlantic shelf. Population structure and migrations of the offshore species (*Leucoraja* spp. and *Dipturus* spp.) are not known.

4.3.2.2 Surveys

The main survey of interest to skates in the Bay of Biscay are the French EVHOE in divisions 8ab survey and the Spanish Demersale survey in Division 8c. These survey provide biomasss indices for the Thornback ray and the cuckoo ray. Other rays are caught in two small numbers to obtain reliable yearly indices and year-by-year data, however, data aggregates over several years may be informative on spatial and depth distribution, sex-ratio, length distribution. Some other surveys in coastal and estuarine habitats may include additonal data but these a re have not been used so far for stock assessment of population trends purposes.

4.3.2.3 Commercial catch

ICES has compiled international landings data of skates (ICES, 2018). This effort appears to be challenging and various issues are found in the data (e.g. species misreporting, confusing vernacular names), further ICES workshops are planned to improve the data where possible. The main reason for the reporting of skates landings by family rather than by species is that the price depends on size (higher price per kg for larger fish) and not on species. Estimating discards is also challenging. First, skates are overall observed in moderate to small numbers in on-board observations, making the raised estimates of discards more uncertain than for major teleost stocks. Because The discarding rate varies with species because a higher proportion of the catch of small-bodied species is discarded. In particular in recent years, when the TAC became constraining fishers have landed larger fish only.

4.3.2.4 Stock assessment

Data on all skates stocks are mostly insufficient for stock assessment purposes because until 2009 landings were not reported by species but as "skates and rays". The situation is particularly poor for the Undulate ray which is mostly caught by small-scale coastal fisheries owing to its spatial distribution. These species was banned to landings from 2009 to 2014 and a small TAC to allow for bycatch only was open in 2015. In addition of being not species-specific, landings from small-scale fisheries were probably not reliable historically. As a consequence, unlike for other species no landings data (even uncertain) before the ban for landings in 2009 is available.

ICES provided catch advice for four stocks (Thornback ray in Subarea 8, Spotted ray in Subarea 8, Cuckoo in subareas 6 and 7 and divisions 8abd, cuckoo ray in Division 8c) based on the ICES precautionary approach using survey trends (ICES, 2016). One or two surveys out of the Spanish Demersales, the French EVHOE and the Irish IGFS are used to estimate the stock trend. The stock units used for these assessments are based on the spatial distribution of survey and commercial catches were breaks in the geographical distribution of occurrence are considered as boundaries between units.

The long-term population trajectory of the thornback ray of the Bay of Biscay was investigated by fitting a bayesian state-space biomass production model with a Schaefer production function to a hypothetical catch time series for the period 1903-2013 and survey catches for 1973, 1976 and 1987-2013 (Marandel et *al.* 2016). This modelling suggested that the stock biomass is currently below possible MSY levels. However, results cannot used for ICES advice and management as several assumptions were necessary to create the long catch time series and to define informative priors, notably for the intrinsic growth rate.

4.3.2.5 Management

Because of their rarefaction, the white skate, blue skate and flapper skate are "prohibited species" in regions of EU waters where they occur. This prohibition status implies that when accidentally caught these species, species shall not be harmed and individuals shall be promptly released. Other skates species in the Bay of Biscay are subject to a TAC for "skates and rays" in ICES subareas 8 and 9 (note that in these subareas shelf and slope areas at depth where the cited species may occur are fully included in EU waters). The TAC regulation requires that catches of cuckoo ray, blonde ray and thornback rays shall be reported separately. Undulate ray is subject to species specific TAC, separately for ICES subareas 8 and 9. The TAC for undulate ray in Subarea 8 is however not aligned on ICES stocks units where two distinct stocks are considered in divisions 8ab in the one hand and Division 8c in the other hand. Lastly, the requirement for species-specific reporting of landings of cuckoo ray, blonde ray and thornback rays as well as undulate ray, implies that the other four species may still be landed as "skates and rays". In practise, most fish auction markets are now equipped with species identification sheets and employees have been trained to species identification. In particular the close monitoring of undulate ray, which landings are restricted to vessels holding a licence, have encouraged fisher to sort skate catches by species (and to be able to discards fish that they are not allowed to land).

Activities in PANDORA to fill the gaps (or needs) – Bay of Biscay

4.3.3 Blackspot seabream

In the context of the landing obligation, the blackspot seabream is a potential choke species because a single catch event may overshoot the national quota for vessels of Countries other than Spain (for which quotas in 2019 and 2020 and 84 and 94 tonnes respectively. Quotas of other countries, Ireland, France and UK are in the order of magnitude of one single incidental catch of a pelagic or bottom trawl haul. Before the landings obligation, big incidental catches were discarded, with the landings obligation such catches might imply the closure of the major fisheries. Although, at the low stock level the fastest rebuilding would be achieved with a zero fishing mortality, a complete absent of bycatch is not realistic. Therefore in the context of the landing obligation, it seems necessary to allow a level of unavoidable bycatch to be landed. Otherwise any catch of the species implies the closure of the fishery. This is particularly crucial as the TAC level is on a decreasing trajectory over time.

In PANDORA acoustics surveys aiming to estimate the local biomass of blackspot seabream are being carried out. The main objective is to estimate the biomass and to produce a survey protocol that can be realized by the industry. These surveys cover a few small area to the North of ICES Division 8a, where bycatches are the most frequent. During surveys, handline fishing operations are made to identify species producing echoes in the acoustic backscatter. A subsample is collected for biological data including length-weight relationship, sex and maturity-at-length, stomach contents, otoliths and scales for age readings, tissue samples for genetics, stable isotopes and fat content.

4.3.4 Skates

Acitivities in PANDORA to fill the knowledge gaps include multispecies modelling of the skate assemblage in the Bay of Biscay; survey data analyses to derive long-term trends; close-kin mark-recapture (CKMR, see e.g. Skaug, 2011; Bravington et al., 2016) to estimate to abundance of the thornback ray and age estimation of a small sample of the thornback ray. The multispecies modelling addresses the aspect of aggregated landings data for all skate species together and derives stock trajectory for the main species in recent catch in the Bay of Biscay. The analysis of survey data aim at estimating trends in occupancy by species. The CKMR aspect is carried out as finalizing work in the four year GenoPopTaille project funded by the French national agency for Research (ANR). The age estimation is carried out in collaboration with the SUMARIS project as as research to develop method for age estimation of skate species.

4.4 The Mediterranean Sea

In this section we refer to five species in the Mediterranean Sea, 3 demersal species and 2 pelagic species: European hake (*Merluccius merluccius*), Red Mullet (*Mullus barbatus*), Deepwater pink shrimp (*Parapeneus longirostris*), Albacore (*Thunnus alalunga*), Atlantic bluefin tuna (*Thunnus thynnus*). For each species the areas considered are:

1. European hake (Merluccius merluccius): Aegean Sea and Western Mediterranean
2. Red Mullet (*Mullus barbatus*): Aegean Sea and Strait of Sicily
3. Deepwater pink shrimp (*Parapeneus longirostris*): Strait of Sicily
4. Albacore (Thunnus alalunga): Western Mediterranean
5. Atlantic bluefin tuna (Thunnus thynnus): Western Mediterranean

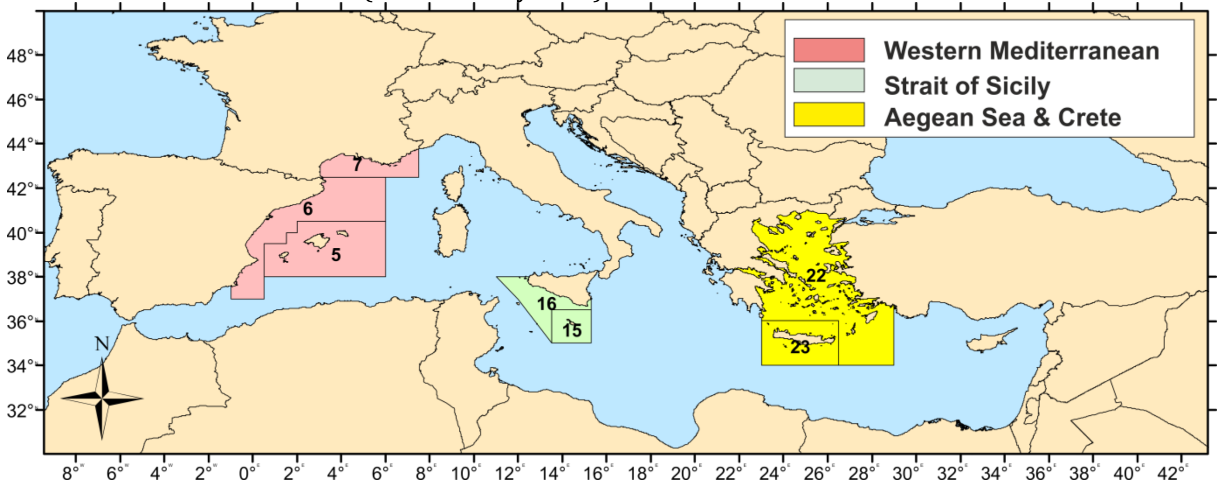


Figure 4.4.a. An overview of the regions covered in the PANDORA project.

Existing knowledge relevant to the needs- The Mediterranean Sea

4.4.1 *Merluccius merluccius*, European hake

General status European hake, *Merluccius merluccius* L., 1758, is a demersal fish species distributed throughout the Mediterranean Sea and in the eastern Atlantic from the Barents Sea to the Mauritanian coast. In the Mediterranean, hake is a species of high economic importance as it is one of the main target species of most bottom-trawl fisheries (Papaconstantinou & Farrugio, 2000). Genetic studies have shown that a clear genetic difference exists between the Atlantic and the Mediterranean hake (Pla et al., 1991; Roldan et al., 1998), a finding also supported by morphometric studies (Inada, 1981; Lo Brutto et al., 1998). Recent research goes beyond large genetic differenciation using neutral genetic markers and found fine-scale population structure using information adaptive markers (Milano et al. 2014). Besides considerable efforts delineate stock boundaries in the Mediterranean Sea (e.g. STOCKMED), recent evidence suggest a more complex popuations structure and transboundary populations over the current managent areas supported by alternative methods (e.g. oceanographic dispersion models) in the western Mediterranean (Hidalgo et al. 2019a). Beyond current needs to curb overexploitation in the whole Mediterranan, there is a lack of biological knowledge for stock assessment.

Hake in the Aegean Sea In the Aegean Sea, hake is generally more abundant in the 100–450 m bathymetric zone (Tserpes et al., 2008). Juveniles seem to be mostly distributed over the continental shelf, as it happens all over the Mediterranean. An increasing trend was evident up in the mid 2000's in the examined abundance indices and this finding was in agreement with the reported total catch levels of hake of the Greek fisheries that showed a similar trend (Tserpes et al., 2007). Probably, the progressive reduction of the total Greek fleet capacity, accompanied by the increase of the trawl-net mesh size over the past decades, have resulted in stock level increases that are reflected in the MEDITS survey abundance indices. Environmental changes such as water temperature increase due to global warming may have also favored hake recruitment, and consequently stock size increase.

Hake is an important commercial species in the Greek small scale fisheries sector, as well as the industrial bottom trawl fleet, reaching as much as 10% of total catches. The stock is exploited by bottom trawlers and various artisanal fisheries using gillnets and demersal longilnes but the majority of landings (~60%) is coming from bottom trawlers. Since 2009, fishing mortality (F) and spawning stock biomass (SSB) were considered to be outside optimal levels and currently the stock is considered to be overfished (Anonymous, 2017; GFCM, 2017) with a B/Bmsy < 1 and F/Fmsy > 1 (Figure 4.4.b). As a result, a national multi-annual management plan targeting fisheries exploiting the hake stock has been put in place since 2014 (Anonymous, 2013).

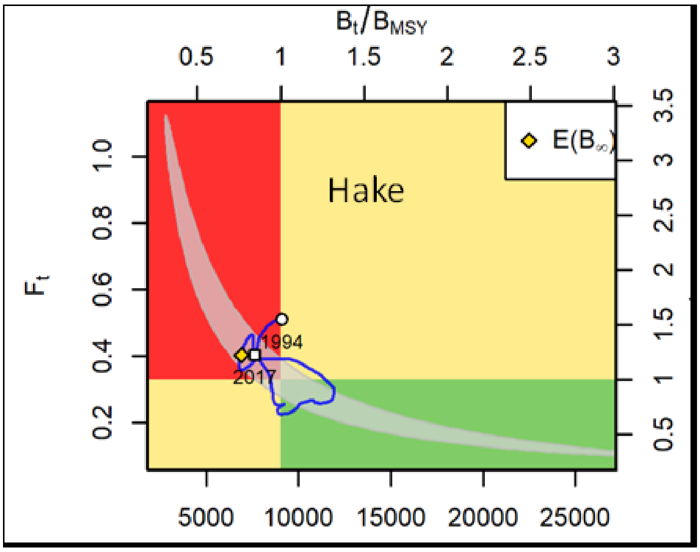


Fig. 4.4.b. Kobe plot depicting evolution of Aegean Sea hake stock status .

Hake in the Western Mediterranean This is the most important factors that can be included in the regular assessment and management:

- Environment-dependent estimates of recruitment.
- Improve the role of density-dependence.
- Time-varying information to improve natural mortality vector.
- Improve the knowledge of ecological and environmental processes spatially structured to inform management measures.

- A scientifically-based definition of stock boundaries, but also intra-stock structure.

Several environmental processes in the Western Mediterranean can be included in stock-recruitment relationships. The most relevant are: i) larval dispersal and self-recruitment success affecting the first weeks-months of life and, ii) the strength of winter conditions in the NW Mediterranean that drives numerous processes over the first six months of life (Fig. 4.4.c; Hidalgo et al 2011, 2019a).

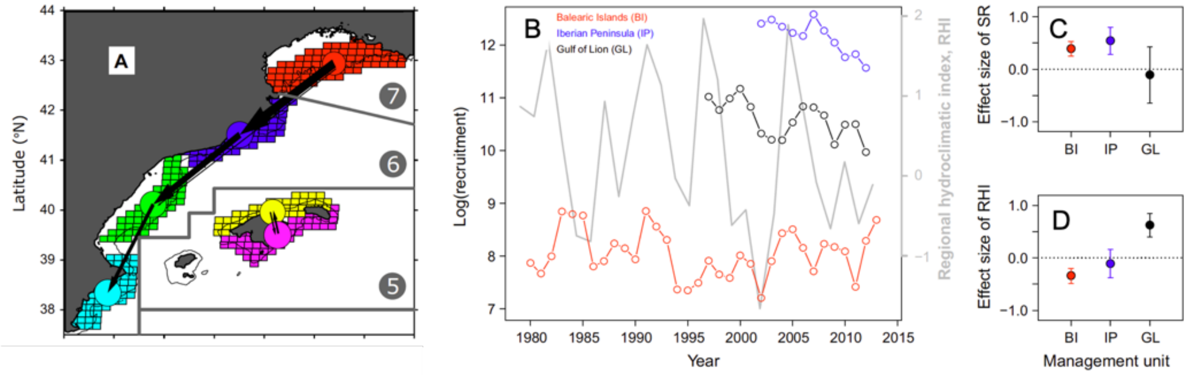


Fig. 4.4.c A. Estimates of hake larval exchanges (arrows) and retention (colored circles) among the different subpopulationsof hake. In general term, GSA 6 and 7 have a unique and independent dynamics of GSA 5. B. Time-series of annual recruitments from fisheries assessment in the three management units (Balearic Islands, BA, red colors; Iberian Peninsula, IP, blue colors; Gulf of Lion, GL, black colors) and the regional hydroclimatic index (RHI, gray curve). Strength of connectivity (self-recruitment, SR) (C) and hydroclimate (RHI) (D) effects on recruitment for each management unit using a global statistical model (adapted from Hidalgo et al. 2019a).

The role of density dependence (DD) is, to date, a black box for the European hake, since for most areas large individuals (e.g. spawners) are not captured - underestimating both spawning potential and density-dependent control of the populations. Recently, Hidalgo et al. (2019b) showed that DD affected growth and indirectly survival between recruits and juveniles (Figure 4.4.d). However, it is still not resolved at which scale scale and on which ontogenetic stage DD affect recruitment success and population growth on the European hake (Andersen et al 2017).

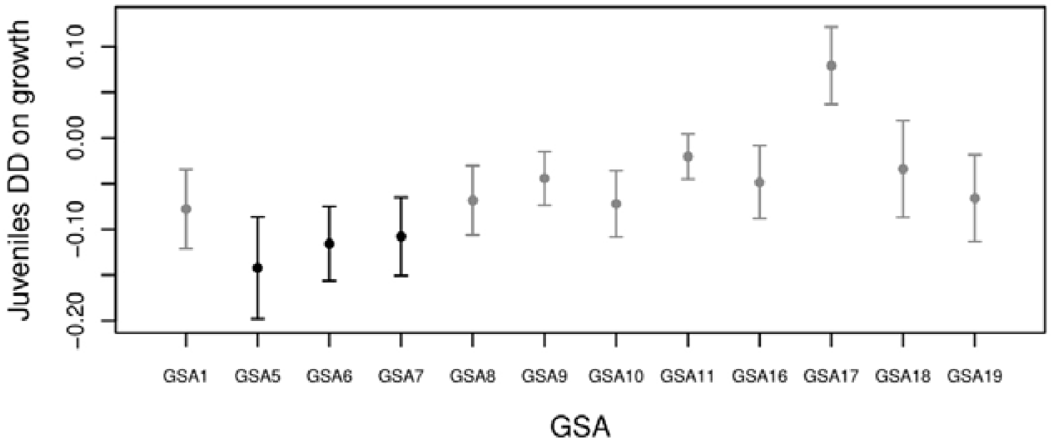


Fig. 4.4.d. Density-dependent effect of juvenile growth (from recruits to juveniles). Black symbols represent significant effects (p<0.05) and grey symbols non-significant effects (p>0.05) for 12 European GSA in the Mediterraean Sea. Note that the three significant areas are those in the Mediterranean Sea (adapted from Hidalgo et al. 2019b).

Survival, understood as natural mortality in terms of fisheries assesement, is also a critical ecological process commonly omitted (i.e. temporally invariant) in regular assessment. Recent research show that in the Western Mediterranean survival from recruits to juveniles is highly dependent on the size of recruits using survey data (Hidalgo et al. 2019b). This opens new avenues to approach dynamic parametrization of natural mortality. Other processes might be considered also, such as body condition which as been demostated to have a potential role in the recruitment dynamics of hake in the GSA 6 (Ibarian peninsula) (Figure 4.4.e, Ordines et al. 2019).

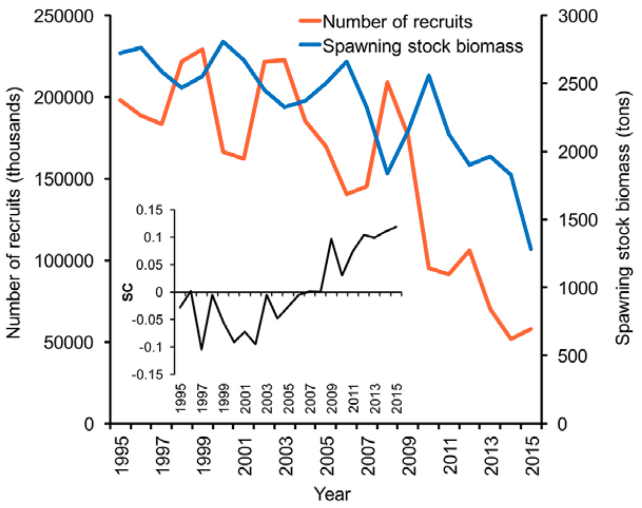


Fig. 4.4.e. Hake recruitment and spawning stock biomass trends reported for the GSA 6 along with the trend of the mean annual values of hake recruit somatic condition (SC) in GSA 6 (inset)(from Ordines et al. 2019).

The Mediterranena Sea is a regional sea in which most ecological and environmental processes are spatially structured. The same occurs at population level, and in particular for European hake in the Western Mediterranean, including nursery areas (Druon el al. 2015), key retention (Hidalgo et al. 2019a) and feeding areas (Ordines et al. 2019). This is also aligned with the current strong demand to provide a biological meaningfull definition of the stock boundaries as well as modeling tools that allow for intra-stock spatial complexity, which is known as one of the main source of bias of biological reference points (Goethel and Berger 2019).

4.4.2 *Mullus barbatus*, red mullet

General status of Red Mullet. Red mullet is distributed in the Eastern Atlantic, along the European and African coasts from the North Sea and England to Senegal and in the Mediterranean and Black Sea (Fischer et al., 1987). It is a benthic species, frequently found on muddy bottoms at depths between 5 and 250 m (Voliani, 1999) with the highest concentrations on the continental shelf (10-150 m). Red mullet is one of the most important species for Mediterranean coastal fisheries. The total estimated landing in Mediterranean and Black Sea was 16000 ton in 2016. It is exploited by otter trawlers and artisanal vessels using trammel nets and gillnets (Voliani, 1999) representing the main component of the trawl catch on the deep shelf (50-150 m depth) along with *Merluccius merluccius* (European hake), *Pagellus spp.* (seabreams, pandoras), horse mackerels (Trachurus spp.), *Octopus vulgaris* (common octopus), *Sepia officinalis* (common cuttlefish), *Eledone spp.* (horned and musky octopuses), and *Lophius spp.* (anglerfish).
Genetic studies showed the occurrence of single demes locally and partially separated, in which individuals coming from different areas (e.g. Gulf of Lions, Tyrrhenian Sea, Strait of Sicily, Ionian Sea) cannot be considered as belonging to a single large homogeneous population (Maggio et al., 2009). However, the results of the EU project STOCKMED supported the hyphotesis of three main stock units in the region: Western basin-Ionian Sea, Adriatic-Aegean Sea, Levantine Sea. The ongoing stock assessments are generally carried out at the GSA spatial scale in the Western and Central Mediterranean and joining GSA 17 and 18 in the Adriatic Sea. The issue of stocks delimitation for management purposes of red mullet and other commercial species is therefore still discussed and the MED_UNITs EU project has recently been granted to provide new knowledge on the subject. Most of the assessed stocks are overfished, with a few exceptions.

According to Voliani (1999), the maximum total length (TL) of red mullet in the Mediterranean is 28–29 cm for females and 23 cm for males, however specimens from 10 to 20 cm TL are generally found in the commercial fisheries landings. In the northern sector (GSAs 15 and 16); the observed maximum length is 25 cm TL for females and 25 cm TL for males. The species is fast growing and reaches more than half of its total size during its first year of life (Voliani et al., 1999).

Red mullet reproduction in the Strait of Sicily occurs near the coast, from May to June–July (Gharbi and Ktari, 1981; Levi et al., 2003). Eggs, larvae and post-larvae up to 30–35 mm, of *M. barbatus*, are pelagic and live in the surface waters. According to Sabatés and Palomera (1987), larvae are found only in surface waters (0–1.5 m depth), mainly in areas influenced by river outflow. Larvae were found in the Mediterranean mainly between June and July (Sabatés and Palomera, 1987). Juveniles up to 4–5 cm TL are pelagic, have a blue livery and may be collected several miles off the coast. Above this size, juveniles move to the coastal areas and become demersal. Recruitment is massive and take place in summer, followed by a gradual dispersion towards deeper waters (Lo Bianco, 1909; Voliani, 1999).

Red Mullet in the Aegean Sea. In the Aegean Sea red mullets differentiate by size as well as areas. Despite their distribution overlap, depth and temperature selection differ considerably between the size classes. In general, fish size increased with depth, and smaller individuals tended to occur in shallower and warmer water. Abundance increased in mid-shelf waters during spring, indicating a movement across the shelf towards deeper water, associated with the spawning behaviour of the species. The factor controlling the timing of that movement to deep waters seems to be the maturity of individual fish (Machias & Labropoulou, 2002). Conspicuous morphological differences between the North and South Aegean sub-populations is attributed to the diverse sea bottom geomorphology and large scale oceanographic features (Mamuris et al., 1998)

Red mullet is exploited by bottom trawlers and various artisanal fisheries using gillnets but the main bulk of catches is coming from bottom trawlers over 18m of length. The Greek bottom trawl fishery has multi-species characteristics and captures more than 100 commercial species. However, red mullet is one of the most important targets. All assessment models predict that the Aegean red mullet stock is currently being fished below Fmsy. Moreover, fishing mortality shows a declining trend since 1996, and current F/Fmsy is below 1 (Figure 4.4.f) (STECF, 2017).

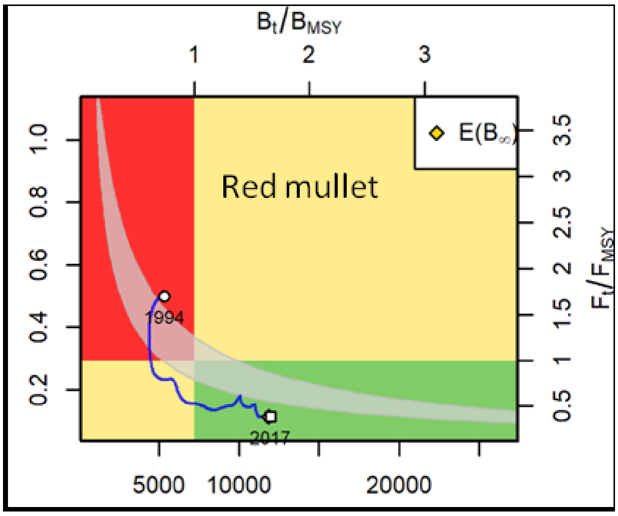


Fig. 4.4.f. Kobe plot depicting evolution of Aegean Sea red mullet stock status .

Red Mullet in the Strait of Sicily. In the GSA 12-16 (Southern coast of Sicily, Tunisia coasts, Malta shelf: SoS) red mullet is fished almost exclusively by trawlers operating on shelf bottoms. The landing due to artisanal vessels is low. The total average annual landing in GSA 16 in the period 2006-2017 was about 568 tons with a decreasing trend (Figure 4.4.g), Milisenda et al., 2018). Numerical simulations revealed a weak degree of connectivity between the Sicilian–Maltese and the African sides of the SoS. Furthermore, red mullets around Maltese Island was weakly connected with those living off the Sicilian coast. Based on this new information during the last GFCM benchmark assessment red mullet inhabiting the area was assessed considering 3 stocks distributed respectively in GSAs 12-14 (Tunisia), GSA 15 (Malta), GSA 16 (Sicily). The stock along the south coast of Sicily (GSA, 16) and Tunisia (GSA 12-14) are in overfishing, Connectivity between spawning and nursery areas of red mullets in the Strait of Sicily were simulated using a physical oceanographic model (Gargano et al., 2017).

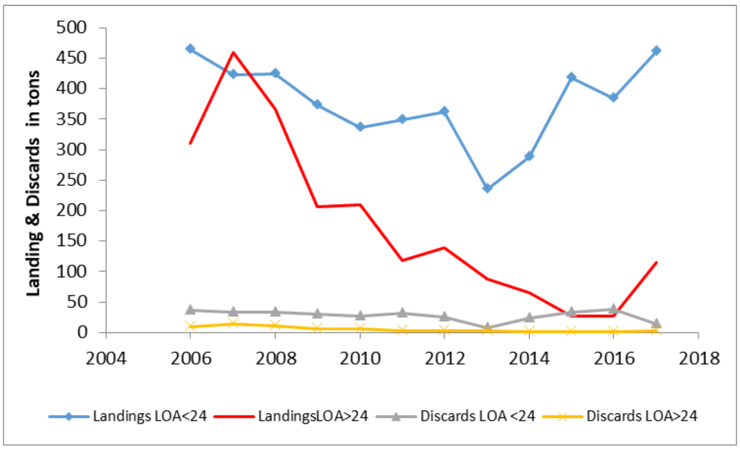


Figure 4.4.g. Landings and discards in tons of red mullet from 2006 to 2017 in the south of Sicily(GSA 16).

4.4.3 *Parapeneus longirostris*, Deepwater pink shrimp

General status of deepwater pink shrimp. Deepwater rose shrimp (DPS), *Parapeneus longirostrus*, Lucas 1847, is a large decapods crustacean. DPS is distributed in the eastern Atlantic from Angola to Portugal and in the West Atlantic from Guyana to Massachusetts. It inhabits the entire Mediterranean (Fisher et al., 1987). Deepwater rose shrimp can be found at depths between 20 and 700 m, but it is common and abundant on sandy-muddy bottoms between 100 and 400 m (Bombace, 1972). After spawning, the planktonic larval phases (nauplius, zoea and mysis) develop; the postlarva, similar to adults, reaches the sandy-muddy bottoms on the continental shelf and begins the bentho-pelagic cycle (Heldt, 1938). In the Mediterranean Sea, pink shrimp is fished only with bottom trawl nets. Although the biggest specimens have greater commercial value, the mean-sized shrimps over 20 mm carapace length are marketable.
Genetic studies have shown a high genetic variation among the populations of the Mediterranean sea. Data especially revealed the presence of a gradual discrepancy along a west–east axis (Lo Brutto et al., 2013). *P. longirostris* is a warm-temperate and fast growing species with a life cycle of 3-4 years. It reaches the highest biomasses in the south and central Mediterranean Sea decreasing along a south–north gradient. In the last 10 years the species is showing a fast northward expansion and its biomass is increasing in relation to the ongoing trend in water temperature (Colloca et al., 2014). DPS is now one of the most important resources for Mediterranean bottom trawlers exploiting deep shelf and upper slope fishing ground and its annual landing was about 15.000 tons in 2017 (source FAO FIGIS, www.fao.org/figis).

Deepwater rose shrimp in the Strait of Sicily. The stock in the region is exploited by Italian, Tunisian, Maltese, Libyan and Egyptian trawlers. The annual landings range between 7000 and 10000 tons and the stock is regularly assessed by the GFCM working group on stock assessment (Figure 4.4.h). The most recent assessments indicate overfishing, with the spawning biomass fluctuating without a clear trend.

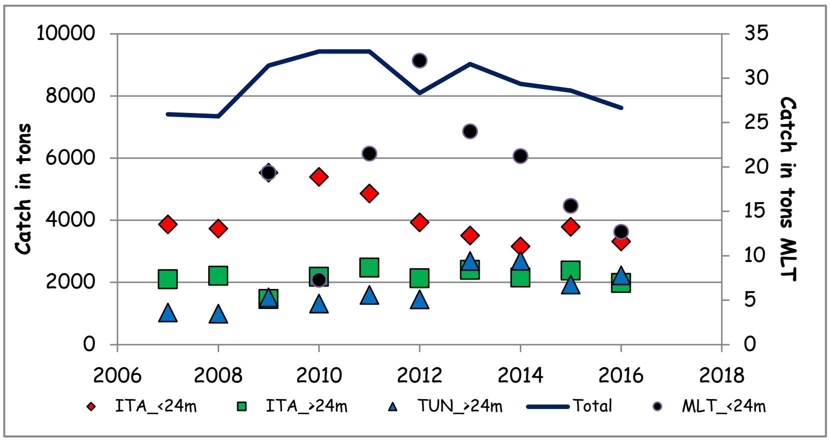


Figure 4.4.h. Catch of DPS from 2007 to 2016 in the Strait of Sicily, Central Mediterranean (GSA 12 - 16) by country (ITA: Italy, TUN: Tunisia, MLT: Malta) and fleet segment (haul length > or < 24m) (source GFCM stock assessment form). MLT_<24m catch data refer to secondary axis (on the right).

Recommendation GFCM/42/2018/5 on a multiannual management plan for bottom trawl fisheries exploiting demersal stocks in the Strait of Sicily (geographical subareas 12 to 16) applies the precautionary approach to fisheries management, ensuring that exploitation levels of European hake (*Merluccius merluccius*) and deep-water rose shrimp are at MSY by 2020 at the latest. It includes inter-alia the following measures: i) protection of nursery areas and essential fish habitats that are important for European hake and deep-water rose shrimp stocks in the Strait of Sicily through FRAs and temporal closures; ii) gradual elimination of discards by avoiding and reducing, as far as possible, unwanted catches; iii) measures to adjust the fishing capacity of the fleets to fishing mortality levels consistent with the MSY.

4.4.4 *Thunnus alalunga*, Albacore

General status of Albacore. The albacore tuna is a large pelagic species that can perform long migrations. The Mediterranean population is managed as a single stock separated from the Atlantic. This spatial structured management is supported by genetic studies (Nikolic et al. 2017). Albacore tuna has a high relevance in Mediterranean surface long line fisheries with important fishing activity, especially in Italy, but it also supports a variety of fishing types in different countries (Figure 4.4.i).

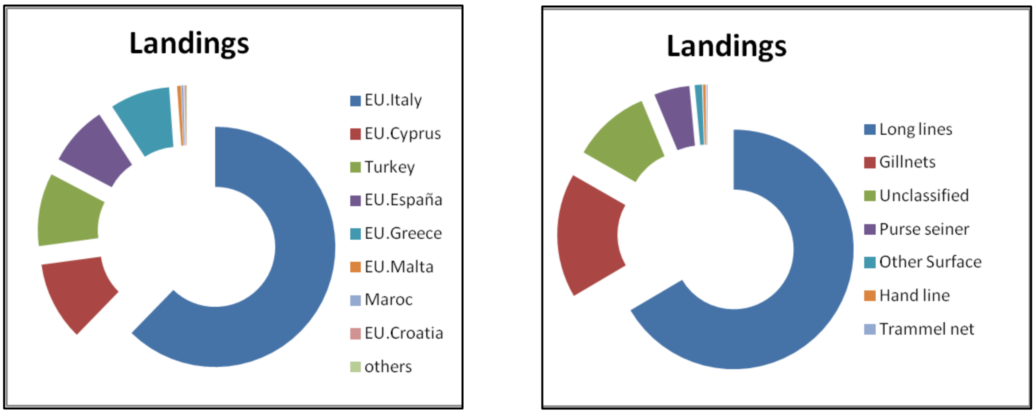
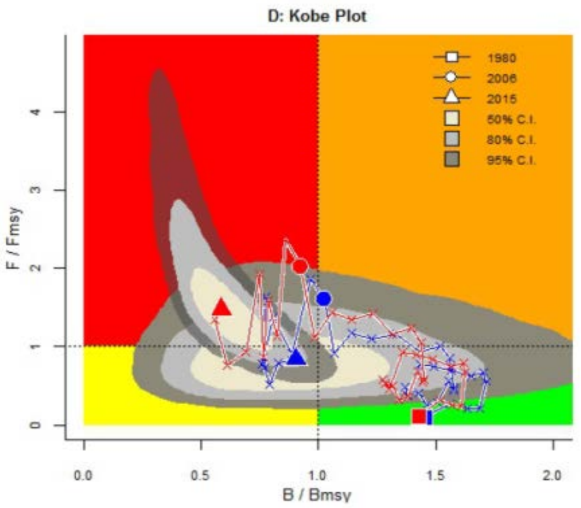


Figure 4.4.i. Ratio of landings per country (left) and gear (right) for the Mediterranean Albacore (Data provided by ICCAT database).

The Mediterranean albacore stock was last assessed in 2017, with updated catch data up till 2014 (ICCAT 2017). The approach used for the population assessment were based on data poor methods based on catch based and production models. The results of the 2017 assessment, showed that the status of the stock is highly uncertain with respect to both fishing mortality and biomass, with different output scenarios when different assessment models are considered(Figure 4.4.j). The Albacore Working group of the ICCAT/SCRS set the first warnings on the status of the stock and recommendation to institute management measures designed to avoid increases in catch and effort.



Figure(4.4.j). Kobe 2 phase plot with uncertainty using CPUE data till 2014, and projection till 2015 using observed catches in 2015. In blue assessment using a Catch based method (CMSY), in red the assessment using a CMSY bayesian method (ICCAT, 2017)

Albacore in the Western Mediterranean. In the Western Mediterranean the albacore tuna is mainly targeted by the Spanish long line fleet. This fishing activity mainly concentrates around the Balearic archipelago during the reproductive season in summer, the main spawning ground in the region (Figure 4.4.k).

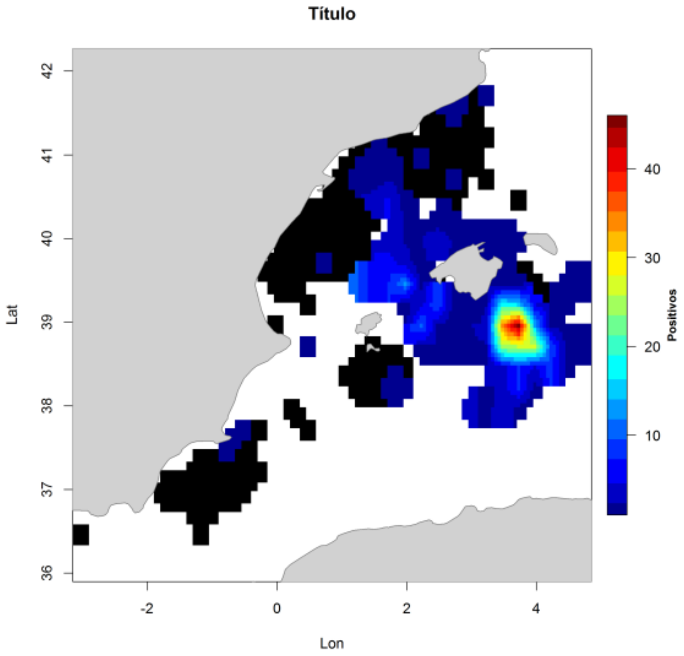


Figure 4.4.k. Positive catches of adult Albacore tuna in the long line fishery in the Spanish coast (number of catches). Catches accumulate in the same area as the spawning grounds.

The aggregation of adult individuals in this area make the case for the development of a albacore tuna larval abundance index obtained from ichthyoplankton surveys during June-July. Following a similar concept as the “egg production methods”, the larval index provide information on the spawning stock biomass (SSB) trends, which is the only index available independent of the fishery for the albacore Mediterranean stock (Alvarez-Berastegui et al. 2018).

The adequate standardization of the larval abundances to obtain a valid abundance index informing about the SBB, and the development of more accurate population assessment models relays on the background information on the albacore biology and the effects of environmental variability on the reproductive ecology and early life stages. More specifically, the key information for advancing in this two lines are:

For the improvement of larval abundance indices:

1. Standardization to the main sources of uncertainty from changes in sampling
2. Identification of the mesoscale oceanography driving the spatial distribution of larval habitats.
3. Identification of the biological and oceanographic processes affecting larval survival and growth.

For improving the general process of population assessment, the gaps were identified in the PANDORA workshops conducted in Ispra (Italy, Se deliverable 5.3).

1. Better understanding of the historical evolution of the albacore catch series.
2. Reviewing and recovery of historical catch time series for the main fleets.
3. Reviewing and recovery of information on the catch composition (lengths, ages).
4. Reviewing and integrating the information on the species growth and reproduction biology
5. Developing indices of relative abundance. Particularly those tracking the recruitment to the fishery.
6. Gaining more knowledge about the environmental impact in the status of the Meditarrean albacore stock.
7. Boosting cooperation between scientists in charge of sampling programs for standardization of methods.

4.4.5 *Thunnus thynnus*, Atlantic Bluefin tuna

Atlantic bluefin tuna is a highly migratory species that inhabits the Atlantic Ocean and adjacent seas. It is currently managed as two separated stocks although mixing of both stocks is expected but still being quantified. The Western Mediterranean area is the major spawning ground for the Eastern stock and the fishery in this area particularly targets mature adults that arrive to reproduce during spring-summer.

Bluefin tuna in the Western Mediterranean. Due to overfishing during the 90's, ICCAT, the international RFMO in charge of this species, established a 15-year recovery plan with the objective to ensure the sustainability of the fishery by 2022 (Porch et al. 2019). This plan involves reducing TACs, closed fishig seasons, increasing minimum landins size and prohibiting the use of airplanes and helicopters. Latest assessments of the stock confirm the stock is recovering and abundances are increasing regarding previous years (Figure 4.4.l).

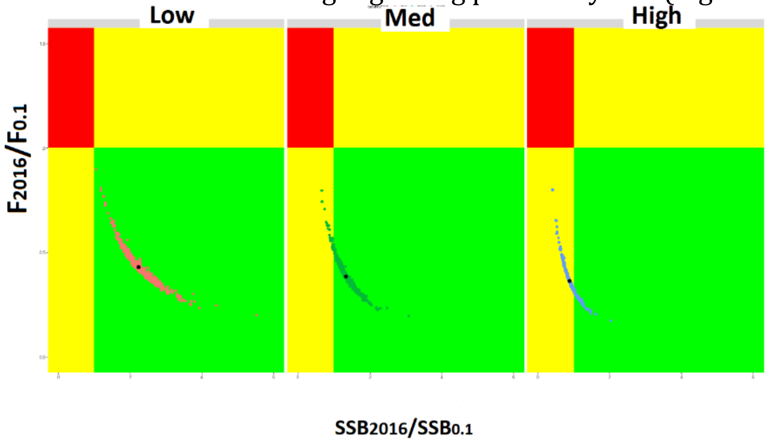


Figure 4.4.l. Kobe plot of the latest assessment of bluefin tuna (2017) Eastern and Mediterranean stock status from VPA run under three different recruitment scenarios (ICCAT,2017).

One general issue to improve the assessment for this species is the development of fisheries independent abundance indices. The recent improvement in knowledge of the ecology of this species has allowed the development of an abundance index independent of the fishery based on icthyoplankton surveys conducted annually in the Western Mediterranean (Alvarez-Berastegui et al. 2018). This has been included in current assessment models and need to be updated annually. Improving the knowledge of the relationship between the environmental variables and the spatial distribution of the larvae can integrate how environmental variability influence the larval abundance indices. Current assessments do not include recruitment indices. Better knowledge on the variables that influence larval survival and recruitment, particularly temperature (Ingram et al 2017 ; Reglero et al. 2018), can help to develop recruitment indices. The variables driving the reproductive phenology of the species are beginning to be understood (eg. Reglero et al. 2019) but need to incorporate the adults' routines to understand the occurrence of this species in the Western Mediterranean and quantifying the importance of this spawning ground. Current availability of infrastructures that allow rearing this species has improved our knowledge on the variables that influence growth and survival of the early life stages (eg. Blanco et al. 2018; 2019) and can help to parameterize mechanistic models.

Activities in PANDORA to fill the gaps (or needs) – The Mediterranean Sea

4.4.6 The Aegean Sea case study

Within PANDORA, the goal of the Aegean Case Study was to improve current assessments by incorporating the environmental effects in the stock & ecosystem evolution and moreover investigate the plausible impact of climate change on demersal species (hake & red mullet).

To this end, an exhausting search was exerted on all available datasets to compile data on:

a) abundance indices,
b) environmental preferences and,
c) relevant climatic data

Based on the MEDITS survey data series (Bertrand et al., 2002), dating back to 1994, fishery independent abundance estimates were associated with in-situ ambient temperature and salinity measurements concurrently recorded by CTD during the experimental fishing campaigns.

Additionally, 35 environmental indices of physicochemical variables for the Aegean Sea were acquired through the work completed in CERES project (CERES, 2018a). Historical data sets covered the period from 1960 up to date, while future predictions based on two climate scenarios (RCP4.5 and 8.5) included years up to 2098. An association between historical hake abundance and environmental variables allowed for identifying the most influential factors driving the stock as well as predicting plausible future trends.

4.4.7 *Merluccius merluccius*, European hake

Aegean hake was found throughout the water column, however the peak of abundance was within the continental shelf and in depths around 100m (Table 4.7). Juveniles resided in much shallower waters compard to the adults and in more productive waters. Thermal preference was quite restricted around 13^{o} C.

Table 4.7. Environmental preferences of hake in the Aegean Sea based on MEDITS survey

Hake – Aegean Sea			
Population	*Larvae*	*Juvenile (0-1 age groups)*	*Adult + juveniles (0-9+ age groups)*
Period	2004-2013	1994-2011	1994-2008
Temperature (C)	20.4-22.7	11.8-15.0	12.0-14.0
Chl-a (mg/m3)	Not clear	0.1-0.9	Not clear
Salinity (psu)	34.7-37.7	Not clear	37.0-40.0
Depth (m)	0-50	28-385	20-540 (80)
Abundance (kg/km2)	-	8.4	48.27
Abundance (Nb/km2)	-	-	741.1
Northern distribution	41.08	40.51	40.51
Southern distribution	38.43	35.19	35.19

Based on Generalized Additive Modelling approaches, gross primary production, water temperature and pH were found to be crucial drivers of hake abundance indices in the past (1960-2016) and depending on the climatic scenario hake stock will either steadily decline up to the 2050s, levelling afterwards till the end of the century or fluctuate largely oscillating within the observed historical levels (Figure 4.4.m).

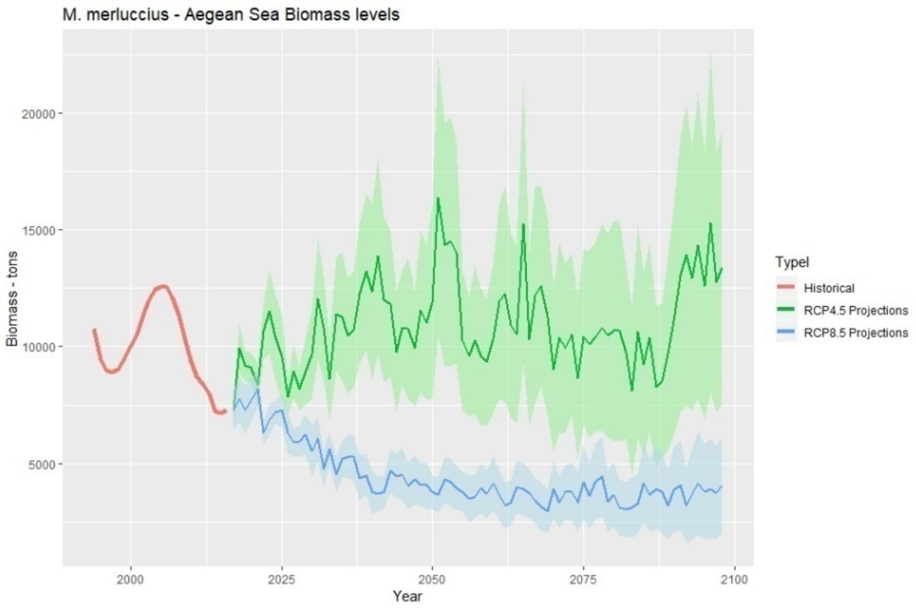


Figure 4.4.m. Historical and projected stock biomasses of hake in the Aegean Sea under RCP4.5 and RCP8.5 climatic scenarios (source: CERES 2018b).

Spatial distribution was also investigated through MaxEnt linking presence/absence of hake in the Aegean with environmental factors. Analyses revealed a patchy pattern with hot-spot areas of high abundance (Figure 4.4.n). Moreover, future predictions suggested a significant increase of the favourable areas for hake in the Aegean Sea (Table 4.8.)

Table 4.8. Fraction of suitable habitat for hake in the Aegean Sea at three time slices (present, 2050s and 2090s) under two scenarios RCP45 and RCP85 (±1sd intervals in parenthesis).

	present	**2050s**	**2090s**
RCP45	0.55 (0.13-0.96)	0.92 (0.62-0.99)	0.82 (0.54-0.97)
RCP85	0.64 (0.12-0.98)	0.95 (0.63-1.00)	0.98 (0.90-1.00)

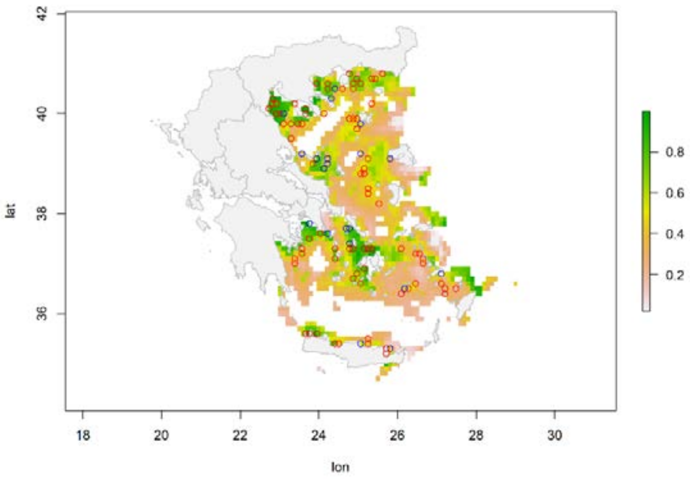


Figure 4.4.n. Prediction of MaxEnt representing the relative probability of occurrence or habitat suitability for hake in the Aegean sea (source: CERES 2018b)

4.4.8 *Mullus barbatus*, red mullet

Aegean red mullets resided in depths up to 500m, however in shallow waters (around 60m) is where they were found in higher abundence (Table 4.9). Thermal preference was much higher than hake, around 20^{o} C.

Table 4.9. Environmental preferences of red mullet in the Aegean Sea based on MEDITS survey

Red mullet – Aegean Sea		
Population	*Larvae*	*All (adults & juveniles)*
Period	1994-2011	1994-2008
Temperature (C)	19.1-26.6	17.0-22.0
Chl-a (mg/m3)		
Salinity (psu)	31.4-39.1	39.0-40.0
Depth (m)	0-50	20-540 (60)
Abundance (kg/km2)	-	18.9
Abundance (Nb/km2)	-	875.4
Northern distribution	41.08	40.51
Southern distribution	38.43	35.19

Gross primary production, benthic dissolved organic carbon and pH were the main drivers of red mullet abundance indices in the past (1960-2016). The two different climatic scenarios gave very dissimilar projections for red mullet abundance: under RCP8.5, red mullet stock will remain at the most recent levels indicating that climate variability will not affect the stock. Under RCP4.5 red mullet biomass will increase almost monotonically up to 2100 with the stock doubling in size compared to the current state (Fig. 4.4.o).

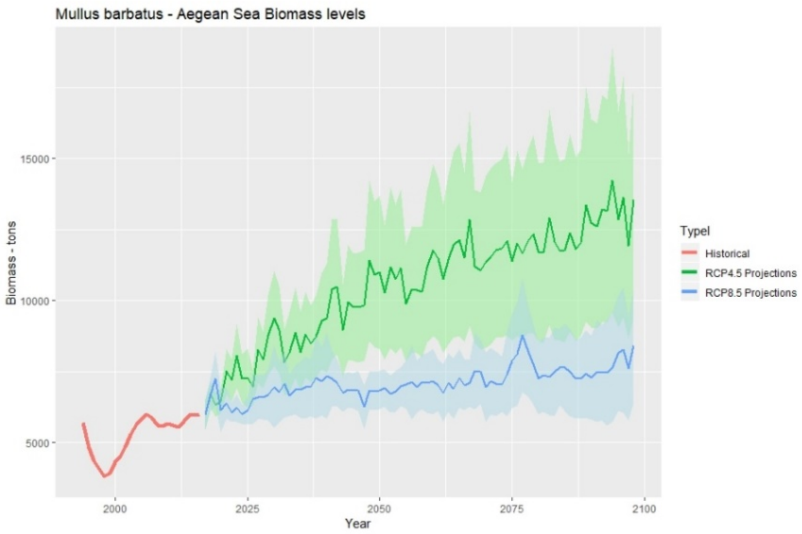


Figure 4.4.0. Historical and projected stock biomasses of red mullet in the Aegean Sea under RCP4.5 and RCP8.5 climatic scenarios (source: CERES 2018b).

Spatial distribution of red mullet was not investigated.

The results acquired for the Aegean CS within T.1.2 will be used as an input in WP2 to answer the following research questions:

- **Can we enhance current stock assessment tools to incorporate environmental variation (e..g. climate change) impact? How?**
    - **direct climate change (CC) effect on stock-recruitment relationship,**
    - **direct climate change (CC) effect on natural mortality**
    - **direct climate change (CC) effect on intrinsic growth rate**
- **Can we mitigate climate change impact and maximize sustainable long-term yields?**

4.4.9 Strait of Sicily Case Study (red mullet and pink shrimp)

While previous work on red mullet and pink shrimp distribution in relation to environmental factors has been based on ecological data (Fortibuoni et al., 2010, Levi et al., 2003, Ungaro et al., 2006), within PANDORA, the aim of the Strait of Sicily Case Study is to expand the predictive ability on the relationship between distribution and warming by using ecophysiology to assess the potential effects of climate change on the thermal habitat suitability of two key species (*M. barbatus* and *P. longirostris*). This will be accomplished through ecophysiological laboratory experiments on the effects of temperature on the energetics (metabolic scope) and thermal tolerance (Marras et al., 2015). This will provide a mechanistic basis (Teal et al., 2018) for modeling habitat suitabiities based on oceanographic data for present and future scenarios, which will then feed into potential distributions projections. Distribution profiles from the MEDITS survey data series will be compared to the habitat suitability based on the coupling between the ecophysiological data and the oceanographic models. This will allow to map the correspondence between potential habitat and habitat utilization in both red mullet and pink shrimp, thus allowing to assess the reliability of predictions derived from the model based on both the energetic performance curve and the thermal limits. Furthermore, laboratory derived thermal tolerance relationships will also be incorporated into an end-to-end ecosystem model Atlantis (Fulton et al., 2004). Atlantis is an ecosystem box-model intended for use in Management Strategy Evaluation. It is composed by a set of submodels. It features a deterministic biophysical submodel, which is spatially resolved in three dimensions using a map made up of polygons and vertical layers. Physical forcing fields (currents, temperature and salinity) are included using results of an external hydrodynamic model.

This model will be used to reproduce the structure and functioning of the ecosystem, represented by 58 functional groups and 8 fleets, with particular focus on commercially important species, to explore the potential effetct of climatic or man-induced changes (eg harvest control rule) on marine habitats and ecosystem, and use it for scenario testing and trade-offs evaluation related to the application of different fisheries management scenarios on the marine ecosystem and on the socio-economic compartments of the Strait of Sicily. Activities in this workpackage will focus on the retrival of relevant data on biological, fisheries and economic value for target species.Future physical data (temperature, salinity, currents, etc) will be gathered from the projections for the RCP4.5 and 8.5 warming scenarios produced within the CERES project (CERES, 2018a).

4.4.10 The Western Mediterranean Case Study

Within PANDORA, the goal of the Western Mediterranean Case Study is to improve current assessments of European hake and red mullet by 1) incorporating the short term environmental effects in the stock, and 2) providing ecological basis to the dynamics of natural mortality vector by considering density dependence, size dependence and body condition. These procceses will be investigated in both hake and red mullet of the Geographic Subarea 6 (Iberian Peninsula) in the Mediterranean Sea. In the case, of the incorporating short-term environmental variability, a first paper has been published recently evidencing that, with the currenty available data, annual recruitment can be estimated attending to oceanographic modeling and hydroclimatic conditions in winter (Hidalgo et al. 2019a).

For albacore, the goal of the Western Mediterranean Case Study In order to tackle the different gaps identified regarding new data and biological knowledge for the improvement of the sustainability of the Mediterranean albacore tuna different activities are being conducted in the framework of PANDORA. Regarding the improvement of larval abundance indices used as proxy for spawning stock biomass the activities are focused on:

-The analyses of the spatial and temporal distribution of the spawning ground locations of Albacore tuna in the Western Mediterranean. This activity will allow to assess whether the larval sampling distribution covers the spatial location of the spawning grounds of this speceies, and to assess the temporal overlap between the sampling and the spawning time.

- The analyses of the relation between the larval spatial distribution and the distribution of water mases around the Balearic Sea. The identification of this reation between the local mesoscale oceanography and the early life ecology of albacore tuna will allow to standardize the captures of larvae to the mismatch between the smpling distribution and the larval habitat distribution.

- The analyses of the Catchability of larvae among different fishing gear methods apply along the time series of ichthyoplankton surveys in the Balearic Sea. This will allow to construct standardized CPUEs along time to assess the temporal trends of spawning stock biomass.

Regarding the general improvement of population assessment, the activities to tackle the identified gaps are:

-Reviewing the current knowledge on the Mediterranean albacore tuna reproduction biological parameters to set a valid ogive function to assess maturation.

-Revise the current data bases of catch at length distribution available in ICCAT for the Albacore working group of the Standing Comission for Research and Statistics (SCRS).

-Develop environmental indices in the Western Mediterranean spawning ground around the Balearic Sea to assess the interannual varaiblity. The temporal trends on the environmental varaiblity will be applied to improve the prediction of the age 1 termpoal trend used in catch at age population assessment models.

- Propel the creation of a research project within ICCAT focused on the Mediterranean albacore, setting the research priorities identified (see previous section).

For Atlantic bluefin tuna the proposed activities include:

- Integrating environmental variability in the larval abundance index independent of the fishery. There is already knowledge of the environmental variables to be taken into account that is not being considered in the indices. The methodology would be used non-linear models and Bayesian models to estimate the indices.The process this gap is related to is the dynamic spatial distribution of the larvae and the mortality curves.

- Collaborate in genetic analyses of larvae collected from the Western Mediterranean oceanographic campaign in 2019 to seek the feasibility of close-kin analyses for bluefin tuna.

- Design a recruitment indices that besides integrating temperature as a key variable driving larval growth and survival it also considers food availability and predators. The methodology would be to improve current knowledge on the relationship between the larval survival and the food availability and the predators by developing statistical and mechanistic modelling and integrate such knowledge in the already available recruitment index temperature-dependent. The process considered in the influence of environmental and biological variables in the spatial and temporal distribution of eggs and larvae and their effect in their growth and survival.

-Improve knowledge on the reproductive biology of the species by including the adults' perspective into the understanding of the bluefin tuna reproductive phenology. This understanding could be incorporated in the MSE model that is being developed by ICCAT for Atlantic bluefin tuna.

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Annex 1

Review on environmental effects on recruitment dynamics of commercially important North Sea stocks

Authors: Bernhard Kühn and Alexander Kempf

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Introduction

Fish stocks and the yield of the fishery have always been subjected to fluctuations, which gave rise to different hypotheses of the potential causes. One of the first to link these fluctuations to environmental variability was Johan Hjort in his famous work “Fluctuations in the great fisheries of Europe” from 1914. He noticed that environmental conditions during early life stages strongly affect the number of young fish (recruits) entering the stock at a later point (Hjort 1914). His main hypotheses focused on vulnerability of larvae to availability of suitable prey at the onset of first feeding (termed “Critical period” hypothesis) and susceptibility to hydrodynamic factors (termed “Aberant drift”-hypothesis. Building on his work many more hypotheses regarding stock and recruitment variability arose. Most of them were a refinement of Hjorts “Critical Period”-hypothesis e.g. “Match/Mismatch” (Cushing 1990), “Stable Ocean” (Lasker 1978, 1981) and “Optimal environmental window” (Cury & Roy 1989) – the latter two focusing on the role of the hydrodynamic environment in prey availability. Others emphasised the role of hydrodynamics determining dispersal of early life stages (e.g. Migration Triangle (Harden Jones 1968), Member Vagrant (Iles & Sinclair 1982, Sinclair 1988)). The Ocean Triad hypothesis of Bakun (1996, 1998) combines these viewpoints by emphasising the role of hydrographic features in “enrichment, concentration and retention” of prey and fish larvae. However these hypothesis focus only on bottom-up process whereas top-down processes such as predation and trophic interactions mediated by the environment are believed to be of uttermost importance, but still are often neglected (Bailey & Houde 1989, Bax 1998). Today fishery scientist are aware that the recruitment problem is multidimensional and an integrative holistic approach is needed, rather than pursuing one single hypothesis (Houde 2008, Hare 2014). Traditional fisheries assessment on the other hand does not make use of this and seldom incorporates environmental effects. Only 24 cases out of 1250 reviewed stocks globally (Skern-Mauritzen et al. 2016) and 24% of 206 US-stocks (Marshall et al. 2019) incorporated ecosystem drivers into stock management. This is in part due to the understanding that the fishery is the most important driver of the stock, which originated in the work of Ricker, Beverton and Holt in the 1950s (Ricker 1954, Beverton & Holt 1957). The authors conveniently linked the parent stock size to the number of recruits surviving with a single model (termed “stock-recruitment-relationship”) to quantify the exploitable part of the population to the fishery. Since then traditional stock assessment made use of this “black box” without the need to understand early life cycle dynamics (Ulltang 1996). However in reality a weak link between the stock and the recruits is the exception rather than the rule (Cury et al. 2014, Szuwalski et al. 2015), with environmental variability accounting for most of the variance in the stock-recruitment relationship. Additionally the attempt of incorporating environmental information into recruitment forecasting was accompanied by many failures, as most of the relationships were weakened or broke down when retested with new data (Myers 1998). As (Keyl & Wolff 2008) pointed out the reasons lie in the complex nature of marine ecosystems (nonlinearity, time lags, spatial scale, direct and indirect effects, multidimensionality) as well as population effects and the occurrence of spurious correlations. Changes in the systems state (“regime shifts”) due to human ecosystem alteration or climate pose an additional challenge even if the underlying relationships are causative (Tamburello et al. 2018). Data limitations in the stock (Pepin 2016) as well as inaccuracies in predicting environmental covariates (Walters & Collie 1988, Xu et al. 2018) add to the difficulty of successfully predicting stock recruitment. Due to the difficulties some authors even questioned the usefulness of environmental recruitment research for management purposes (Walters & Collie 1988, Myers 1998). Still the awareness of the many pitfalls lead to numerous publications reviewing the current state of recruitment research in the recent past. They addressed environmental influences on the recruitment process (Köster et al. 2003, Houde 2008, Hare 2014, Haltuch et al. 2019), specific species (e.g. Dickey-Collas et al. 2010, Ottersen et al. 2014) and advances in modelling (Needle 2002, Megrey et al. 2005, Subbey et al. 2014), aiming to contribute to a possible solution and future directions. Common ground exists that recruitment research should be based on a conceptual framework with a priori hypothesises, rather than a pure exploratory analysis as well as the use of robust statistical methods and the need for model validation. For the North Sea, many commercially important stocks are believed to be influenced by environmental drivers with strong effects on the fisheries. Especially the recent warming (Belkin 2009) and a change in the plankton community (Beaugrand 2004, Alvarez-Fernandez et al. 2012) exert their effects on higher trophic levels including fishes (Beaugrand et al. 2003, Payne et al. 2009). Therefore understanding the drivers of fish stock fluctuations for the North Sea and incorporation into assessment can help in sustainable management of the stocks. Consequently, this work within PANDORA aims to (i) review current work on important commercial stocks (cod, herring, haddock, whiting, saithe) in the North Sea and identify potential drivers of recruitment and (ii) try to incorporate these into stock-recruitment relationships by means of conventional and new statistical methods.

Methods

As a basis for future analysis the existing literature on effects of the environment on the recruitment of important commercial North Sea stocks (cod, herring, haddock, saithe, whiting) were reviewed. The structure of each review was chosen to reflect the life cycle stages (egg, larvae, juveniles, adults) to identify the time, spatial characteristics and extent each life stage is influenced by environmental drivers. Through this, relevant recruitment bottlenecks as well as knowledge gaps have been identified. The literature search was organised by using the search engines “Google scholar” and “Web of Science” for peer reviewed documents. For the aim of a comprehensive cover of the topic suitable general key words for each species were used (Table A1.1). Additionally, references found within references were scanned for further information. The ICES database was used to acquire documents from ICES working groups, stock assessments, cooperative research reports as well as grey literature in the form of Conference and Meeting (CM) documents.

Table A.1.1: Keywords used for literature search (not limited to and with various combinations)

General key words:	Recruitment, recruits, North Sea, egg, larvae, juvenile, adult, SSB, stock, life cycle, fecundity, maturation, maternal/parental effects, spawning grounds, growth, survival, temperature, salinity, currents, wind, drift, IBM, NAO, North Atlantic Oscillation, AMO, Atlantic multidecadal Oscillation, SPG, Subpolar Gyre, fronts, Atlantic inflow, circulation, turbulence, prey, phytoplankton, zooplankton, predation, density, competition, habitat, migration, stock structure
Species specific key words: Cod (*Gadus morhua*)	Cod, Gadus morhua, gadoid outburst, Calanus finmarchicus,
Herring (*Clupea harengus*)	Herring, Clupea harengus, autumn spawner, winter spawner, Downs, Orkney Shetland, Bushan, Dogger, Banks, HAWG, Paulik, microzooplankton, cannibalism, stock collapse
Haddock (*Melanogrammus aeglifinus*)	Haddock, Melanogrammus aeglefinus, eddy, gyre
Saithe (*Pollachius virens*)	Saithe, Pollachius virens, coalfish, Köhler, stock mixing,
Whiting (*Merlangius merlangus*)	Whiting, Merlangius merlangus, jellyfish, medusae

Annex A.1.1 Recruitment of North Sea cod

Life cycle of North Sea cod (*Gadus morhua*) and processes that might affect recruitment variability

1. Effects of the Spawning population

1.1 Stock structure

Cod in the North Sea (subarea IV) is managed together with cod from the eastern English Channel (7.d) and the Skagerrak (3a.20) as a single stock. However the benchmark report WKNSEA (ICES 2015) discussed if the North Sea cod stock is composed of more than one population. Evidence from tagging studies (Robichaud & Rose 2004, Wright et al. 2006, Neuenfeldt et al. 2013, Neat et al. 2014), genetic analysis (Hutchinson et al. 2001, Knutsen et al. 2004, Nielsen et al. 2009, Poulsen et al. 2011, Heath et al. 2014, Barth et al. 2017) and analysis of otholith chemistry (Wright et al. 2006, 2018) indicate considerable spatial differentiation within the North Sea stock. Genetic analysis point to at least two distinct subpopulations residing in the North Sea, comprising the Viking population in the North East and one occupying shallower areas (Hutchinson et al. 2001, Heath et al. 2014). Some gene flow also exists between the North West and Viking as well as within southern populations of the German Bight, southern Bight and Flamborough Head (Hutchinson et al. 2001). Heath et al. (2014) pointed out that mature cod from West of Scotland showed high genetic similarity with cod from shallower North Sea region. Investigations of migration pattern of adult cod found adiitional structuring on finer spatial scales with exchange between the southern Bight and eastern English Channel, but no evidence for exchange between the southern and northern North Sea, as well as between West of Scotland and the north-western North Sea (Wright et al. 2006, Neuenfeldt et al. 2013, Neat et al. 2014). Signals from otholith chemistry of cod juveniles indicate a high degree of stationarity in juvenile life separating the North and the South, however both populations showed intermixing with the Skagerrak area (Wright et al. 2018). Cod in the Skagerrak population shows considerable connection to the adjacent eastern North Sea stock, via transport of eggs and larvae into the Skagerrak (Knutsen et al. 2004, Stenseth et al. 2006, Jonsson et al. 2016, Barth et al. 2017). Juveniles grow up there and migrate back into the North Sea later in their life as juveniles and spawners (Pihl & Ulmestrand 1993, Svedäng et al. 2007), joining the Viking population to a large extent, but also populations in the central and southern North Sea (Wright et al. 2018). The general interpopulation flow of early life stages between the north and the south seems to be limited, although the area around Fisher Banks received recruits from both northerly (Viking and Moray Firth) and southerly (Dogger, Flamborought) spawning grounds in a drift model by Heath et al. (2008). The general picture points towards low levels of stock mixing during the adult phase, but some exchange due to drift of early life stages especially in the eastern North Sea around Fisher Bank and the Skagerrak

The SSB for the whole North Sea peaked in the 1970s together with other gadoids termed the “gadoid outburst” and is decreasing since then, with a recent recovery since 2005. Recruitment follows more or less the trend in SSB, but with an overall low recruitment since the last 15 years, despite some recovery in SSB. Within the North Sea there is considerable spatial variation in SSB trends (Holmes et al. 2008, 2014, ICES 2015, 2019). Hedger et al. (2004) noticed a shift in cod abundance between the 1980s and 1990 changing from a more southerly distribution (southern Bight, German Bight, Dogger Bank) towards the Northeast around the east of Shetland, Viking Bank and Utsira high. Until 2005 the southern and northwestern North Sea SSB follows the main decreasing trend of the whole North Sea, whereas in the deeper Viking area the population is stable (Holmes et al. 2014). After 2005, the substocks recovered until a peak in 2016 – 2017 and declined thereafter, whereas in the southern North Sea the substock decline persisted over the whole period (ICES 2019). The shift is hypothesised to result from increasing temperatures in the southern North Sea, either through direct adverse effects on spawners and recruits or indirect through reduced feeding conditions (Dulvy et al. 2008, Nicolas et al. 2014, Engelhard et al. 2014, Núñez-Riboni et al. 2019). Rather than directed adult movement of cod to colder, deeper areas the observed pattern is a reflectance of the state of each subpopulation (Neat & Righton 2007). A recent analysis of suitable thermal habitat for cod in the North Sea found especially the North east of the North Sea and the

Skagerrak to increase in suitability for cod, whereas habitat suitability in the south decreases under recent warming and climate projections (Núñez-Riboni et al. 2019).

1.2 SSB effect

The variance explained by the stock-recruitment relationship in North Sea cod is low and follows an overall compensatory response with increasing stock numbers (e.g. Pécuchet et al. 2015, Akimova, Núñez-Riboni, et al. 2016). Although some authors (Macer 1983, Rijnsdorp et al. 1991) found lack of evidence of density-dependent growth in the adult stage of North Sea cod, Cook et al. (1999) found the year-class effect in their weight-at-age model to be correlated with total and spawning stock biomass. This point towards density-dependent effects in younger life stages, however, the exact mechanisms are not resolved yet. Results of Macer (1983) suggested density-depend effects exerted on juvenile cod in their second year through competition with older age classes, whereas Van Alphen & Heessen (1984) found competition within a year class during their first three years to be most likely.

1.3 Parental effects and fecundity

Age of reproducing females is affecting the reproductive outcome of a population mainly in two ways – through fecundity and maternal effects. Fecundity relates to the number (quantity) of offspring generated within a season, whereas maternal effects summarize the effect each individual female has on the quality (size, viability, survival) of its offspring (Solemdal 1997, Trippel 1999). Older females lay more eggs than younger ones, due to increased body size (Hixon et al. 2014, Barneche et al. 2018). However, the relationship between body size and reproductive energy output is not linearly scaled in many fish, but increases disproportionally (Barneche et al. 2018). Also eggs of first and repeat spawners are qualitatively different, with smaller eggs, lower fertilisation and hatching rates for younger females (Trippel 1998). These characteristics propagate further in life as egg weight is related to later larvae size and size of their mouth gape (Knutsen & Tilseth 1985). Due to smaller size, the authors suggested larvae of first spawners to have difficulties at the onset of exogenous feeding. A simulation model by Palakovich Carr & Kaufman (2009), taking into account maternal effects on offspring viability, found the reproductive effort of first-time and second-time spawners in Gulf of Maine cod to be low compared to their overall high biomass in the population. Additionally differences in buoyancy properties between eggs (Kjesbu et al. 1992, Vallin & Nissling 2000) and early larvae (Saborido-Rey et al. 2003) from different aged females exist. For Baltic Sea cod in the Bornholm Basin more neutral buoyancy at lower salinities for eggs of older females (Vallin & Nissling 2000) relates to increased survival probability as eggs are less likely to sink into the anoxic layer, which is characteristic for the Baltic Sea (von Dewitz et al. 2018). Stige et al. (2017) found higher mean age and size of females within the Barent Sea cod population to be positively linked to a wider spatiotemporal distribution of cod eggs in the region, possibly related to different buoyancies. However, to what extent this affected recruitment remained unclear. Timing of spawning also differs with age, with older females spawning earlier for North Sea cod (Kjesbu et al. 2010, Morgan et al. 2013) and over an extended period (Kjesbu et al. 1996). This might mitigate mismatch dynamics as temporal overlap with suitable larval-prey becomes more likely (Kjesbu et al. 1996). Combining all these effects of age on fecundity, egg properties and spawning duration points to a general positive effect of old spawners on offspring survival probability, which seems to be underestimated in the classic spawning-stock biomass representation especially under the increasing maturity rate for young North Sea cod (i.e. age 2) in the last decades. Strong age and size truncation of fisheries removing older females from the population can have profound effects, which are not captured by treating all individuals as identical (Hixon et al. 2014).

1.4 Maturation

From the 1970s on cod in the North Sea mature at younger ages and smaller sizes (Marty et al. 2014). The authors made increased fishing pressure responsible for the observed shift, which seems to be the case in male cod. However, the decreasing trend in cod females could not be explained by fishing and might be due to a negative effect of temperature experienced earlier in life during the juvenile phase. Differences in maturation schedules is also evident on an intrastock level within the North Sea. Laboratory studies indicates a marked north-south gradient, with individuals from the southern North Sea maturing later at larger sizes and with greater fecundity than individuals from the North West under same conditions (Harrald, Wright, et al. 2010). However, elevated temperatures and higher growth in the south might counterbalance differences between substocks in the wild leading to approximately the same age at maturation. At much smaller spatial scales, Yoneda & Wright (2004) found increased fecundity of cod in the inshore region compared to the offshore region at the Scottish Coast in recent times. Wright et al. (2011) linked these regional differences in maturation and fecundity of cod within the North Sea to changes in fishing pressure, moving from coastal to offshore regions over the last fifty years. Additionally, temperature had a positive effect on the probability to mature early leading to a strong increase in maturity rates of young cod. Currently a large proportion of cod in the northwest and south in the North Sea spawn at age 2, whereas individuals from the northeast do not (Wright et al. 2011).

1.5 Environmental effects on reproduction potential

Temperature experienced by females during vitellogenesis in autumn did affect spawning time in spring for North Sea cod (Kjesbu et al. 2010, Mcqueen & Marshall 2017). Higher temperatures resulted in faster oocyte growth and in consequence in an earlier spawning. Another profound influence on reproductive potential plays the individual’s condition. Individuals from stocks in warmer water showed better condition than individuals from stocks in colder waters, with positive influence on recruitment and productivity (Rätz & Lloret 2000, Thorsen et al. 2010). The authors attributed these differences to enhanced growth under elevated temperatures and better prey availability. In Barent Sea Cod, Kjesbu et al. (1998) showed a positive relationship between prey availability (capelin), elevated temperatures during vitellogenesis and fecundity.

1.6 Timing of Spawning

There exists a north-south gradient in spawning, with individuals spawning earlier in the south than the north. Brander (1994) reported peak spawning season (abundance of stage I eggs) ranging from the end of January in the English Channel and progressively increasing through the Southern Bight in mid-February, to beginning of March in the west-central North Sea and German Bight. González-Irusta & Wright (2015) assessed spawning by occurrence of cod in the spawning stage. The authors found peak spawner abundance in the southern North Sea occurring in mid-February, whereas spawner in the northwest were abundant at the end of February. Individuals from the North-East North Sea (Viking) spawned latest from mid-March onwards. Interestingly, an analysis of roe-landings data and calculation of peak roe month in the north and central North Sea by Mcqueen & Marshall

(2017) showed that the north-south divergence in spawning times occurred just recently in the early 90ies. They made increased autumn temperatures responsible for the shift.

1.7 Spawning grounds

There exists a large variability in the extent of spawning grounds in the North Sea. Although all historical spawning grounds are still in use (Wright et al. 2003, Fox et al. 2008, González-Irusta & Wright 2015, Höffle et al. 2017), their temporal and spatial extent varies between years. In a review by Wright et al. (2003) the authors summarized information on the main spawning ground from 1950 onwards. Early work identified main spawning grounds in the northwest and central North Sea to the west and north of Doggerbank as well as southeast and southwest of the Fladen Ground along the Scottish coast. Areas in the southern and central North Sea namely between Flamenborough and Dogger Bank, Horns Reef area and the Southern Bight were most important in the 1970s and 1980s. In the 90s the German Bight to the northwest of the Dogger Bank in the south and at the north western region around Moray Firth and the northeast of Scotland were used as spawning areas. (see references in Wright et al. 2003). In the years 2004 (Fox et al. 2008, Höffle et al. 2017) and 2009 (Höffle et al. 2017) distributions of stage I eggs concentrated in the southeast of the North Sea mainly on the Dogger Bank, German Bight, Fisher Bank and along the Norwegian Trench north to Utsira High and Viking Bank. A recent study on spawning fish in the years 2009 – 2014 found higher spawner abundance in the southern North Sea in 2009, whereas higher concentrations of spawners occurred in the northwest around Orkney and Shetland in later years (González-Irusta & Wright 2015). The authors explained inter-annual variability in spawning ground use mainly with changes in temperature and salinity. Northern spawning grounds experienced much more stable conditions during the time studied, whereas in the southern North Sea large inter-annual differences in temperature and salinity may have led to observed patterns. Temperatures between 5 – 7 °C, higher salinities and coarse sand areas were favourable conditions for spawning cod, whereas strong tidal currents limited spawning (González-Irusta & Wright 2015). This is in accordance with other studies, who found higher egg densities in shallower regions with low temperatures and higher salinities (Lelièvre et al. 2014, Höffle et al. 2017).

2. Eggs

2.1 Temperature effects on growth, development and mortality

Temperature directly affects development times in eggs. Although increased temperature reduced the time spend in the egg stage, as well as drift periods (Peck et al. 2009), increased predation pressure under elevated temperatures possibly cancels out these benefits (Akimova, Hufnagl, et al. 2016). However Drinkwater (2005) suggested the opposite effect with lower temperature, leading to higher vulnerability to predation, due to longer stage duration.

2.2 Transport

A North Sea wide study conducted in winter/spring 2004 on the distribution of cod eggs identified four main regions namely the south of Dogger Bank, Fisher Banks and along the Norwegian Trench and northern Scotland (Munk et al. 2009). In these regions, egg abundances were associated with salinity fronts. This indicates that spawning itself either occurs in close proximity to these regions or that frontal zones help in retaining eggs at places, that itself are again favourable for later larvae stages in terms of retention and prey availability. Information from two ichtyoplankton surveys in 2004 and 2009 indicates that drift during the egg phase is limited with quite stable distribution pattern between stage I and stage IV eggs (Höffle et al. 2017).

2.3 Predation

Predation by small pelagics was shown for Baltic Sea cod with strong consequences on recruitment (sprat and herring (Köster & Möllmann 2000)) and was suggested as important mechanism also for other populations (Barent sea: herring (Ottersen et al. 2014), Grand Bank: mackerel (Paz & Larrañeta 1992), Gulf of St. Lawrence: mackerel and herring (Swain & Sinclair 2000), Irish Sea: sprat (Pliru et al. 2012)). A North Sea wide study found younger herring (2-3 years old) (*Clupea harangus*) frequently preying on eggs of demersal fish, including cod in the southern part of the North Sea in February (Daan et al. 1985). Pommeranz (1979) found herring and sprat to prey on cod eggs in the southern Bight. Northern areas, associated with older age classes of herring, had neglectable predation during February (Daan et al. 1985). However this can be due to the low availability of cod eggs, as peak spawning occurs later in the season (~March) in the northern North Sea (González-Irusta & Wright 2015, Mcqueen & Marshall 2017). Additionally, feeding is generally limited during this time of year (De Silva 1973, Daan et al. 1985, Last 1989, Van Ginderdeuren et al. 2014). However, based on assumed spring feeding grounds of herring by Corten (2002) in a wide area around the Norwegian Trench in the north eastern North Sea in April/May a strong spatial overlap of cod eggs and larvae with herring is likely. For the southwest of the North Sea, Segers et al. (2007) found Herring in February to forage on cod eggs when other food sources are scarce. Predation related mortality of cod eggs could therefore be strongly depend on the temporal and spatial occurrence of crustacean zooplankton. For eastern Baltic See cod abundance of cod eggs and vertical as well as horizontal overlap determined the strength of herring predation on cod eggs (Neumann et al. 2014).

3. Larvae

From the current picture in the literature, larvae are believed to be the most vulnerable stage, originating from ideas like the Critical Period/Match Mismatch hypothesis and aberrant drift.

3.1 Temperature

Temperature is the main factor affecting growth and development in ectotherms. Cod larvae show reduced development times with higher temperature. In the laboratory optimal growth for younger larvae stages was under lower temperatures (9.7 °C) than for larger larvae (12.3 – 13.4 °C) (Steinarsson & Björnsson 1999). Survival was dome-shaped with an optimum around 8.5 – 8.8 °C for all sizes. Modelling studies of Fouzai et al. (2015) indicated that elevated temperatures favour growth and therefore survival in cod larvae, but only under sufficient food conditions. Otherwise risk-taking behaviour to satisfy increased metabolic rates lead to higher predation mortality. Similarly Akimova, Hufnagl, et al. (2016) showed a positive effect of increased temperatures on larval survival with a biophysical-IBM if the effect of increased growth is able to counterbalance the increased temperature dependent mortality. Larvae and juveniles in the North-eastern North Sea in April and May 2001 showed a positive effect of faster growth on survival (Nielsen & Munk 2004). An analysis of match-mismatch dynamics of larval cod and their prey with an IBM and temperature data for the North Sea, showed higher duration of overlap between larvae and zooplankton prey during warm years (Kristiansen et al. 2011). This is due to earlier bloom dynamics caused by increased temperature. However, the authors did not account for effects of changing prey composition under elevated temperatures.

3.2 Transport

Oceanographic features can strongly affect the dispersal of larvae via drift and their orientation in the water column. Brander (1992) noticed a marked change in distribution of cod larvae between the period of 1948 to 1956 as well as 1974 to 1983. In the earlier years, cod larvae occurred mainly in the German Bight and the Northwest of the North Sea, whereas in the latter large abundances of larvae were found in the North and Central East along the Norwegian Trench. Proposed explanation was the northward shift of spawning since 1950. Rindorf & Lewy (2006) evaluated the time 1983 to 2003 and noticed a northward shift in distribution, too. Their hypothesis was that northward drift of eggs and larvae in winter due to a series of higher temperatures and southerly winds lead to this change. These drifted individuals remained in the north during their juvenile life and recruited to the local stock, therefore shifting the general spawner distribution to the North.

3.2.1 Drift related to internal North Sea circulation

Larvae drift in winter and spring in the North Sea is determined through the internal circulation. Main influences comprise the temporal and spatial variation in wind pattern, Atlantic water inflow, temperature and salinity differences as well as large scale oceanic influences such as the North Atlantic Oscillation (NAO). Many field studies on larval drift focus on the Skagerrak population. There eradication of local cod populations resulted in low spawner abundance (Cardinale & Svedäng 2004). However high abundance of juvenile cod points to possible source-sink dynamics with drift of eggs and larvae towards the Skagerrak from North Sea populations (Cardinale & Svedäng 2004, Stenseth et al. 2006, Svedäng & Svenson 2006). Knutsen et al. (2004) combined DNA analysis and hydrographic modelling of southward inflow into the Skagerrak and found the composition of the local juvenile population related to the variability in inflow events. Recent studies on larval drift in the North Sea used IBMs (Individual based models) coupled to ocean circulation models to simulate potential drift paths of cod larvae (Peck et al. 2009, Jonsson et al. 2016, Sundby et al. 2017, Huserbråten et al. 2018). For the southern North Sea large scale atmospheric pattern are believed to play a crucial role as shown by an association between the NAO, temperature and the spread of drift trajectories in the model of Peck et al. (2009). Colder temperatures under negative NAO experienced in the egg and larvae stage might prolong development times and therefore increase spread and drift duration (Peck et al. 2009). Positive NAO and warm temperatures resulted in stronger retention. However most retention in the model was observed to be in years where the NAO-index was close to zero, which indicates other oceanographic processes unrelated to the NAO to be important. Drift of larvae from the southern North Sea to the Skagerrak is higher in years with a high NAO-index, especially if spawning is early (Jonsson et al. 2016). This contradicts genetic studies of Knutsen et al. (2004), who found 2001, a year with a strong negative NAO, related to high inflow and large transport of larvae of North Sea origin into the Skagerrak. The drift model of Huserbråten et al. (2018) found a large proportion of larvae originating from spawning sites in the northern North Sea to settle along the western Norwegian shelf of the Viking Bank area from 1995 - 2016. Cod larvae spawned over the Northern North Sea plateau showed a high retention, making the area between Viking bank, Fladen grounds and Utsira High the most important settlement area in the study. Larvae originating from Fisher Bank showed a drift into the Skagerrak following a “Skagerrak loop” with high retention within the area. However, the authors pointed out considerable variability in drift and retention between years. This was also shown by a drift model of Kvile et al. (2018) who found considerable inter-annual as well as spatial differences in retention at settlement, with higher retention in the South than in the North East (Viking). 2012, a year with positive NAO-winter index showed less simulated retention than 2013, a year with negative NAO-winter index. Transport from the south in 2012 was mainly towards the Skagerrak and from the North East to the North West. In 2013 export from the Viking occurred to the North in direction of the Norwegian Sea out of the study area. This is in accordance to Pingree (2005), who showed negative NAO associated with southerly to south easterly winds, reducing Atlantic water inflow in the north, weakening North Sea internal circulation pattern and increasing outflow through the Norwegian Trench. In conclusion, positive or negative NAO index are not uniformly affecting cod early life stage transport for the whole North Sea. Instead, conditions that result in higher drift of southern populations might result in higher retention in the North and vice versa. However, linking flow events and circulation pattern to the NAO might be considered with caution as correlations for volume transport and temperature are weakened for regions with Atlantic inflow in the Southern North Sea (Hjøllo et al. 2009, Mathis et al. 2015). Additionally, different circulation modes are positively correlated with the NAO with different strength (Mathis et al. 2015) making links between NAO and larvae drift difficult.

3.2.2 Frontal zones and their role in retention

An important feature of shelf seas are frontal zones, where water of different origin meet. At fronts transport processes are slowed down, providing an area of retention for various life forms (Bakun 1996, 2006). Within the North Sea fronts develop near the continental shelf due to differences in bottom topography (shelfbreak fronts) e.g. at the Norwegian Trench, in the north where inflowing Atlantic water meets more basin/coastal influenced water and in the south due to freshwater discharge of rivers entering the North Sea from the continent. Various studies of Munk (Munk 2007, 2014) and Munk et al. (Munk et al. 1995, 1999) examined the relationship between cod larvae and hydrographic features of fronts in the North Sea. Most of these studies focus on the area around Fisher Banks and the Skagerrak at the vicinity of the shelf-break front at the Norwegian Trench. Here fronts form between relatively warm water of intermediate salinity coming from the Danish Coast via the Jutland Costal Current (JCC) and low salinity and intermediate temperature water masses flowing along the Norwegian coast as the Norwegian Coastal Current (NCC), both overlaying colder and more saline water masses of Atlantic water within the Norwegian Trench (Munk et al. 1995, Munk 2014). At the southern shelf slope upwelling of cold water occurs (Munk et al. 1995). Cod larvae were found almost evenly distributed along the front and peaked in close proximity or directly within the hydrographic front with the zone of inclining pycnoclines in May 1992 (Munk et al. 1995). Munk (2014) reported cod larvae showing a relatively wide spread distribution in shallower inshore waters (30 – 40m in depth) across the front in May 1997. Larvae size varied also across the front – with smaller larvae appearing directly inshore of the front with increasing size at off-and onshore direction. Fronts in the southern part of the North Sea are freshwater-driven-haline fronts in winter and early spring before stratification develops. Warmer, more saline water from the Atlantic enters the North Sea from the north and meets these low salinity waters influenced from river discharge at the vicinity of the German Bight/ Horns Reef and the south-western part of the Dogger Bank (Munk et al. 2002). Munk et al. (2002) found cod larvae in March associated with haline fronts at the southwest and northeast of the Dogger Bank as well as the German bight. In the North a study of Höffle et al. (2013) evaluated the occurrence of hydrographic features and cod larvae between April and May. Larvae were associated with haline fronts and zooplankton concentration at the western and eastern margins of the region. The region is influenced by Atlantic water inflow. Regardless of the known association of eggs and larvae with frontal zones, the mechanisms, which drive variability in recruitment, are not fully understood.

3.3 Diet and feeding conditions

3.3.1 Prey species utilized

Last (1978) examined food items of cod larvae in the eastern English Channel and southern Bight in the southern North Sea. Feeding already started in the yolk-sac stage, with primarily on diatoms. Larger larvae > 4mm mainly feed on *Pseudocalanus minitus* and *Paraclanus parvus* nauplii as well as *Acartia clausii* nauplii. With increasing size, they started to feed on copepodits of *Pseudo/Paracalanus*. Larvae diet in the northern North Sea around the Shetland Islands (Economou 1991) consisted of copepod nauplii and eggs of *C. finmarchius* in the early stages and changed to copepodits of the small copepod *Oithona similis*, *Acartia clausii* and *Pseudocalanus elongatus* with medium larvae size. *C. finmarchius* was dominant in the diet of older larvae. The difference in diet between northern and southern cod sub-stocks in the North Sea is part of a bigger pattern of northern stocks relying on *C. finmarchius* as main food item, whereas southern stocks use *Para/Pseudocalanus* for their diet (Heath & Lough 2007). Pitois & Fox (2008) questioned a reliance on *C. finmarchius* for the whole North Sea, because cod was shown to be successful in areas where *C. finmarchius* was never abundant. Rothschild (1998) noticed that large year classes of cod in the North Sea required either large year classes of *Calanus* or *Paracalanus/Pseudocalanus*, but a high abundance of *Calanus* or *Paracalanus/Pseudocalanus* did not necessarily resulted in a large year class of cod. The community change of zooplankton during the North Sea regime shift around 1987 due to increased temperature and in the following a reduction in the boreal *C. finmarchius and euphausiids* as well as an increase in more temperate Atlantic species indicated by *C. helgolandicus* (Beaugrand et al. 2003, Beaugrand 2004), is believed to be the main cause of impaired cod recruitment in the North Sea. Additionally Alvarez-Fernandez et al. (2012) detected a decrease and change in seasonal pattern of dinoflagellates and dominant neritic zooplankter like Para/Pseudocalanus spp. and Temora sp. from 1998 on. The authors linked these changes to the recruitment failure of several North Sea fishes, including cod.

3.3.2 Microturbulence, Frontal Zones and Prey

Different hypothesis exist, which hydrodynamic features in the ocean are favourable for the encounter of larval fish and their prey. On the one side of the spectrum is Lasker's "Ocean stability" hypothesis (Lasker 1978, 1981) originating from his work with anchovy in the upwelling system of the California Current. The author found strong winds and upwelling disrupting stable mesoscale hydrographic structures associated with larval anchovy food aggregations to be detrimental for larval survival. On the other hand wind and tide induced microturbulence can enhance prey-encounter rates of fish larvae and their prey (Sundby & Fossum 1990, Mackenzie & Leggett 1991, Sundby et al. 1994). For Northeast Arctic Cod at the Lofoten (Sundby & Fossum 1990, Sundby et al. 1994) found an increase in feeding rates with increased wind speeds. However Sundby et al. (1994) also noticed a decrease in prey concentration with increasing wind speeds due to stronger mixing. Theoretical work of Mackenzie et al. (1994) showed that the relationship between feeding success and turbulence is dome-shaped, as prey items become harder to pursuit with increasing turbulence. An IBM for cod and haddock larvae at Georges Bank showed detrimental effects of medium to high turbulence on feeding success of larvae (Werner et al. 2001). The authors noted that these ranges of turbulence are frequently observed at Georges Bank. For the North Sea, no studies on microscale turbulence and cod larvae exist to this moment. Many studies linked recruitment with the large-scale atmospheric pattern NAO. However as the NAO strongly affects other environmental variables such as temperature, the effect of wind-induced turbulence is not easy to resolve. North Sea cod larvae are strongly associated with the development of stable frontal zones (see paragraph "*Frontal zones and their role in retention*"), which reduce advection and show increased abundance of zooplanktic prey and therefore enhancing growth for cod (Munk 2007). In their analysis of lipid biomarkers in larvae and juveniles cod of the North Sea, St. John & Lund (1996) could show prey utilisation near frontal zones, indicative by a more diatom based diet, lead to better condition in juveniles than utilisation of food sources from stratified waters. Disruption of these zones due to prevailing strong winds or episodic events such as storms might have negative impacts on larvae survival. However, studies looking on between year variability in front formation, zooplankton concentration and recruitment are rare until today.

3.4 Calanus finmarchicus and Inflow of Atlantic water

The "gadoid outburst" in the 1960s and 1970s as well as the ongoing decline lead to a number of studies, who linked recruitment success in North Sea cod to the abundance of the copepod *Calanus finmarchius* (Cushing 1984, Rothschild 1998, Beaugrand et al. 2003, Beaugrand & Kirby 2010), as it represents an important food item for cod or at least a proxy for favourable conditions. Here we review in short the dynamics of *C. finmarchicus* in the North Sea and adjacent Seas to get an idea how a change in the abundance of this zooplankter could affect the recruitment in cod. Within the North Sea there is no self-sustaining population of *C. finmarchicus*, as the species overwinters in deep regions (> 500m depth), which are only found in the Norwegian Trench area in the North Sea. Therefore, the North Sea population relies mainly on inflow of *C. finmarchius* from adjacent seas. Advection of *C. finmarchius* into the North Sea is hypothesised (see hypothesis of Backhaus et al. (1994)) to originate mainly from the Faroe-Shetland Channel in the North West (Heath & Jónasdóttir 1999, Harms et al. 2000) and southern Norwegian Sea via the Norwegian Trench in the North East (Madden et al. 1999) - two main overwintering habitats for adult *Calanus* (Heath et al. 2004). They represent the southernmost edge of the deep source population within the southern Norwegian Sea gyre. *C. finmarchicus* adults emerge from diapause by ascending towards intermediate layers starting in February were they mate and spawn around March. Adults, eggs and naupli are then transported into the North Sea, where they function as important food source for cod early life stages. The dynamics of *C. finmarchicus* in the North Sea therefore strongly depend on the temporal and spatial dynamics in the source regions, variability in *C. finmarchicus* abundance within inflowing waters into the North Sea and variability of the inflow itself.

3.4.1 Changes in the source region

Calanus finmarchicus population are not varying uniformly over the eastern North Atlantic. While *C. finmarchius* populations have decreased across the European Shelf including the North Sea since the late 50s (Planque & Fromentin 1996, Beare, Batten, et al. 2002, Beaugrand et al. 2003, Papworth et al. 2016), Atlantic populations further south of Iceland increased between 1958 and 1996 (Beare, Gislason, et al. 2002). However, in the south eastern Norwegian Sea the spring abundance of *C. finmarchius* decreased from the year 2000 onwards (Dupont et al. 2017). In addition, the spring peak occurred earlier and the duration decreased. Similar observations were made in the south western part of the Norwegian Sea north of the Faroe Islands. In this area overwintering *C. finmarchicus* decreased and younger stages increased since 2003 (Kristiansen et al. 2016, 2019). *C. finmarchicus* in this area is positively correlated with the Subpolar-Gyre-Index lagging one year (Kristiansen et al. 2019), which determines the Transport of Atlantic water masses into the Norwegian Sea. The weakening of the SPG in the mid 1990s, with a low state in 2003 allowed warmer water masses of Atlantic origin to expand further north (Häkkinen & Rhines 2004, Hátún et al. 2005) leading to a retreat of *C. finmarchicus*. Other large scale phenomena might play a role too, as *C. finmarchicus* population in the Norwegian Sea is positively reacting to an increased Norwegian Gyre circulation (Kristiansen et al. 2019), associated with stronger wind stress curl over the area reflected by positive NAO phases (Chafik 2012).

3.4.2 Variation in North Sea inflow and Variability in abundance of C. finmarchicus

The amount of *C. finmarchicus* being advected into the North Sea depends strongly on the flow regime in the Faroe-Shetland channel. There Norwegian deep water flows in southerly direction from which *C. finmarchicus* ascends and gets entangled in the Continental slope current near the surface flowing in north-easterly direction and part of it branching into the North Sea (Backhaus et al. 1994, Heath 1999). The main instream path of Atlantic water to the northern North Sea are the Fair-Isle Current between Orkney and Shetland, the inflow east of the Shetland islands and at the western slope of the Norwegian Trench (Winther & Johannessen 2006), with the magnitude of inflow over the Norwegian Trench equal the other two sources (Winther & Johannessen 2006). Analysis of CPR-data from 1958 to 1993 pointed to the Norwegian Trench inflow as main intrusion route of *C. finmarchicus* into the North Sea (Heath et al. 1999). Two main factors are described by Heath et al. (1999) to result in successful invasion of *C. finmarchicus* into the North Sea – the supply of Norwegian deep water, bringing *C. finmarchicus* into the Faroe-Shetland Channel and favourable wind conditions mostly from North West to result in *C. finmarchicus* getting caught in the inflow path into the North Sea. The occurrence probability of both conditions declined since the late 1960s. The authors noted that both factors respond to changes in the NAO, however, with the Norwegian deep water reacting slower on decadal time scales. The inverse relationship of *C. finmarchicus* with the NAO found by Fromentin & Planque (1996) was believed to reflect the inflow over the Norwegian Trench. However the relationship broke down in 1996 (Planque & Reid 1998). Reid et al. (2003) attributed the cause of this breakdown to the reduction of *Calanus* in the overwintering areas, rather than a reduction in inflow, which the authors still understood to be a response to the NAO. Additionally temperature changes of the Continental slope current entering the North Sea are believed to reflect the abundance of *C. finmarchicus* in the inflow. Several authors concluded that an advection of *Calanus* into the North Sea from the North Atlantic is accompanied by a decrease in temperature (Sundby 2000, Beaugrand et al. 2003, Reid et al. 2003). In the region of the Faroe-Shetland Channel Atlantic waters of different origins meet (Hansen & Østerhus 2000, Hansen et al. 2017). One is the Continental slope current/shelf edge current coming from Rockall through in the south and carrying warm saline waters of subtropical origin and the other coming from the west carrying colder and fresher waters of subpolar origin. During a strong subpolar gyre, the flow of subtropical water is more confined to the shelf edge and Atlantic water of subpolar origin already mixes in the vicinity of the Rockall Channel, whereas under a weak gyre subtropical water extends farther North (Hátún et al. 2005). Beare, Batten, et al. (2002) explained the higher temperature, the decrease in *C. finmarchicus* and an increase in more temperate Atlantic species in the North Sea with the stronger influence of the Continental Shelf slope water entering the North Sea via the Fair Isle current.

3.5 Predation

Pálsson (1994) reviewed the predation pressure on cod early life stages. Important fish predators on larval cod were mostly anchovy, herring and sandeels (Garrod & Harding 1981). Lindley et al. (2003) found an inverse relationship between cod recruitment and abundance of young fish in CPR data of the North Sea, either indicating an opposite response to the environment, competition or predation on early life stages. Modelling of Speirs et al. (2010) showed that especially herring could play a crucial role in the decline of cod due to predation on early life stages in the North Sea. Even under low fishing pressure, recovery of the stock was impaired. Medusae and ctenophores like *Aurelia aurita* were also frequent predators on both eggs and larvae of cod. Especially young larvae were vulnerable to predation (Bailey & Batty 1984, Titelman & Hansson 2006). Koenigstein et al. (2017) integrated predation by jellyfish in a recruitment model of cod in the Barent Sea. However in shelf seas like the North Sea jellyfish abundance starts to increase in May and June (Gibbons & Richardson 2009), where abundance of cod larvae is already decreasing.

4. Juveniles

4.1 Temperature and effects on growth

Temperature plays a crucial role in the juvenile stage. Within the first 1.5 years of their life growth in juvenile cod is positively correlated to temperature (Rindorf et al. 2008). Harrald, Neat, et al. (2010) found growth rates of cod juveniles from the western North Sea to increase from 8 °C to 12 °C and still far from the optimum temperature. Tirsgaard et al. (2015) showed for small juveniles from the Kattegat area to have a higher optimal temperature than older age classes (14.5 °C for 50g, 11.8 °C for 200g and 10.9 °C for 450g cod). This is in accordance with laboratory studies, which showed optimal temperatures for growth of reared cod decreasing exponentially with weight ranging from approximately 15 - 17 °C for 2g fish to 7 - 9.2 °C for fish weighting 2000g (Björnsson et al. 2001, 2007, Björnsson & Steinarsson 2002). The observed warming of the North Sea might therefore have different consequences on different life stages and as such on recruitment. Studies on growth conditions for cod juveniles of the Skagerrak coastal population, which is distinct from the offshore population within the North Sea, indicate detrimental effects of temperature since the 2000s. Summer temperatures regularly exceeded the optimal window for growth, resulting in growth reduction (Laurel et al. 2016).

4.2 Habitat and Density dependence

The 0-group is the time in the life cycle of cod where they change from a pelagic to a demersal lifestyle. Settlement for cod at least in the northern North Sea takes place in a pulse lasting about a month in shallow near shore waters (Bastrikin et al. 2014). At the bottom density-dependent effects are shown to take place for different cod stocks (Robichaud & Rose 2006, Lough 2010) possibly due to the limited availability of suitable bottom habitat in terms of feeding and shelter from predation. A modelling study by Walters & Juanes (1993) emphasised this. The authors showed that properties of classic Ricker or Beverton-Holt stock-recruitment relationships emerged simply by considering habitat related energy balance of juvenile fish between foraging and predator avoidance. The latter is also evident in field studies. Settlement of cod did not differ between substrate types in juvenile cod of Nova Scotia, however survival and growth rates did (Tupper & Boutilier 1995). This does not necessarily fall together, showing a trade-off between suitable feeding and predator avoidance. Therefore, structural complex habitats, with feeding grounds and shelter in close proximity are more favourable for juvenile cod (Tupper & Boutilier 1995, Borg et al. 1997, Persson et al. 2012, Grabowski et al. 2018). Macrophytes are shown to be associated with both suitable feeding (Tupper & Boutilier 1995) and as shelter habitat (Borg et al. 1997, Laurel et al. 2003, Persson et al. 2012). Especially eelgrass (*Zostera marina*) have been shown to be of paramount importance as nursery habitat for cod (Lilley & Unsworth 2014). For relief types finer grained sand bottom is preferred over vegetation covered (Persson et al. 2012) or coarser grained types in the absence of predators (Gotceitas & Brown 1993), due to increased foraging efficiency (Persson et al. 2012). However in the presence of predators coarser substrate types such as gravel and cobble are chosen (Gotceitas & Brown 1993, Lough 2010). For Georges Bank Cod Lough et al. (1989) and Lough (2010) suggested that the availability of coarse gravel habitat and predator distribution over the area represented an important recruitment bottleneck for the cod population. The availability of cover in laboratory experiments was also shown to mitigate effects of cannibalism by older age classes on 0-group cod (Theodorou et al. 2013). In the North Sea, only few studies evaluated the influence of habitat on juvenile cod. Most of these are done for coastal populations in the Skagerrak/Kattegat area (e.g. Borg et al. 1997, Fromentin et al. 2001). Fromentin et al. (2001) found differences in density-dependence between patches of coastal populations of cod in the Skagerrak area and explained them with differences in the bottom flora. Pihl et al. (2006) found 0-group cod densities largely reduced at sites where former *Zostera marine* habitat disappeared. The authors concluded that the 60% area loss of *Zostera marina* in the Swedish Skagerrak area lead to a severe impairment of recruitment in cod. Loss of suitable nursery habitat can therefore greatly increase density-dependent effects, felt by the juvenile population. To date the effects of bottom habitat for the life cycle and recruitment of demersal fishes is mainly ignored in assessments (Caddy 2008, 2014). This might be due to the understanding that bottom habitat is somewhat stationary, with limited inter-annual changes and therefore not responsible for fluctuations in fish recruitment. Albeit Frederiksen et al. (2004) found substantially change in the spatial distribution and coverage of eelgrass patches in the Kattegat area over the course of seven years. Therefore understanding changes in bottom habitat could potentially improve our understanding of bottlenecks in the life cycle of cod.

4.3 Diet

The food composition of cod was extensively evaluated by Daan (1973). During their life, cod changes from a crustacean based towards a fish based diet, with considerable differences between the southern and northern North Sea. In the southern part, juvenile cod between 5-20 cm in size were mainly feeding on invertebrates with crustaceans comprising the paramount quantity (55 – 65% of their diet) and polichaetes and mollusca to a lesser extent. The main crustaceans were in decreasing importance Pandalidae and Crangonidae, Paguridae and Portunus. Fish comprised approximately 17 – 27% of their diet, mainly sandeel, sprat, common dab and cod. In the northern North Sea cod juveniles in the size class 5-20cm were more dependent on crustaceans (70 - 95%), however with a great amount of unidentified food items. Information from Demain et al. (2011) from the northwestern North Sea, found cod between 5-10cm in length feeding mainly on crustaceans – early on mostly on the Copepods *Temora longicornis* and *Calanus finmarchicus* and later cyprids, decapod larvae and *Crangon crangon.* The proportion of fish in their diet, mainly sandeel, increased during transition to deeper waters. This is in accordance with Bastrikin et al. (2014), who showed cod < 3cm exclusively feed on copepods and later in an increasing extent on benthic food items comprising a variety ranging from *Crangon crangon*, megalopa larvae of craps, euphausiids, molluscs and amphipods to sandeel and plaice as dominant fish prey.

4.4 Competition

In general, feeding competition in cod might occur in the settlement period as well as in the bottom habitat. There other juveniles of demersal species are likely to interfere with cod through competition for food and space. However, the extent of competition is strongly dependent on timing and spatial overlap and cannot only be resolved from similar feeding niches. Although cod and whiting (*Merlangius merlangus* L.) showed strong niche overlap across the North Sea (Hop et al. 1994, Fjøsne & Gjøsœter 1996, Shaw et al. 2008), increasing feeding niche separation with progression from a pelagic to a more benthic lifestyle (Demain et al. 2011) as well as different duration and timing in settlement period (Bastrikin et al. 2014) makes feeding competition for these two species only possible for a short period during the pelagic stage (Shaw et al. 2008, Demain et al. 2011). Which of these species has the competitive advantage over the other is not entirely clear as studies showed either whiting or cod having a larger feeding niche than the other (e.g. Fjøsne & Gjøsœter 1996, Shaw et al. 2008).

The degree of competition between cod and flatfish is not resolved yet. The strong increase in plaice in the southern North Sea in recent years might exert considerable competition with 0-group cod over benthos. Plaice showed a different diet than cod, mainly consisting of polychaeta, as well as crustaceans – mainly amphipoda and decapoda, mollusca and Echinodermata (De Clerck & Buseyne 1989). Large plaice consumed also fish species, mainly sandeels. If there is competition between cod and plaice it might be over crustacean species as well as sandeels. However as 0-group cod are able to feed on 0-group dab and plaice (Daan 1973, Ellis & Gibson 1995, 1997, Bastrikin et al. 2014), possible negative effects of flatfish presence on cod might be mitigated.

Van Denderen & Van Kooten (2013) incorporated feeding competition of juvenile stages of Cod and Herring into a mechanistic model showing possible explanations for the “gadoid outburst” due to the herring collapse and a release from competition in the past.

4.5 Predation

Information on piscivorous predation on cod in the North Sea was summarised by (Pálsson 1994) showing whiting (Hislop et al. 1991), horse mackerel (Dahl & Kirkegaard 1987) and grey gurnard (De Gee & Kikkert 1993, Floeter et al. 2005) to be important predators. Cannibalism of cod by older conspecifics is also a strong factor (Daan 1973).Whiting as the main piscivorous predator in the North Sea and with a ubiquitous distribution feeds regularly on small 0-group cod, with predation mortality in some years almost as much as cannibalism by cod (Pope & Macer 1996). Horse mackerel migrate to the northern and eastern North Sea for feeding in summer. As population parameters like stock size and age structure (only large horse mackerel 4+ migrate) as well as inflow events of warm Atlantic water largely determine these migrations (Iversen et al. 2002), predation pressure on juvenile cod might be quite variable between years. The increase in grey gurnard since the late 1980s in the North Sea exerted considerable predation pressure on 0-group cod. Results of a multispecies virtual population analysis (MSVPA) indicated 60% was due to predation by grey gurnard (Floeter et al. 2005). Kempf et al. (2013) assessed temporal and spatial overlap of 0-group cod with grey gurnard via Species distribution modelling (SDM) and found recruitment success negatively correlated with spatial overlap of both species. The authors attributed the increase in population numbers of grey gurnard from the 1990ies onwards and a general northward expansion of the species due to increased water temperatures to the stronger predation pressure on cod. However low salinity waters like in the Skagerrak area and temperatures < 14°C might act as a refuge for cod from predation by grey gurnard. Comparison of stomach analysis between 1991 and 2013 for grey gurnard found fewer 0-group cod in the diet of Grey gurnard in 2013, possibly attributed to the lower abundance of juvenile cod (Huwer et al. 2014). In the SMS stock assessment model key run for cod 2017 (ICES 2017), piscivorous predation by grey gurnard comprises the largest fraction of predation mortality on 0-group cod since the 1990s, with whiting and cod predation being much smaller. In the age class 1, cannibalism is the almost solely remaining piscivorous predation pressure. Additionally predation by harbour porpoise and grey seals make up a large fraction.

5. Summary

Cod recruitment in the North Sea is understood to be a result of a multitude of effects comprising the whole range from bottom up to top down processes (Table A.1.2). The most prominent processes comprise the change in spatial dynamics of North Sea cod, the heterogeneous stock structure, effects of a warming North Sea, transport/retention processes of either early life stages or their food related to hydrographical structures (fronts, Atlantic inflow) as well as predation pressure exerted during egg, larvae and juvenile phase. There is a large extent of studies, which focused on the effects of temperature, as it is strongly affecting cod early life stages both directly and indirectly with the overall effect to be negative. This is most likely attributed to a combination of the direct effects of a distributional change, growth and mortality and indirect effects due to interaction with zooplankton and/or Atlantic water inflow. Additionally the role of zooplankton prey and match-mismatch dynamics got a lot of attention and it is believed to be one of the recruitment bottlenecks. Predation pressure by clupeids and grey gurnard also received attention in the recent years. However, which of these processes dominate to shape recruitment dynamics of North Sea cod is poorly resolved and interactions and/or masking effects of different environmental drivers make it difficult to pinpoint real causal relationships.

Table A.1.2: Correlative/statistical studies, taking into account environmental variables on recruitment

Environmental variable	Region	Relationship	Explanation/Proposed mechanism	Author
SSB	North Sea	Compensatory response	Recruitment level determined by SSB, density-dependent effects	(Brunel & Boucher 2007, Hjermann et al. 2013, Pécuchet et al. 2015, Akimova, Núñez-Riboni, et al. 2016)
	North Sea	Compensatory or Over-Compensatory response	SSB-effect additionally modified by food availability	(Olsen et al. 2011)
Temperature	North Sea	-	Either direct effect or a proxy for food abundance, Atlantic inflow, … (see various chapters)	(Dickson et al. 1974, Dippner 1997, Planque & Frédou 1999, O’Brien et al. 2000, Brander 2000, Clark et al. 2003, Planque et al. 2003, Cook & Heath 2005, Brunel & Boucher 2007, Kempf et al. 2009, Olsen et al. 2011, Hjermann et al. 2013, Nicolas et al. 2014, Pécuchet et al. 2015,

				Akimova, Hufnagl, et al. 2016, Sguotti et al. 2019)
	North Sea	-	Reduced inflow of warm Atlantic water	(Svendsen et al. 1991)
	Skagerrak	Dome-shaped	Optimal temperature for development	(Cardinale & Svedäng 2004)
Salinity	North Sea	-	Reduced influence of low salinity Norwegian coastal water in the North West North Sea	(Svendsen et al. 1991)
Wind	North Sea	+	Wind-induced turbulence during the first quarter	(Svendsen et al. 1991)
	Skagerrak	+	Frequency of westerly winds and transport of cod eggs from the North Sea into the Skagerrak via drift	(Cardinale & Svedäng 2004)
Currents	North Sea	Not reported	Effect of mixing and turbulence or transport processes	(Pécuchet et al. 2015)
Nutrients (NO_3)	North Sea	Not reported	Eutrophication	(Pécuchet et al. 2015)
Zooplankton:				
Calanus finmarchicus (and related indices)	North Sea	+	Favourable feeding conditions through *C. finmarchicus* and/or associated zooplankter for cod early life stages	(Cushing 1984, Pepin 1990, Beaugrand et al. 2003, Beaugrand & Kirby 2010, Fauchald 2010, Olsen et al. 2011, Nicolas et al. 2014)
Para/Pseudocalanus index	North Sea	None		(Beaugrand & Kirby 2010)
Predation:				
Herring biomass	North Sea	-	Predation of eggs and larvae	(Pepin 1990, Fauchald 2010, Minto & Worm 2012, Hjermann et al. 2013)
CPR-young fish	North Sea	-	Effect via predation or competition	(Lindley et al. 2003)
Predation index	North Sea	-	Spatial overlap with the main predators of cod juveniles (Cod, Whiting, Grey gurnard)	(Kempf et al. 2009, 2013)

Jellyfish	North Sea	None	Shelter effect as observed for whiting, proposed for cod	(Lynam & Brierley 2007)
Large scale Indices:				
AMO (Atlantic multidecadal Oscillation)	North Sea	-	Influence of warm Atlantic water	(Sguotti et al. 2019)
NAO (North Atlantic Oscillation)	North Sea	none	A multitude of effects on local environmental variables in the North Sea like temperature, wind pattern, currents, inflow of Atlantic water and abundance of zooplankton	(Cardinale & Hjelm 2003)
	North Sea	-		(Dippner 1997, Lindley et al. 2003, Brander & Mohn 2004, Stige et al. 2006)
GSI (Gulf Stream Northwall index)	North Sea	-	Influence of Atlantic warm Atlantic water propagation into the North Sea	(Lindley et al. 2003)

6. Knowledge gaps

Apart from all the known influences and hypothesis on cod recruitment in the North Sea there is still a gap in identifying the causes for the current low recruitment and the related bottleneck(s) in the life cycle of cod. As many processes are interlinked and “everything correlates with everything”, especially temperature, it is hard to identify real causal interactions. Correlative recruitment studies look either on local abiotic indices or large scale indices. However, mechanisms that exert their effect on cod recruitment within the North Sea might have their origin elsewhere (e.g. Atlantic water inflow and *C. finmarchicus*), which requires one to look beyond the boundaries of the stock’s distribution.

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Annex A.1.2 Recruitment of North Sea autumn-spawning herring

Life cycle of North Sea autumn spawning herring (Clupea harengus) and processes that might affect recruitment variability

1. Effects of the Spawning population

1.1 Stock structure and spawning components

In the North Sea several different herring stocks with different spawning strategies reside, which mix throughout the year. There are the autumn and winter spawners, which are managed as a single stock (ICES subarea 4, devisions 3a and 7d). On the west coast of Norway the southernmost tip of the large Norwegian spring-spawning herring stock are found (ICES subareas 1, 2, 4, 4a, 14a). Additionally there are the spring-spawners from the Skagerrak, Kattegat and western Baltic (ICES subdevisions 20-24). Stock mixing between spring spawners from the Skagerrak/Kattegat/Baltic and autumn spawners is especially apparent in the Skagerrak in summer and winter, whereas in the northern North Sea mostly the autumn spawners and Norwegian-spring spawners mix (Ruzzante et al. 2006). However during the spawning time the different stocks are separated, due to return of herring to their spawning origin, possibly based on learned behaviour (McQuinn 1997, Corten 2002). As the autumn and winter spawning stocks comprise the largest fraction of herring in the North Sea their life cycle is discussed. The autumn spawning stock is composed of three spawning components namely the Shetland/Orkney herring at the north east of Scotland, the Buchan component at the Coast of Aberdeenshire, and the Banks herring at the north east of England and the southwest of the Dogger Bank. The winter spawning herring comprise only one component, the Downs herring situated near the Strait of Dover. Spawning starts at the end of summer (August/September) for the Shetland/Orkney and Buchan component and successively continues in September and mid of October for Banks and November/December/January for Downs herring (Zijlstra 1973, Nash & Dickey-Collas 2005, Schmidt et al. 2009). There is considerable variability in the spatial extent of spawning grounds. With the collapse in North Sea herring in the late 1960s to 1970s spawning was almost exclusively limited to the area of Shetland/Orkney (Schmidt et al. 2009). Due to the eradication of the Buchan herring stock, spawning grounds were abandoned and recovered in 1983 on Aberdeen Bank (Corten 1999). Southern spawning sites west of Dogger Bank, Downsing and Sandettie in the southern Bight were not recolonised after recovery of the stock (ICES 1977, Corten 2002). Although the herring stocks recovered, the Shetland/Orkney component dominated until the early 1990s, with the Downs herring recovery being the slowest. Another episode of low recruitment happened in the early 90s. From the late 90s on populations increased also in the central and southern North Sea, however the Dogger Bank was not recolonised. From 2000 onwards the most northern components decreased drastically, whereas the Downs stock increased and contributed most to the herring larvae in the North Sea in recent years . (Schmidt et al. 2009, ICES 2019). The different recruitment pattern of the spawning components as well as inter-annual variability in mixing of autumn and winter spawners during most of the catch season, poses a considerable challenge for maintaining spawners diversity of the total stock (Bierman et al. 2010, Dickey-Collas et al. 2010, Kerr et al. 2017).

1.2 SSB effect

For the North Sea herring stocks, different results of the extent of density regulating mechanisms exist. Some studies showed negative correlation of the combined abundance of the North Sea stocks with growth in adult herring (Burd 1984, Heath et al. 1997, Hunter et al. 2019). The overall stock-recruitment relationship shows a compensatory response under large SSB, even an over-compensatory response if one considers only the period after the great herring collapse in the 1970s (Nash et al. 2009, Corten 2013). The author explained the difference, due to a change in the stock structure and stronger vulnerability to cannibalism after 1970. The stocks in the south were reduced and the Orkney/Shetland and Buchan stock contributed the most; however, their long drift period to the nursery areas in the German Bight made them more vulnerable to predation. Others showed no evidence of density-dependent growth (Saville et al. 1984, Brunel & Dickey-Collas 2010) and pointed towards the effect of e.g. temperature shaping growth in the North Sea herring population (Brunel & Dickey-Collas 2010).

1.3 Parental effects

As for cod, similar age effects exist for herring. Fecundity increases in a hyperallometric fashion with increasing body-size in summer spawning Icelandic herring (Óskarsson & Taggart 2006, Barneche et al. 2018). However, studies on North Sea herring indicate a linear relationship between weight and fecundity (Baxter 1959, Burd & Howlett 1974). Additionally, there is evidence that fecundity shows a concave relationship with age in North Sea herring (Hickling 1940, Baxter 1959). Within a spawning group, egg weight was positively related to the size of the female, but this effect was only apparent for younger fish (Blaxter & Hempel 1963, Hempel & Blaxter 1967). Larger eggs result in larger larvae with larger yolk-sac reserves, higher growth after hatching and the ability to withstand longer periods of starvation before complete yolk-sac absorption (Blaxter & Hempel 1963). Paternal effects also contribute to larvae quality (see references in Dickey-Collas et al. 2010). The different spawning strategies in autumn and winter for North Sea herring stocks result in different reproductive investment and fecundities with autumn spawners having smaller, but more eggs, whereas winter spawners have fewer, but larger eggs (Hempel & Blaxter 1967, Zijlstra 1973, Sinclair & Tremblay 1984, Sinclair 1988, Damme et al. 2009). Changes in the relative proportions of the different spawning components can therefore greatly alter the reproductive outcome, which is not adequately represented by SSB.

1.4 Maturation

Currently maturation is between 2 and 3 years (Petitgas 2010), with a phase of late maturation (3- 5 years) from 1950 to 1960 (Cushing 1967). Maturation with age changed only little between 1970 – 2012, with most of the individuals becoming mature at age 2 (Hunter et al. 2019). Two aged individuals from the southern North Sea matured at smaller length (15 – 23 cm) than individuals from the North (21 – 25cm). The effect was possibly due to an effect of temperature and density-dependence, as herring matured earlier under rising temperatures and increased abundance particularly for males. The maturation ogive used in the assessment is derived from acoustic surveys and shows most variation in the age classes 2 and 3, with an all-time low of 37% mature at age two in the recent year 2018 (ICES 2019).

1.5 Environmental effects on spawning potential

1.5.1 Effect of feeding conditions on fecundity

Only few studies on autumn and winter spawning herring in the North Sea and reproductive investment exist. (Almatar & Bailey 1989, Bailey & Almatar 1989) noted considerably inter-annual variation in the fecundity/length relationship not attributed to density dependent effects. The authors suggested environmental effects such as food availability or temperature to be responsible. The major literature is on spring spawning herring from populations outside the North Sea. Several studies showed that low fish condition (indicated by Fulton's K) due to poor feeding conditions resulted in a reduction of fecundity and higher rates of atresia in Norwegian spring spawning herring (Óskarsson et al. 2002, Kennedy et al. 2010, 2011) and Icelandic summer spawners (Óskarsson & Taggart 2006). Dos Santos Schmidt et al. (2017) showed that low fecundities could prevail over subsequent seasons even if fish showed no impaired present condition. The authors suggested this lag effect to be responsible for the low reproductive investment in North Sea herring, possibly linked to changes in zooplankton biogeography and productivity. In the North Sea oocyte development for both autumn and winter spawners starts already in April-May, with fecundity being down-regulated via atresia, dependent on actual fish condition (Damme et al. 2009). Low feeding conditions during this time can therefore strongly affect North Sea herring reproductive investment. Adult North Sea herring mainly feed in the northwest North Sea around Orkney and Shetland, which is influenced by inflow of Atlantic water. Changes in inflow pattern as well as zooplankton composition might affect herring feeding in this area. Adult herring shifted their summer feeding further north in 1988-1990, possibly to changes in temperature and reduced abundance of *C. finmachicus* in the North Sea (Corten 2001). Indeed herring in this area were found to be associated with frontal zones, waters from the Slope current and biomass of zooplankton also actively pursuing the movements of zooplankton below the thermocline (Maravelias & Reid 1997).

1.5.2 Temperature

Temperature can also affect spawners reproductive investment directly. Increased temperature positively affected growth rate (Hunter et al. 2019) and was shown to be positively related to SSB in the North Sea (Akimova et al. 2016). A study of spring-spawning pacific Herring (*Clupea harengus pallasi)* found winter temperatures experienced before spawning, positively affecting fecundity but with the trade-off of decreasing egg weight (Tanasichuk & Ware 1987). From examination of data of Dogger-Bank herring, the authors suggested also temperature to be related to variability in fecundity. As winter temperatures influenced fecundity, the authors could rule out the possibility that this effect might be due to food availability. On their analysis on egg weight across several Atlantic herring stocks (Hempel & Blaxter 1967) found fecundity related to temperature and spawning strategy, with higher temperatures leading to higher fecundity but smaller eggs. For autumn-spawning Baltic Sea herring, elevated temperatures in late summer and autumn (August – October) were shown to cause abnormalities in ovaries (Ojaveer et al. 2015). In addition, timing of spawning might be affected, as gonad development is positively linked to temperature (Dragesund (1960), Jakobsson (1969) in Corten (2001)). To ensure spawning at the same time, North Sea herring actively adapts to increased water temperatures by migration to colder waters (see Corten (2001) and references therein).

2. Eggs

2.1 Temperature

Temperature was shown to affect hatching success in North Sea herring. Within the range between 5.5 °C to 14.5 °C the percentage of successful eggs hatching is dome-shaped with highest hatching rates between ~ 10 - 13 °C (Blaxter (1956) in Postuma (1968)). Building on this work Postuma & Zijlstra (1974) correlated temperatures at spawning sites at Dogger Bank and the Downs area with larvae abundance and found a negative relationship for Dogger and a positive for Downs herring, resembling the overall dome-shaped temperature response for eggs found earlier.

2.2 Bottom habitat

As herring are demersal spawners that attach their eggs to structures at the sea bottom, dynamics affecting the seabed as well as habitat type become crucial for egg survival. Herring eggs are typically laid over sand and gravel beds as well as attached to makrophytes (overview and several references in de Groot, 1980). These sites are normally characterised by strong current velocities preventing fine sediments to depose over the egg mats. However, gravel extraction over herring spawning grounds lowers the depth of the seabed and decreases the tidal current (de Groot 1980), which increases sedimentation. Storm events leading to increased turbidity and sediment swirling as well as subsequent sedimentation might result in considerable sediment deposition on eggs. This can lead to anoxia, which negatively affects herring embryogenesis (Braum 1973). Laboratory studies on Baltic Sea herring testing the effect of suspended silt due to increased turbidity near egg mats found no negative effect on egg survival and hatching (Kiørboe et al. 1981). However in the field sedimentation processes might still play a role as Morrison et al. (1991) observed mass mortality of herring eggs in the Firth of Clyde due to a diatom bloom and subsequent sedimentation resulting in low oxygen levels in the water surrounding the egg mat.

2.3 Drift

Drift processes in the egg phase are not frequent as eggs are attached to the bottom substrate. However, severe storm events can cause dislocation of herring eggs from their spawning grounds and washing up on nearby shores as it was shown for Pacific herring (Hourston & Rosenthal 1976, Hay & Miller 1982) and spring spawners in the Baltic Sea (Moll et al. 2018). Morrison et al. (1990) observed strong disruption of egg mats of spring spawning herring in the Firth of Clyde in the Irish Sea after a storm event. The authors, however, noted that autumn-spawning herring are less susceptible to storm-induced flushing as they spawn in deeper waters than spring spawners.

2.4 Predation

Predation on herring eggs by other demersal fish is common. Tibbo et al. (1963) reported substantial predation of winter flounder (*Pseudopleuronectes americanus*), sculpins (*Myoxocephalus sp.*), skate (*Raja sp.*) and smelt (*Osmerus mordax*) on spring spawning herring eggs in Chaleur Bay, Northwest Atlantic. Egg predation by haddock (*Melanogrammus aeglefinus*) is a common phenomenon observed for herring at Georges Bank (Richardson et al. 2011), Norwegian spring-spawning herring (Toresen 1979, Høines & Bergstad 1999) as well as the northern North Sea (Bowman 1922). Haddock predation on eggs was shown to be one explanation for impaired recovery for Georges Bank herring, as population model output as well as results of ichtyoplankton surveys indicated spatial and temporal overlap between age 1+ haddock and herring larvae (Richardson et al. 2011). Bowman

(1922) noticed considerable predation of haddock on herring eggs around Scotland. The author used information on catches of these “spawny” haddock, with a unique appearance to indirectly deduce spawning grounds of herring (de Groot 1980). In the North Sea age-1 and adult haddock abundance was shown to be highest in the North West area (Hedger et al. 2004, Asjes et al. 2016), a region where important spawning habitats for herring are situated (Orkney/Shetland and Buchan component). Therefore, predation is highly likely. Also other gadoids like cod (*Gadus morhua*), saithe (*Pollachius virens*) and pollack (*Pollachius virens*) were frequently found to prey on herring eggs of Norwegian spring-spawners (Høines & Bergstad 1999). Rankine & Morrison (1989) observed considerable predation of sandeel (*Ammodytes marinu* and *Hyperoplus lanceolatus*) on herring eggs and larvae. Cannibalism of herring on their own eggs at the end of the spawning season was observed for North Sea spring spawners at the Norwegian coast (Skaret et al. 2002).

3. Larvae

Weak year classes of herring were associated with reduced survival within the larval stage, indicated by a Paulik diagram (Nash & Dickey-Collas 2005). Especially the period between 1988 and 1990, as well as a recent phase of low recruitment from 2002 on was characterised by low early larval survival (Nash & Dickey-Collas 2005, Payne et al. 2009).

3.1 Temperature effects on growth, development and survival

The larval phase in autumn spawning and winter spawning herring is exceptional long, lasting around seven month for autumn spawners and six month for winter spawners until metamorphosis in April – June (Sinclair & Tremblay 1984 and references therein). During this time, they experience large variation in temperatures. Development and growth of herring larvae are temperature dependent, with faster growth under higher temperatures. Under sufficient food availability, growth rates of larvae in autumn are high, due to high temperatures, but decrease together with photoperiod towards winter (Gamble et al. 1985, Johannessen et al. 2000). The growth pattern follows more or less a dome-shaped response (Johannessen et al. 2000). Although herring larvae can withstand long periods of low productivity (Johannessen et al. 2000, Geffen 2009) the question remains which growth pattern and temperature regime is favourable for herring larvae. The upper limit of thermal tolerance for North Sea herring larvae in the yolk-sac stage was ~23 °C (Blaxter 1960, Yin & Blaxter 1987), but starvation could reduce thermal tolerance to around 19 °C (Yin & Blaxter 1987). Although not yet relevant in the northwestern North Sea, as temperatures are colder at the end of summer a further warming of the North Sea can increase thermal pressure on herring larvae. Results of a biophysiological IBM showed increasing survival of autumn and winter spawning herring under decreasing water temperatures in autumn and winter, with high losses already under mean temperatures > 11°C (Hufnagl & Peck 2011). Fässler et al. (2011) found a positive correlation between temperatures experienced during the first 30 days after hatching and increased mortality in larval herring for the autumns spawning stock components in the North Sea.

3.2 Drift

The role of drift in the lifecycle of herring of different populations was and still is under considerable debate. One can differentiate between two groups – the ones emphasising the importance of larval drift to lifecycle closure in herring and the ones underlining the role of retention within the spawning area as crucial. Historically drift was considered important in the lifecycle of herring. Field data indicate a transport of larvae from the western North Sea to nursery grounds in the south east with the prevalent circulation pattern (Bückmann et al. 1950, Corten 1986, Cushing 1986, Bartsch et al. 1989). For the North Sea Corten (1986) hypnotized failure of the North Sea circulation to be responsible for the low recruitment of 1972 to 1978, as only few larvae reached their nursery areas within six month in the south-eastern North Sea and Skagerrak. Reason for this was probably reduced Atlantic inflow into the north-western North Sea (Corten 2013). Comprehensive modelling studies of larvae drift using hydrographic models identified favourable circulation patterns that lead to sufficient transport to nursery grounds as an important driver of recruitment variability (Bartsch & Backhaus 1988, Bartsch et al. 1989, Bartsch 1993). Bartsch & Backhaus (1988) and Bartsch et al. (1989) made the disruption of the typical cyclonic circulation within the North Sea due to southerly and south-easterly winds as well as reduced inflow of Atlantic water between Orkney and Shetland responsible for failed advection from spawning grounds in the North West to the south-eastern North Sea. Kauker & von Storch (2000) as well as Sündermann & Pohlmann (2011) identified four different circulation pattern for the North Sea linked to the prevailing wind direction. The prevailing westerly to south-westerly winds result in a counterclockwise (anti-cyclonic) circulation pattern, typical for the North Sea, which reverses under easterly and north-easterly winds. Indeed the latter regime was observed by a drifter study in the first quarter of 2018, where persistent easterly winds resulted in displacement of drifters from the German Bight to the east coast of England (Stanev et al. 2019). South-easterly and north-westerly winds result in a stagnant regime with limited exchange between the northern and southern North Sea.

Iles & Sinclair (1982) as well as Sinclair (1988) argued that minimisation of drift in the first few month is important for herring recruitment success. Autumn herring spawn in rather consistent areas in the North Sea along the west coast of Great Britain with specific hydrographical features representing frontal or transition zones between stratified and well-mixed waters (Richardson et al. 1986, Kiørboe et al. 1988). Their stability during the first few month of the larval phase determines how well larvae are aggregated within an area. Indeed did Heath (1990) found the distribution of larvae around Orkney/Shetland to be highly correlated with the interannual variability of the major salinity front, characterising the Fair Isle inflow. Although larvae from the Buchan area (Munk et al. 1986, Kiørboe et al. 1988) were observed to drift southward, they were retained within the frontal region. This was confirmed by modelling of larval transport and vertical movement of larvae by Bartsch & Backhaus (1988) indicating that larvae in the Buchan area can be retained in the area and settle in the Firth of Forth. Sætre et al. (2002) identified retention areas for Norwegian spring-spawning herring and concluded that both drift to nursery areas as well as retention plays a crucial role in determining year class strength. Years with high recruitment were correlated with slow northward transport and rather high retention within the Norwegian coastal current. Contradictory Skagseth et al. (2015) held increased northward transport with the Norwegian coastal current responsible for favourable recruitment. Results from 22 years of larval herring surveys of northwest Atlantic Herring in the Bay of Fundy indicate strong larval retention over several month regardless of tidal residual flow as well as strong inter-annual consistency in larval herring distribution (Stephenson et al. 2015). An analysis of herring larvae surveys throughout the North Atlantic indicates that dispersal of larvae during the first two to three month, indicated by their centre of distribution between different ages of larvae, is limited (Sinclair & Power 2015). Results of a hydrodynamic modelling study by Dickey-Collas et al. (2009) of herring larvae transport from the Southern Bight (Downs component) in winter to the German Bight and comparison with inter-annual variation in recruitment also confirmed this general view. Years of high recruitment fell together with years of increased modelled retention, rather than successful delivery to nursery grounds.

3.3 Interpopulation flow

North Sea herring are connected to other populations via larval drift. Considerate inflow of larvae from the west of Scotland to the area around Orkney and Shetland with the Scottish Coastal and Fair Isle current was described by Heath & Rankine (1988). Although both regions are managed separately, (ICES VIa, IVa) recruitment overlap needs to be taken into account (Saville & Morrison 1973). Another inflow of larvae exists in the Skagerrak-Kattegat area with herring larvae coming from the North Sea (Johannessen & Moksness 1991) and mixing with individuals from the western Baltic Sea (Ulrich et al. 2012). Observations of North Sea herring at the Norwegian coast up to 70°N (Bjørke & Sætre 1994) as well as model results suggest that outflow of herring larvae to the Norwegian Sea occurs frequently even under “normal” North Sea circulation patterns (~ 20% loss) (Bartsch 1993).

3.4 Diet

3.4.1 Frontal Zones and Microturbulence

As for cod larvae in spring, herring larvae of autumn spawning herring have been observed to be associated with fronts in the North Sea. The frontal region in the North West North Sea around September/Oktober showed enriched numbers of eggs and immature copepods suitable for herring larvae feeding (Kiørboe et al. 1988). Similar associations between zooplankton, herring larvae and frontal zones have been observed by Kiørboe & Johansen (1986) in the Buchan area. Cushing (1986) argues that frontal structures might break down before herring hatch occurs, however Kiørboe et al. (1988) observed relative stability of thermal fronts up to late October, providing suitable feeding habitat over an extended period. Additional storm events occurring during the sampling time enhanced copepod egg production probably due to increased mixing and availability of nutrients for phytoplankton growth. Small scale turbulence in tidally well-mixed areas is additionally increasing encounter rates between herring larvae and their prey as shown for autumn spawning herring of Nova Scotia (Muelbert et al. 1994). Gallego et al. (1996) found a dome shaped effect of wind-induced turbulence on growth rates of larval herring in the Orkney-Shetland area with a maximum response at wind speeds of 14.5 m/s^{-1}.

3.4.2 Prey items of larvae

Larvae of late summer and autumn spawning herring benefit from the phytoplankton autumn bloom dynamics and associated zooplankton. Food items for herring larvae in the northern North Sea were mainly eggs, nauplii and copepodid stages of small copepods dominated by the calanoid species *Para-* and *Pseudocalanus sp.* (Heath et al. 1989, Lusseau et al. 2014). Also *Temora sp.* had a large portion on the diet of small herring larvae, with decreasing importance as larvae grew (Heath et al. 1989). The calanoid *Acartia sp.* was only rarely consumed or negatively selected (Checkley 1982, Heath et al. 1989, Lusseau et al. 2014). The prey species composition in autumn can have effects on larvae abundance in late winter. Alvarez-Fernandez et al. (2015) found *Pseudocalanus sp*. in October and *Temora sp.* in November had a positive relationship with larvae abundance in the northern North Sea in February, whereas abundance of *Acartia sp*. had a negative influence. The effect of cyclopoid copepods on larvae diet is not entirely clear. Heath et al. (1989) reported *Oithona sp. nauplii* not present in any larvae guts, although comprising ~ 20% of the nauplii encountered. Others found *Oithona sp.* to comprise a large fraction of larvae diet, similar to calanoid copepods (Lusseau et al. 2014) as well as increasing importance for later stages (Checkley 1982). The general pattern is similar to the diet observed for other populations of autumn spawning herring. Wilson et al. (2018), who examined feeding of autumn-spawning herring in Newfoundland, Canada, found *Temora longicornis* and *Oithona similis* being important for early larvae and *Pseudocalanus sp.* for mid-sized larvae. For late larvae stages *Calanus sp.* became important. Larvae of the Downs component hatch in mid-winter, where they encounter different temperatures as well as different prey-composition as their conspecifics further north. There do not exist many studies on winter zooplankton composition and feeding of herring larvae in winter. Just recently the importance of small plankter (micro- and mesoplankton) in the diet of marine fish larvae was rediscovered, although already known for around a century (de Figueiredo et al. 2005, 2007, Montagnes et al. 2010, Friedenberg et al. 2012, Illing et al. 2015, Denis et al. 2016, Bils et al. 2017). Denis et al. (2016) found smaller larvae (8-13mm) of Downs herring in winter to feed on a variety of prey types comprising small copepods and nauplii (the cyclopoid *Oncanea spp*. and the harpacticoid *Euterpina acutifrons*), diatoms, dinoflagellates and invertebrate eggs. Larger larvae (>13mm) fed mainly on the copepods *Temora longicornis* and *Paracalanus parvus* and dinoflagellates. *Pseudocalanus elongates* as well as *Temora longicornis* were negatively selected. A critical phase represents the shift from an omnivorious to a carnivorious diet at around 13 mm as larvae experience slower growth and reduced condition (Denis et al. 2017).

3.4.3 Food availability

Several mechanisms for the low herring recruitment since 2002, despite a recovery in spawning stock biomass, have been proposed. Many authors make low overwintering survival due to a decrease in food abundance responsible (Payne et al. 2013, Lusseau et al. 2014, Hufnagl et al. 2015, Alvarez-Fernandez et al. 2015). Payne et al. (2013) found a strong reduction in growth rates, not only attributed to temperature, of larvae mostly originating from the Banks and Buchan component during the winters 1998-2004. The authors attributed this reduction to a change in quantity or quality of prey. Combining field data with a hydrodynamic, biophysical IBM of herring larvae at the different spawning components revealed a decrease in length of larvae over time (Hufnagl et al. 2015). One process was the increased inflow of Downs herring larvae into the southern North Sea region, however, length was observed to decrease for all sub-stocks. Alvarez-Fernandez et al. (2015) found decreased abundance of *Pseudocalanus* in October after 1998, especially in the Northern North Sea, co-occurring with the decrease in herring larval abundance*. Acartia sp*. also decreased throughout the North Sea, except for the English Channel and Skagerrak where it increased. Analysis of the plankton changes in the North Sea seen in CPR data for the period 1970 – 2008 found a reduction in dinoflagellates and neritic zooplankter (*Temora longicornis*, *Para/Pseudocalanus spp*., *Centropages hamatus*) together with an increase in diatoms and warm-water copepods after 1998 (Alvarez-Fernandez et al. 2012). This effect was particularly pronounced in autumn and winter, indicating strong effects on herring due to a loss of their preferred prey. Corten (2013), however, questioned the change in plankton observed by (Alvarez-Fernandez et al. 2012) to be responsible for the herring recruitment depression since 2002, due to the four years of mismatch.

3.5 Predation

It is believed that autumn and winter spawning of herring is an adaptive response, among others, to reduce predation on larvae due to low activity of potential predators during winter (e.g. Hufnagl et al. 2015). Therefore, most predation pressure experienced in the larvae phase might be for the earlier spawning components during late summer and autumn. Most predators already preying on herring eggs are also preying on larvae such as sandeel (Christensen 1983, Fuiman & Gamble 1988, Rankine & Morrison 1989). Cannibalism by older year classes might also occur, as it was frequently observed under laboratory conditions (Fuiman & Gamble 1988, Fuiman 1989) and within the North

Sea (Daan et al. 1985, Last 1989, Gröger et al. 2010). On their way to their overwintering habitats in the north-eastern North Sea, the adult herring stock largely overlaps with drifting larvae in the central North Sea. One hypothesis concerning the recruitment reduction after 2000 was increased cannibalism from the adult stock during the larvae phase (Corten 2013). Predation by the jellyfish *Aurelia aurita* was shown in the laboratory (Bailey & Batty 1983, 1984). In the Baltic Sea, Kiel fjord, predation by *A. aurita* was observed mainly during the yolk-sac stage in May (Möller 1984). Sites with high jellyfish densities as well as years with high jellyfish abundance showed low abundance of herring larvae. For the North Sea several species of medusae (*A. aurita* and *C. capillata*) as well as overall medusa abundance co-varied with herring larvae (Lynam et al. 2005). However different signs of correlation, made the mechanism of a potential link unclear with possible explanations being competition, predation or similar reaction to environmental forcing (NAO).

4. Juveniles (after metamorphosis)

Analysis of survival between different life stages via a Paulik diagram indicated that exceptional high year classes were linked to processes affecting the transition between the larval stage (0-winter-ringer) and juveniles (1-winter ringer) (Nash & Dickey-Collas 2005).

4.1 Temperature

As for larvae elevated temperatures negatively affect 0- and 1-winter ringers, shown by a negative correlation with bottom temperature (Nash & Dickey-Collas 2005). Contrary earlier work by Postuma (1968) found higher temperatures in spring and pre-summer in the coastal nursery habitat to be favourable.

4.2 Diet

Several studies on diet of juvenile herring showed strong reliance on calanoid copepods, especially *Temora sp.* (De Silva 1973, Last 1987, 1989, Van Ginderdeuren et al. 2014). Other copepods consumed were *Calanus finmarchicus* and to a lesser extent *Pseudocalanus sp.* From the post-metamorphosis up to herring of two years their diet gradually approaches that of adults (De Silva 1973). 1-year olds showed a stronger reliance on mysids, euphasiids and fish larvae than younger ones (De Silva 1973). Last (1987) reported large amounts of post-larval sprat taken by young herring > 5cm. In addition, post-larvae sandeel (*Ammodytes sp.*) were commonly found for herring > 15 cm (Last 1989).

4.3 Predation

Predators of juvenile herring are numerous including whiting (*Merlandius merlangus*) (Hislop et al. 1991, Pedersen 1999), cod (*Gadus morhua*) (Daan 1973, Hüssy et al. 2016), saithe (*Pollachius virens*) (Engelhard et al. 2014), mackerel and horse mackerel (Dahl & Kirkegaard 1987).

4.4 Competition

Young sprat and herring showed strong diet overlap, particularly for copepods, cladocerans and the appendicularia *Oikopleura* in an area west of Scotland (De Silva 1973). However as herring grow their diet strongly diverged from that of sprat, indicating lower probability of competition. Van Ginderdeuren et al. (2014) found a high diet niche overlap between herring and sprat, indicated by the Schoener Index, in the Belgian North Sea. Additionally other clupeids (mackerel, horse mackerel) showed overlap with herring diet in MDS (Multidimensional scaling)-analysis of stomach contents, with herring having the widest niche, which might help in reducing effects of potential competition. Contrary Raab et al. (2012) found a small feeding niche for juvenile herring (12 – 15cm) in the German Bight. The authors found intermediate levels of diet overlap between herring and sprat, with likely competition over the copepods *Temora sp*. and *Calanus*. Anchovy, an emerging species in the North Sea, showed only low overlap with herring juvenile's diet.

4.5 Parasite infestation

Fish diseases can be an additional stressor on recruitment of a stock. In Pacific herring of Prince William Sound Alaska several fish diseases including *Ichthyophonus hoferi,* a mesomycetozoen parasite*,* contributed largely to reduced recovery of the stock due to higher natural mortality (Marty et al. 2010). For North Sea herring a strong infection with *Ichthyophonus hoferi* was reported in the years 1991- 1993 (Mellergaard & Spanggaard 1997). Eighty percent of young age classes (1+ and 2+) were infected, whereas fish below 20 cm showed low infection rates. The authors hypothesised that the herring stock reduction in the beginning of the 90s was a result of increased fishing pressure, combined with increased mortality of spawners and recruits due to the parasite. In 2017 and 2018 additional outbreaks occurred in the northern North Sea, with primarily age class 0-4 being infected in 2017 and in 2018 also higher age classes (5-7) (ICES 2019).

5. Summary

The autumn spawning herring in the North Sea represents a stock with a complex life cycle due to its separation into different spawning components, highly migratory life stages as well as mixing with other stocks. Environmental influences on subsequent recruitment act already on the adult stage, possibly through suitable feeding conditions. Recruitment is believed to be determined between larval and juvenile stage, but with considerable variation between years. Strong year classes were determined mainly in the juvenile phase, whereas the recruitment failure in recent years is believed to originate from a bottleneck in the larval phase. However due to the multitude of effects acting within this stage, comprising drift, temperature, feeding conditions and predation, several equally plausible hypothesises exists explaining the current recruitment failure in herring. Additionally it is likely that spatial differences in environmental effects on the whole herring population in the North Sea exist (see Table A.1.3), due to the complex stock structure and different spawning times (Downs vs. Orkney-Shetland).

Table A.1.3: Correlative/statistical studies linking recruitment in herring to environmental drivers

Environmental variable	Life stage	Region/ substock	Relationship	Explanation/Proposed mechanism	Author
SSB	various	North Sea	Compensatory or Over-compensatory	Strong stock-recruitment relationship	(Pepin 1990, Svendsen et al. 1991, Nash et al. 2009, Corten 2013, Hjermann et al. 2013,

					Alvarez-Fernandez et al. 2015)
Temperature	Early larvae (MLAI)	North Sea	+	Northern North Sea winter bottom temperature positively affects larvae (possibly direct through growth)	(Nash & Dickey-Collas 2005)
	Late larvae (MIK)	OSBB-herring	Non-linear (negative)	Temperatures in October during the Yolk-Sac stage negatively affect larvae	(Alvarez-Fernandez et al. 2015)
	Age-0-recruits	North Sea	-	Overall negative effect of averaged North Sea temperature on recruitment	(Ottersen et al. 2013)
	Juveniles (age 1-wr)	North Sea	-	Negative effect (either direct or indirect) of northern North Sea winter bottom temperatures on juveniles	(Nash & Dickey-Collas 2005)
	Age-1-recruits	North Sea	-	Negative temperature effect at the autumn spawning grounds and Skagerrak	(Hjermann et al. 2013)
	Age-1-recruits	North Sea	+	Positive temperature effect at southern and German Bight	(Hjermann et al. 2013)
	Age-3-recruits	Banks herring	-	Temperature during spawning in autumn	(Postuma 1968)
		Banks herring	+	Temperature in their nursery habitat	(Postuma 1968)
	Age-3-recruits	Downs herring	+	Temperature during spawning in winter and in their nursery habitat	(Postuma 1968)
Wind	Age-0-recruits	North Sea	+	Effect of directional wind for transport in winter and mixing on turbulence and possibly food availability in spring	(Svendsen et al. 1991)

	Age-1-recruits	North Sea	Not reported	Effect of mixing and turbulence on food availability	(Pécuchet et al. 2015)
Currents	Age-1-recruits	North Sea	Not reported	Indicator of transport	(Pécuchet et al. 2015)
		Downs herring	+	Recruitment strength positively related to travelled distance in a drift-IBM	(Dickey-Collas et al. 2009)
Phytoplankton:					
Diatom abundance	Age-1-recruits	North Sea	-	Not explained	(Pepin 1990)
Zooplankton:					
Calanus	Age-1-recruits	North Sea	+	Suitable prey conditions	(Pepin 1990)
Para/Pseudocalanus index	Age-1-recruits	Downs herring	+	Suitable prey conditions	(Cushing 1992)
	Age-1-recruits	North Sea	-	Not clear	(Cushing 1995)
	Late Larvae (MIK)	OSBB-herring	Non-uniform in space	Abundance in October positive in northern and negative in southern North Sea	(Alvarez-Fernandez et al. 2015)
Acartia sp.	Late Larvae (MIK)	OSBB-herring	Non-uniform in space	Abundance in October	(Alvarez-Fernandez et al. 2015)
Predation:					
Cod recruitment	Age-1-recruits	North Sea	-	Predation pressure	(Pepin 1990)
Gadoids	Age-1-recruits	North Sea	Not reported	Predation pressure	(Pécuchet et al. 2015)
Cod biomass	Age-1-recruits	North Sea	-	Negative effect of abundance of large cod at the nursery grounds	(Hjermann et al. 2013)
	Age-1-recruits	North Sea	+	Positive effect in the central North Sea, but mechanisms unknown	(Hjermann et al. 2013)
Jellyfish	Early larvae	North Sea	+	Similar response of jellyfish and herring	(Lynam et al. 2005)

	(LAI)			larvae to common environment	
	Age 0-wr	North Sea	-	Predation or competition	Lynam et al. 2005)
Large scale Indices:					
AMO (Atlantic multidecadal Oscillation)	Age-1-recruits	North Sea	+	Effect exerted on larvae stage	(Gröger et al. 2010)
NAO (North Atlantic Oscillation)	Age-0-recruits	North Sea	Weak	A multitude of effects on local environmental variables in the North Sea like temperature, wind pattern, currents, inflow of Atlantic water and abundance of zooplankton	(Dippner 1997)
	/	Skagerrak, English Channel	-		(Alheit & Hagen 1997)
	Age-1-recruits	North Sea	-		(Gröger et al. 2010)

6. Knowledge gaps

Although herring is one of the best researched fish stocks in terms of knowledge about its life cycle and scientific survey effort, several unanswered questions remain. Especially processes during winter are not yet or just starting to be examined. One way to gain further insight is to look again at some of the known or hypothesised mechanistic relationships and try to incorporate these into a statistical framework taking into account the unique spatial and temporal characteristics of the substocks. Additional tailoring of local environmental variables to match the spatial and temporal scales of each life stage is needed.

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Annex A.1.3 Recruitment of North Sea haddock

Life cycle of North Sea haddock (*Melanogrammus aeglefinus*) and processes that might affect recruitment variability

1. Effect of the spawning population

1.1 Stock structure/ spatial distribution

Mature haddock within the North Sea occur mainly in the north-western and central part of the North Sea, showing a strong affinity to deeper, warmer and more saline waters (Hedger et al. 2004). It further extends to the region West of Scotland and the Skagerrak. Results of tagging by Jones (1959) at the Scottish east coast showed most haddock to stay along the coast with few undertaking migrations to the west of Scotland. Concluding from parasite infestation (Lubieniecki 1977) also found a northward movement of adult haddock age three or older from inshore waters off the Scottish coast towards Shetland as well as the north-eastern North Sea. First genetic analysis of Child (1988) on haddock population structure indicated a homogenous population, whereas Jamieson & Birley (1989) found two distinct populations co-occurring in the North Sea separated by the prime meridian. According to the authors, the western sub-stock consists of haddock from the Hebrides west of Scotland, Orkney and Shetland and the east coast of Scotland. The eastern stock comprises haddock from Viking and Fisher Bank. Rockall and Faroe haddock seem to be each distinct populations indicated by a high frequency of rare alleles. Investigating potential asynchrony in SSB between the western and the eastern sub-stocks in the North Sea, Holmes et al. (2014) found no difference in SSB trends over time, indicating a more or less homogenous stock. However, one has to keep in mind that a greater proportion of the SSB is located in the west, with possibly greater influence on subsequent recruitment.

1.2 SSB effect

For North Sea haddock the recruitment (Cardinale & Hjelm 2003) as well as recruitment success (log(R/SSB)) (Ottersen et al. 2013) showed a negative relationship with SSB and total stock biomass (Cook & Armstrong 1986), indicating strong compensatory density dependence. Large year classes entering the stock are responsible for the low recruitment in the following years (Cook & Armstrong 1984, 1986). Jones (1983) pointed out that this is likely experienced in the beginning of the demersal life phase via food competition with impaired growth within a strong year class and subsequent ones (see also the juvenile paragraph for more details).

1.3 Parental effects

As for other gadoids, parental effects have been reported for haddock. Larger females do not only produce more, but also larger and heavier eggs (Hislop 1988, Trippel & Neil 2004), which positively influences size, growth and starvation resistance of hatching larvae (Rideout et al. 2005, Probst et al. 2006). Additionally, paternal influence on size and growth have been reported (Probst et al. 2006).

The age composition within the stock also plays a crucial role on offspring viability, as first time spawners produce much fewer and smaller eggs (Hislop 1988) and survivorship was shown to be poor (Wigley 1997, Wright & Gibb 2005). Therefore, no contribution of age classes 0 – 2 to the spawning stock of Northern Shelf haddock is considered to date (ICES 2018). Haddock are serial spawners (Hawkins et al. 1967) with decreasing number and size of eggs spawned later in the season (Hislop et al. 1978, Trippel & Neil 2004, Rideout et al. 2005). Several authors found the temporal pattern of hatching associated with survivability of larvae in later life. Earlier spawning/hatching seemed to be result in higher survival of larvae for various stocks (Head et al. 2005, Lapolla & Buckley 2005, Wright & Gibb 2005, Buckley et al. 2010). This is also in part related to older fish spawning earlier, than younger ones and especially first time spawners (Wright & Gibb 2005, Morgan et al. 2013). Other explanations include effects of favourable environment or reduced predation earlier in the year. A meta-analysis of various north-east Atlantic stocks indicated that reduced age class diversity in haddock leads to higher recruitment variability (Brunel 2010). A possible cause might be less variability in spawning times, which normally buffers against match-mismatch dynamics of feeding larvae and their zooplankton prey. Between 2000 and 2005 mean age of spawners increased together with SSB in North Sea haddock (Morgan et al. 2013), however no strong recruitment years were observed, indicating other effects in determining spikes in recruitment.

1.4 Maturation

Age and length at maturation varied both temporally and spatially within the North Sea. Between the 70ties and 80ties age and length at maturation were highest and decreased since then with haddock maturing at a smaller size (Rochet 2000, Baudron et al. 2011, Wright et al. 2011). This effect is more pronounced in the north-western substock compared to the eastern part of the stock. Although it was first attributed to the effect of increasing temperatures in the North Sea (Baudron et al. 2011, Wright et al. 2011), later work also points towards an evolutionary effect related to higher fishing pressure in the North West of the North Sea (Wright & Tobin 2013, Wright et al. 2014, Marty et al. 2014).

1.5 Environmental effects on reproduction potential

In haddock, the food availability for spawners during the spawning season can greatly influence the reproductive outcome. Hislop et al. (1978) found a reduction of egg numbers and dry weight as a measure of egg quality under low feeding conditions for haddock in captivity. Trippel & Neil (2004), however, found no effect of condition on fecundity, but rather fertilisation rates dependent on male condition. Similarly Marshall & Frank (1999a) reported indices of growth and condition in spawners to be positively related to recruitment in haddock on the Scottian Shelf. For Georges Bank haddock the magnitude and the phenology of the autumn bloom as indirect measure of spawner feeding and condition were proposed as a mechanism to explain recruitment variability (Friedland et al. 2008, 2015, Leaf & Friedland 2014). Payne et al. (2009), however, pointed out that apart from parental condition other processes during the larvae phase might play a role as well in determining year class strength. In the North Sea, haddock preys on a variety of items with great spatial variability. A possible pathway of the effects of parental condition could be sandeel (*Ammodytes marinus)* as haddock shows strong predation in some regions and years (Cranmer 1986, Greenstreet et al. 1998, Temming et al. 2004) and body condition varied with the availability of sandeel (Engelhard et al. 2013). In his investigation on variation in reproductive investment of haddock in the North Sea, Wright (2005) found liver condition of fish to affect maturation. However, the causes for this relationship could not be resolved.

1.6 Timing of spawning

Spawning season in North Sea haddock is between the end of February to May, with peak spawning in March and April (Saville 1959, Blacker 1971, Gibb et al. 2004, González-Irusta & Wright 2016). Higher temperatures experienced during egg-maturation were observed to result in earlier spawning for Georges Bank haddock (Page & Frank 1989).

1.7 Spawning grounds

Gibb et al. (2004) gives a good overview on early work on spawning grounds of haddock. Spawning grounds of haddock are mainly located in the north-western North Sea and along the western Scottish shelf. Early work assigned the whole northern North Sea along the 100m isobar, except for the Norwegian Trench and Moray Firth as suitable spawning habitat for haddock (Thompson 1928). Similarly Saville (1959) found spawning grounds between 1952 and 57 to occupy most of the northern North Sea with the exception of the Fladen grounds and Moray Firth, but with great interannual variability. Egg concentrations in 1992 were similar to the ones observed in the 50s but with a more north and westerly distribution (Heath et al. 1994). Results from recent egg surveys in the North Sea in 2004 (Munk et al. 2009, Höffle et al. 2017) and 2009 (Höffle et al. 2017) found largest concentrations of haddock stage I eggs along the Scottish coast around Orkney in the Moray Firth and east of Shetland north of the Fladen ground. Fewer eggs were found on the edge of the Norwegian Trench towards Fisher Banks in the east and along the Scottish east coast towards the North of the Doggerbank in the South. Later egg stages were more confined to the north-western North Sea surrounding Fladen Grounds. This is in accordance with (González-Irusta & Wright 2016), who inferred spawning grounds by the presence of haddock in the spawning stage from 2009 - 2015. Haddock spawn on sandy and coarser grounds (Asjes et al. 2016, González-Irusta & Wright 2016, Höffle et al. 2017), which explains why the muddy Fladen grounds had less eggs in all these studies. Around the Scottish Shelf spawning occurred in a broad band offshore spanning the west of the Outer Hebrides towards north of Ireland (González-Irusta & Wright 2016). Environmental variables associated with spawning were depth around 100m, temperatures with an optimum around 7 °C and high salinity waters (> 35 psu) coinciding with the area off North Atlantic inflow (Heath et al. 1994, Gibb et al. 2004, González-Irusta & Wright 2016, Höffle et al. 2017) as well as frontal zones (Munk et al. 2009).

2. Eggs

2.1 Temperature

Mortality and development time of eggs in haddock is temperature related (Laurence & Rogers 1976, Martell et al. 2005) with an optimum survival around 7 °C (4 -10 °C) and decreasing development time with increasing temperatures (range: 2 – 12 °C).

2.2 Salinity

Survival of haddock eggs increased with increasing salinities (range: 30 – 36 **‰** (Laurence & Rogers 1976) and eggs near frontal zones were found at the high salinity part of the front (Munk et al. 2009).

2.3 Transport

A North Sea wide study conducted in winter/spring 2004 on the distribution of haddock eggs found an association with salinity fronts (Munk et al. 2009). This indicates that spawning itself either occurs in close proximity to these regions or that frontal zones help in retaining eggs at places, that itself are again favourable for later larvae stages in terms of retention and prey availability. Mapping egg stages I to V in the North Sea from information of the ichtyoplankton surveys in 2004 and 2009 showed strong within-season variability in spatial distribution (Höffle et al. 2017), that might be attributed to drift processes. However not all eggs were prone to drift. Regions with some degree of retention were situated in the north-western North Sea, whereas high variation in egg density were observed near the Norwegian Trench. However relating the egg distribution observed by Höffle et al. (2017) solely to drift, should be done with caution, as other processes (e.g. predation) could be in play. As modelling by Huserbråten et al. (2018) showed for cod eggs, spawning at these locations can easily lead to advection out of the North Sea into the Norwegian Sea through the prevailing currents in the Norwegian Trench. Saville (1959) described the egg distribution in 1956, a particular bad recruitment year, to be largely concentrated along the banks west of the Norwegian Trench, with eggs missing around the east of Shetland. However, sampling of late stage eggs and larvae in 1956 indicated no exceptional strong drift out of the North Sea, indicating other processes to be responsible. Contrary, egg and larvae sampling (Saville 1959) and drift modelling (Heath & Gallego 1998) found eggs spawned north-west of Scotland were advected into the North Sea towards the Shetland Islands.

2.4 Predation

Little is known about predation on haddock eggs. As cod and haddock eggs can only be differentiated in the late stage or by genetic methods (Taylor et al. 2002), early studies on predation on cod eggs (e.g. Daan et al. 1985), might be applicable for haddock. As herring and mackerel thrive in the northern North Sea during spawning of haddock from March to May, especially in the northeastern part (Corten & Kamp 1992, Corten 2002), predation is likely to occur.

3. Larvae

3.1 Growth and Development

3.1.1 Temperature and interaction with other factors

Temperature affects the larvae stage in various ways. Elevated temperatures favour growth and development in larval haddock, but with the cost of higher metabolic demands. Larvae haddock depleted their yolk-sac reserves faster under higher temperatures in the laboratory (Laurence 1978, Martell et al. 2005), which reduces their time to withstand starvation before feeding is initiated. Higher temperatures resulted in faster growth and a reduction of the time spend in each development stage (Martell et al. 2005). In the field, various other factors like photoperiod, food availability and season interact with temperature. Buckley et al. (2004) found a dome shaped relationship of growth in larval haddock on Georges Bank with an optimum around 7 °C. The authors suggested food limitation to be the cause of reduced growth under higher temperatures. Buckley et al. (2006) found a positive correlation between growth in larval haddock and photoperiod as well as temperature. Photoperiod affects both temperature and the onset of the spring bloom, which explains the strong effect on haddock. Additionally as haddock larvae are visual feeders, increased light conditions prolong the time of feeding for the larvae.

3.1.2 Salinity

Laboratory experiments of haddock larvae reared at different salinities found highest survival at salinities around 30 **‰** and low survival under low (25 **‰**) and high salinities (35 **‰**) respectively (Opstad 2003). Growth was optimal under lower salinities of 25 **‰** and similar between 30 – 35 **‰**.

3.2 Transport and retention

3.2.1 Drift

The drift and/or retention hypothesis for haddock dates back to work of Carruthers (1938) and Carruthers et al. (1951) who linked year class strength of North Sea haddock to prevailing wind conditions. However, the relationship broke down after re-examination (Saville 1959). Nevertheless, larval drift is considered to play a role in the life cycle of haddock in the northern North Sea. Bjørke & Saetre (1994) found large proportions of juvenile fish in the Norwegian Sea along the Norwegian coast north of 62° N to originate likely from spawning grounds in the northern North Sea and the west of Scotland. This is also seen in the egg and larval-drift model of Heath & Gallego (1998, 2000), which showed a wider spatial distribution of demersal juveniles compared to initial egg densities ranging from the onset of the Skagerrak along the Norwegian Trench to the Norwegian Sea. How larval drift or retention is affecting recruitment variability in the North Sea is unclear. Evidence from the Georges Bank haddock stock indicates that both retention (Lough et al. 2006, Boucher et al. 2013) or strong drift (Polacheck et al. 1992) can result in exceptional high year classes.

3.2.2 Frontal zones, eddies and their role in drift and retention

As for other fish larvae in the North Sea haddock larvae accumulate at frontal zones (Munk et al. 1999, Munk 2014). However, in contrast to e.g. whiting and cod larvae, which accumulate at the onshore side of shelf-slope front, haddock larvae were found at the offshore side over deeper waters, which might be associated with different requirement for hydrographic parameters. Buckley & Lough (1987) also found haddock larvae on the offshore side of the front on Georges Bank. Munk et al. (1999) also noted that in 1994 during a weak extent of the shelf-slope front in the eastern North Sea almost no haddock larvae were found, indicating either strong dispersal or a change in the spawning. In general, haddock eggs and larvae seem to show a strong association with hydrographic structures in the ocean. In the north-western Atlantic haddock over the Scottian Shelf spawn in or near gyre like structures (Browns Bank (Campana, Smith, et al. 1989), Georges Bank (Smith & Morse 1985, Werner et al. 1993), which help in retaining eggs and larvae on their spawning sites. In his overview work on “patterns in the ocean” and how they shape fish and recruitment dynamics, Bakun (1996) emphasises the role of retention and anti-cyclonic gyres for recruitment in haddock for the population on Rockall Banks and Faroe Banks found by Dooley (1984) and Hansen et al. (1986). For the western Irish Sea a weak cyclonic gyre seems to be important for haddock early life stages (Dickey-Collas et al. 1997), however, its role on retention or dispersal is not entirely clear (Pitois & Armstrong 2014). In the North Sea eggs and larvae are found in an area surrounding the Fladen Ground, but almost never directly within (Saville 1959, Höffle et al. 2017). A series of drift bottle experiments in the northern North Sea in the beginning of the 20th century summarized by Tait (1937) indicated a large eddy like structure in the vicinity of the Fladen grounds. His findings were later confirmed during the autumn circulation experiment from 1987 showing a topographically steered cyclonic eddy (Svendsen et al. 1991, Turrell et al. 1992, Turrell 1992), although much smaller than stated in the work by (Tait 1937) in the order of 100km. It is situated at about 2° E where the 100m isobar takes a sharp turn in south-eastern direction (Svendsen et al. 1991). Saville (1959) mentioned this eddy in the discussion on the wind-recruitment correlation of Carruthers et al. (1951), however judged its role on haddock recruitment to be small. To our understanding, no further research on this topic for the North Sea stock exists, but observations of other stocks justify a deeper investigation.

3.3 Diet and food availability

Prey items of young larvae in the North Sea comprised mainly *Calanoid egg* and *nauplii* as well as various proportions of *Pseudocalanus elongates* and *Oithona sp.,* which increased when larvae grew bigger (Economou 1991). It is general understood that haddock larvae have a large feeding niche and do not show strong selectivity of particular food items (Robb & Hislop 1980, Kane 1984, Economou 1991, Rowlands et al. 2008). Also they do select slower moving organisms (Economou 1991, Auditore et al. 1994), and therefore do not rely on fast swimming *C. finmarchius* as cod does. A study of Buckley & Durbin (2006) also found a zooplankton index derived from abundance of *Pseudocalanus spp.* correlated with larval growth rates of Georges Bank haddock, whereas indices based on *C. finmarchicus* were unrelated. According to the “critical period”-hypothesis, food availability in the first part of the larvae stage is crucial for survival. Buckley & Lough (1987) suggested the highly variable recruitment of haddock at Georges Bank to be the result of a strong reliance of larvae to the high prey densities following spring stratification. Platt et al. (2003) and Trzcinski et al. (2013) were able to link the onset of the spring phytoplankton-bloom inferred from remote sensing data to year class strength, with earlier blooms being favourable for survival. However Trzcinski et al. (2013) pointed out to take general statements about the effect of phytoplankton blooms on recruitment with care, since results were not consistent across populations. This is in accordance with other authors (Head et al. 2005, Rideout et al. 2005, Mountain et al. 2008, Petrik et al. 2014), who emphasised the role of many factors acting over subsequent life stages like spawning time, egg size, transport, hatching rates and reduced predation together with sufficient food supply to result in strong year classes of haddock. For the North Sea, Pepin (1990) found a weak, but positive correlation of haddock recruits with the abundance of dinoflagellates and a colour index, either representing a direct or indirect pathway through zooplankton prey. Indeed did yolk-sac and first feeding larvae of Georges Bank haddock relied on diatoms and the dinoflagellate *Peridinium sp.* at their onset of feeding (Auditore et al. 1994), suggesting a direct impact.

3.4 Predation

Studies on larval distribution and spatial overlap with predators indicate that haddock larvae on Georges Bank are likely to be preyed on by planktivorous fish (Garrison et al. 2000). Especially herring showed a strong overlap with haddock larvae as both species showed the same preference for low temperature, high salinity and stratified waters, whereas the overlap with mackerel was low. For the Irish Sea (Pitois & Armstrong 2014) suggest that the abundance of clupeids like sprat and herring is likely to exert considerate predation pressure on gadoid eggs and larvae. For the North Sea, no study for haddock is known. However, as adult herring and mackerel are abundant in the northern part of the North Sea around the Shetland Islands and the north-eastern North Sea in spring and beginning of summer (Corten & Kamp 1992), predation on haddock larvae seems to be possible.

4. Juveniles

4.1 Habitat and density dependent effects

Haddock change from a pelagic to a demersal lifestyle during the 0-group stage. As recruitment strength for North Sea haddock is believed to be determined during the end of the pelagic/ beginning of demersal phase (Myers & Cadigan 1993, Heath et al. 1999), there is particular interest in possible influences during this life stage. Pelagic juveniles settle in one pulse lasting about two weeks in late May to deeper offshore waters (Bastrikin et al. 2014). Asjes et al. (2016) modelled the distribution of settled 0-group juveniles in quarter 3 in relation to environmental variables and found them mainly distributed along a close band along the Norwegian Trench from Viking Bank and North of the Fladen ground to Fisher and Jutland Bank towards the Skagerrak. Depth between 100 and 120 m, low temperatures and high salinities were preferred, with temperature being a particular constraint for spatial distribution, as juveniles prefer areas < 11°C, which are limited in the North Sea. Any possible intra-cohort competition can therefore be amplified. With increasing age, 0- and 1-year old juveniles approached the spatial distribution of the adult stock. As the spatial distributions of different cohorts as well as size of feeding particles overlap (Wigley 1956, Jones 1983) competition between subsequent year classes is likely to occur. Several authors found growth rates of 0-group juveniles to be negatively affected by abundance of higher age classes (Jones 1983, Cook & Armstrong 1984, Campana, Frank, et al. 1989, Marshall & Frank 1999b). For North Sea haddock the effect of one large year class is likely to affect the next two year classes (Cook & Armstrong 1984, 1986).

4.2 Diet

As for larval haddock, juveniles show also a lack of diet selectivity as well as preference for slower moving organisms (Robb 1981, Auditore et al. 1994). 0-groups in the pelagic phase feed mainly on Appendicularia (Wiborg 1960, Robb & Hislop 1980, Robb 1981), pelagic gastropoda (Limcina spp.) (Wiborg 1960, Bastrikin et al. 2014), fish eggs (Robb 1981) and various copepods (*T. longicornis, para/Pseudocalanus, Metridia lucens, C. helgolandicus, C. finmarchius)* (Robb & Hislop 1980, Bastrikin et al. 2014). A strong reliance on *Calanus finmarchius* as reported for other gadoids seems not to be the case for haddock juveniles (Robb & Hislop 1980, Bromley et al. 1997), although (Bastrikin et al. 2014) reported otherwise. Predation on other gadoids (Norway pout, whiting) and sandeel is also common (Robb & Hislop 1980, Bromley et al. 1997). After settlement their diet is comprised mainly of benthic crustaceans and benthic fish like sandeel and flatfish (Bastrikin et al. 2014).

4.3 Predation

For north-western Atlantic haddock populations predation from 0-group mackerel during the winter is believed to play a crucial role on recruitment (Koslow et al. 1987). However, the authors only used an explorative, correlative approach, with other variables being important as well. From September – December mackerel have the highest overlap with 0-age haddock in the North Sea east of Shetland and along the Norwegian Trench (Uriarte et al. 2001, Asjes et al. 2016). According to the North Sea

SMS run 2017 (ICES 2017), the main predators of 0-age haddock in autumn and winter (Q3 and Q4) are the other gadoids cod, whiting and saithe. In autumn (Q3) predation from grey gurnard is playing an increasing role since the 1980s.

4.4 Competition

Bromley (1989) suggested interspecific feeding competition with Norway pout and mackerel as a possible explanation for slower growth in age-1 haddock in the northern North Sea.

5. Summary

Haddock recruitment shows the most interannual variations among the gadoid stocks in the North Sea. The overall recruitment pattern is strongly driven by density-dependent processes acting in the younger year classes through inter-cohort competition. High year classes of one year result in low recruitment for the following years (2-5 years). However, what causes these exceptional high year classes is not fully understood. It is hypothesised that mostly bottom-up processes shape this process (as seen for western Atlantic stocks) with food availability in relation to bloom dynamics playing a crucial role for both spawners and early life stages. The correlative studies for the North Sea shown in Table A.1.4 support this, with Phytoplankton and herring biomass exerting a positive effect on recruitment. The latter might be due to an effect of herring egg predation on spawners. The negative *Calanus* relationship might point to effects of food composition or large scale oceanic processes for which *Calanus* is only a proxy, as haddock early life stages do not rely strongly on *Calanus* in their diet. Although wind was found to be a spurious correlation with haddock recruitment in the 50s, transport processes (also seen in Table A.1.4 wind, currents, NAO) seem to have a significant impact either directly through beneficial/adverse drift of early life stages or transport of suitable food. Here enrichment processes in relation to frontal zones, gyres and inflow of Atlantic water might be important. Temperature also seems to shape recruitment dynamics in haddock, however the direction of the temperature effect is not clear (compare SST and AMO correlations in Table A.1.4).

Table A.1.4: Correlative/statistical recruitment studies for North Sea haddock

Environmental variable	Life-stage	Region	Time period	Relationship	Author
SSB	Age-3-recruits	North Sea	1936 - 2001	-	(Cardinale & Hjelm 2003)
	Age-0-recruits	North Sea	1963 – 2008	-	(Ottersen et al. 2013)
Temperature (SST)	Age-0-recruits	North Sea	1972 - 1994	none	(Dippner 1997)
	Age-0-recruits	North Sea	1963 - 2008	- (Non-linear)	(Ottersen et al. 2013)
Wind	Age-2-recruits	North Sea	1920 -1949	Non-linear	(Carruthers et al. 1951)
		North Sea	1938 - 1957	none	(Saville 1959)
Currents	Age-0-recruits	North Sea	1963 - 2011	+	(Pécuchet et al. 2015)
Phytoplankton	Age-1-recruits	North Sea	1960 - 1980	+	(Pepin 1990)

Calanus abundance	Age-1-recruits	North Sea	1960 - 1980	-	(Pepin 1990)
Herring biomass	Age-1-recruits	North Sea	1960 - 1980	+	(Pepin 1990)
	Age-0-recruits	North Sea	1963 - 2011	+	(Pécuchet et al. 2015)
Plaice/Sole recruitment	Age-1-recruits	North Sea	1960 - 1980	-	(Pepin 1990)
AMO	Age-1-recruits (low-pass filtered)	Skagerrak-Kattegat	1904 - 1939 1968 - 2003	+ none	(Linderholm et al. 2014)
NAO	Age-0-recruits	North Sea	1972 - 1994	none	(Dippner 1997)
	Age-3-recruits	North Sea	1936 - 2001	none	(Cardinale & Hjelm 2003)
	Age-1-recruits (low-pass filtered)	Skagerrak-Kattegat	1904 – 2004	+	(Linderholm et al. 2014)

6. Knowledge gaps

The greatest problem in understanding haddock recruitment across stocks is the occurrence of these large recruitment spikes 2 to 3 times of the normal magnitude. These spikes become lower and lower over the last decades and the processes behind this observation have not been resolved yet. Based on the understanding of other haddock stocks these likely happen if several favourable effects co-occur. Therefore looking at several environmental drivers and their combined (additive or non-linear) effect might help in finding possible explanations.

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Annex A.1.4 Recruitment of North Sea saithe

Life cycle of North Sea saithe (*Pollachius virens*) and processes that might affect recruitment variability

1. Effect of the spawning population

1.1 Stock structure and migrations

1.1.1 Northeast Atlantic stock structure vs. population structure

To date saithe in the North East Atlantic is managed as four different stocks (1. Icelandic Va, 2. Faroese Vb, 3. Northeast Arctic I and II (Barent Sea stock), 4. North Sea IV, Skagerrak IIIa and West of Scotland/Rockall VI), which does not accurately reflect their underlying population structure. Results from tagging experiments (see Homrum et al. 2013 and references therein), genetic analysis (Child 1988, Eiríksson & Árnason 2015, Behrmann et al. 2015, Saha et al. 2015) as well as parasite infestation (Comiskey & MacKenzie 2000) indicate considerable levels of exchange between stocks. The life cycle of saithe is characterised through offshore spawning areas, recruitment into coastal nursery areas between 1 – 4 years and an offshore migration during their adult life. Young saithe are rather restricted in their movement (Olsen 1961, Jakobsen 1975), probably due to their dependency on shallow coastal habitat (Homrum et al. 2013). Adult saithe undertake longer migrations, which are understood to be related to seasonal feeding and spawning (Homrum et al. 2013). Based on tagging studies there is considerable exchange of adult saithe between the Barent Sea stock and the North Sea stock and to a lesser extent to the Islandic and Faroe stocks. The Faroe stock is mostly exchanging individuals with the Islandic stock (Homrum et al. 2013), while the Icelandic stock shows only few migrations to other areas (Jones & Jónsson 1971, Armannsson et al. 2007, Homrum et al. 2013). The bigger picture drawn by Homrum et al. (2013) based on synthesis of tagging studies of saithe, indicates a general westward movement with a net gain of adult saithe around Iceland and an export from the Faroe islands and the Barent Sea/North Sea stock. Genetic analysis indicate a similar pattern, however with some deviation. Some studies found only no to little differentiation between stocks (Child 1988, Eiríksson & Árnason 2015). Behrmann et al. (2015) found two clusters with one consisting of populations from northern Norway and eastern North Sea and a second from Iceland and the northern North Sea. The authors concluded that in the vicinity of the northern North Sea different populations might mix. This is partly in agreement with a study on seascape genetics by Saha et al. (2015), who found a combined cluster of saithe stemming from west of Norway, the northern North Sea, Viking Bank, West of Scotland, Faroe Islands and Iceland. Subpopulations of saithe from Rockall Banks, the Barent Sea and Canada however seemed to be distinct.

1.1.2 North Sea stock migrations

For the North Sea most of the exchange is with the adjacent Norwegian stock. Here migrations seem to be related to the need of life cycle closure across the stock boundaries. Saithe larvae spawned in the northern North Sea are largely transported out of the North Sea and with the Norwegian Coastal current towards the west and mid Norway, were they possibly recruit to the Barent Sea stock (Bjørke

& Saetre 1994). In earlier years Olsen (1959a, 1961) observed younger fish from the west of Norway between 62 °N and 63.3 °N mainly to move northward along the Norwegian Coast. However, there is also a considerable flow of adults and juveniles back to the North Sea. Studies from Olsen (1959b, 1961) found older mature saithe tagged at the coast of Finnmark in North Norway to move south towards West Norway and the North of the North Sea during spawning season in winter. Analysis of catches from research vessel cruises between 1985 and 1993 indicate that almost no adults of fully mature age classes 7+ remain in the North Sea after spawning (Reinsch 1994). Results of Jakobsen (1975, 1976, 1978, 1981a, 1985) from tagging studies in the 70s indicate that substantial migration of 2-4 year old saithe from the west of Norway between 62 °N and 66 °N in southward direction to the North Sea occurs. Immature individuals between 66° N and 68° N had a tendency to northward migration (Jakobsen 1981a). This pattern was tried to be incorporated into the assessment in earlier years, by assuming that all 1-4 year old saithe between 62° and 64° N recruited into the North Sea stock (Jakobsen 1981b). However, today, no migration is considered in stock assessment of the North Sea stock (ICES 2018). Immature individuals tagged at the west coast of Scotland generally stayed near the coast until they became three years old, where they showed some exchange with the northern North Sea (Newton 1984).

1.1.3 Reasons for adult migration

In the review by Homrum et al. (2013) migration in saithe between stock areas is summarized as an “interplay between spawning and feeding migrations”. As several authors before Olsen (1959b, Jakobsen 1978) they linked the general westward migrations of saithe to follow the migrations of the Norwegian spring-spawning herring to their summer feeding grounds near Iceland. Near the Faroe Islands and Scottish waters around the Hebrides saithe might follow the migrations of blue whiting (suggested by Homrum et al. 2013), as blue whiting is one of the main prey items in these areas (Du Buit 1991). Blue whiting spawning behaviour was shown to be affected by the subpolar gyre (Hátún et al. 2007, 2009). During a strong SPG with colder and less saline water masses blue whiting spawning was more confined to the shelf edge, whereas a weak SPG with warm and saline water extended spawning towards the west of Rockall Bank. Recruitment strength in Faroe shelf saithe was also linked positively to the subpolar gyre (Steingrund & Hátún 2008). The authors concluded that changes in food availability through increased zooplankton abundance as well as blue whiting might play a key role. However, in recent years the relationship between Faroe shelf saithe and the SPG broke down (Steingrund, personal communication). Although blue whiting spawning aggregations do not fluctuate as much with the subpolar gyre near the Hebrides as they do near Rockall and the Faroese (Hátún et al. 2007), effects on the stock to the West of Scotland might occur too.

1.2 SSB effect

Cormon, Ernande, et al. (2016) showed a negative correlation between saithe total abundance and average growth between the age of 5 to 7 in the North Sea, indicating density dependent effects to take place. The same was shown for Faroe shelf saithe, where 50 – 70% variation in growth between age 3 and 6 could be explained by density dependence of the total stock (Homrum et al. 2012).

1.3 Spawning grounds and times

Saithe spawning regions in the North Sea are confined to a narrow band from west of Shetland along the 200 m isobar to the west of the Norwegian Trench and the outlet of the Skagerrak with the main distribution northeast of the Fladen Ground at Tampen, Viking Bank and Utsira High (Damas 1909, Jakobsen 1974, Rogers & Stocks 2001, Sundby et al. 2017). Spawning migrations of saithe from near spawning grounds at the Norwegian coast and mixing with spawners in the Northern North Sea seems to be likely (Reinsch 1994, Behrmann et al. 2015). Additional spawning occurs northwest of Shetland along the shelf edge to the west of the outer Hebrides, extending into the Minch and the North West of Ireland (Reinsch 1976). Recent links of spawning adults with environmental variables in the North Sea were not made, however there is some evidence that the spawning grounds of saithe lie further offshore than observed for other North Sea gadoids (Daan et al. 1990), as well as in the vicinity of warm, saline Atlantic waters between 5.5 and 10 °C and salinities > 35 psu (Reinsch 1976). Spawning time varies from January in the southern regions to May in the northern ones with peak spawning activity in February (Reinsch 1976, Sundby et al. 2017). Skjaeraasen et al. (2017) found a relatively short spawning season for saithe in captivity from west Norway lasting from mid-February to the end of March.

1.4 Parental effects

Egg weight increases with age in saithe (Reinsch 1976), which might indicate higher viability for eggs coming from older spawners, as it was shown for other gadoids. However, no detailed information on parental effects is available for saithe.

1.5 Maturation and fecundity

Saithe of age class three are typically ~100% immature and progressively mature in the age of four (20%), five (65%), six (84%) seven (97%) until they are fully mature at the age of eight (100%) (ICES 2017). There is a difference in age at first spawning between North Sea and Barent Sea saithe (Reinsch 1976) with saithe from the North Sea having a high proportion of first time spawners at the age of seven, whereas saithe from Norway frequently experience first spawning at the age of four. The variable extent of spawners coming from the Barent Sea to spawn in the North Sea in some years might therefore limit our ability to estimate the reproductive output correctly.

1.6 Environmental effects on reproduction potential

1.6.1 Temperature

Oocyte development started in late October – early November for saithe caught at the west Coast of Norway (Skjaeraasen et al. 2017) and temperatures experienced during that time might result in earlier (warm) or later (cold) spawning of saithe as already suggested by (Reinsch 1976) and shown for species like cod (Kjesbu et al. 2010). However, no information for saithe is available to date. Effects on recruitment might occur through match-mismatch dynamics with their planktonic prey during the larval stage.

1.6.2 Parental condition

Effects of feeding success and fish condition on reproductive success in saithe have not been investigated yet. However, Cormon, Ernande, et al. (2016) could show abundance of Norway pout as a main prey item in adult saithe (Bergstad 1991, Du Buit 1991, Høines & Bergstad 1999, Engelhard et al. 2014) to have positive effects on growth. The strong reliance of saithe on Norway pout is also shown in a food web model of Lynam et al. (2017). The authors showed cascading effects of increasing herring abundance in the North Sea, leading to lower Norway pout via competition and in the following to a reduction in saithe biomass. However, as saithe in the North Sea also prey on herring and sandeel, prey switching might happen. Engelhard et al. (2013) showed that body condition of predatory fish (e.g. whiting) varied considerably with the availability of sandeels in the North Sea, which might also be true for saithe. A reduction in their main prey before spawning could result in fewer energy reserves allocated to spawning.

1.7 Competition

The increasing abundance of northern European hake (*Merluccius merluccius*) in the North Sea due to increasing temperatures is believed to exert competition on saithe due to a similar diet. Both species prey on Norway pout (*Trisopterus esmarkii*) and are largely overlapping in the northern North Sea (Cormon et al. 2014, Cormon, Ernande, et al. 2016). Different scenarios showed that competition between hake and saithe on Norway pout might in part explain the recent decrease in spawning stock biomass of saithe (Cormon, Kempf, et al. 2016).

2. Eggs

To date no studies have been conducted looking explicitly on the egg stage of saithe in the North Sea and environmental influences. Spawning and drift processes affecting the egg stage are summarized in the paragraph before and after.

3. Larvae

3.1 Drift

As main spawning grounds of saithe in the northern North Sea at Tampen and west of the Norwegian Trench are in an area characterised by strong currents (Shelf Edge current, East Shetland inflow, Norwegian Trench in/outflow) drift is likely to affect new hatched larvae. Transport in this region is generally eastward towards the Skagerrak and then out of the North Sea along the Norwegian coast via the Norwegian Trench outflow. Jakobsen (1974) suggested that the spawning migrations of adult saithe from the mid-northern Norwegian coast to the North Sea are a way to counter extensive drift during the larvae phase. Indeed larvae and fry of saithe likely originating from the spawning grounds in the North Sea are found along the Norwegian Coast in May implying considerable transport (Furnes et al. 1986, Bjørke & Sætre 1994). Modelling drift of cod early life stages in the North Sea (Huserbråten et al. 2018) showed strong advection directly at the slope of the Norwegian Trench towards the Norwegian Sea and the West coast of Norway in the Svinøy-region. Although parameterised for cod the authors mentioned saithe to follow a similar drift path. This is in accordance to a drift model for saithe early life stages showing rapid eastward and northward movement of eggs and larvae towards the Norwegian coast in March 2012, as well as into the Skagerrak and to the west around the Shetland Islands (Sundby et al. 2017). The latter area showed strong retention over the whole simulation period from February to May. If drift of larval stages is either favourable to reach the nursery habitats at the coast of Norway or disruptive for the North Sea stock is not clear (see Sinclair (1988) for a discussion for herring). An unusual drift event in southerly direction was observed in 1967 where large abundances of young saithe were found in the southern North Sea and caught as bycatch by the brown shrimp fishery in the Wadden Sea (Reinsch 1976). This year was an exceptional high recruitment year. At the same time intrusion of young saithe into the Barent Sea and Spitzbergen occurred, the reason being the propagation of warm Atlantic water via the Norwegian Atlantic current (Reinsch 1976 and references therin). Occasionally drift of young saithe into the Kattegat is observed (Reinsch 1976). As for other gadoid larvae the occurrence of frontal zones in spring play is crucial for retaining larvae in this region. Saithe larvae were associated with fronts in the area around Fisher Banks/Skagerrak area (Munk et al. 1999). They showed a similar distribution as cod larvae, either directly in or at the inshore position of the front. Variability in frontal zone formation can have profound effects of early life stages e.g. in 1994 where weakening of the front resulted in almost no saithe larvae found in the region.

3.2 Diet

Saithe larvae start feeding on calanus eggs and nauplii as well as *Oithona sp.* and *Acartia clausii* (7-10mm), but soon (> 11mm) rely almost solely on *Calanus finmarchius* throughout the rest of the larval stage (Economou 1991). They are able to feed on large and active prey. The distribution of saithe larvae in frontal zones in the northern North Sea indicates an association with large zooplankton as highest concentrations of both groups were found between 40 and 75m depth during the day (Höffle et al. 2013).

3.3 Predation

Predation in the larval stage of saithe is not resolved for the North Sea. As saithe spawning grounds overlap largely with overwintering herring habitats in the region around the Norwegian trench (Corten 2002) predation might occur. Also mackerel as a large predator on fish eggs and larvae is abundant at spawning grounds (Tampen, Viking Bank, Norwegian Trench) in winter since the mid 1980s (Corten & Kamp 1992).

4. Juveniles

4.1 Habitat

When they reach 3 – 5 cm in length, juvenile saithe (0+) move inshore to their nursery habitats along the Norwegian coast. In the western Atlantic juvenile saithe were found to be associated with shallow rocky intertidal habitat with macroalgae for predator avoidance and feeding (Rangeley & Kramer 1995a, b). Also in the North Sea, young saithe were observed to inhabit rocky as well as soft bottom habitats (Pihl & Wennhage 2002) with associated kelp forest (*Laminaria hyperborea*) (Norderhaug et al. 2005). At the coast of North Wales in the Irish Sea, saithe were found in association with seagrass beds (Bertelli & Unsworth 2014). Similar as proposed for cod, availability of suitable nursery habitat can greatly alter intra-and interspecific competition as well as reducing predation pressure.

4.2 Density dependent effects

Density dependent effects in the juvenile stage in saithe seems to be minimised though successive migration from the coast to deeper waters with increasing age (Nedreaas 1987). However Olsen (1966) reported fluctuations in growth rate in saithe from the Norwegian coast, which he assumed to result from high population densities in the 0- and 1-age class.

4.3 Diet

Stomach analysis of juvenile prey indicate a mainly pelagic composition. There is a gradual change from a copepod dominated diet, towards krill (*euphabiacea*) and fish from 5 to 13.9 cm (Robb & Hislop 1980). A similar succession in diet change was reported by Nedreaas (1987) for older age classes one and two off the west coast of Norway within the season from early summer to autumn. This indicates a seasonal effect of prey availability/preference, rather than a solely size effect. The calanoid *C. finmarchius* was the dominating copepod in studies of various authors (Nedreaas 1987, Bromley et al. 1997, Norderhaug et al. 2005). For smaller saithe in the size class < 10 cm, Robb & Hislop (1980) found the copepod species *Anomalocera spp.* and *Caligus spp*. to be most important. Bromley et al. (1997) also reported the copepod *Anomalocera spp*. as food item. Fish species preyed upon consisted mainly of young sandeel (Robb & Hislop 1980, Gislason 1983, Nedreaas 1987), Norway pout (Robb & Hislop 1980, Gislason 1983), yearlings of haddock (Gislason 1983) as well as herring larvae, horse mackerel, yearlings of cod and dragonet larvae (Nedreaas 1987). Norway pout was not frequently consumed in the nursery habitats at the coast of Norway (Nedreaas 1987). For saithe in Faroese waters (Homrum et al. 2012) reported recruitment of saithe at age 3 to be highly correlated with biomass of sandeel fry during their second year and Norway pout fry during their first year of life, indicating a strong reliance on these particular prey species. Nedreaas (1987) found saithe to feed on a more diverse diet from the epifauna and hyperbenthos if pelagic resources were scarce. Here their association with makrophytes (e.g. kelp forests) (Norderhaug et al. 2005) seems to play a crucial role in buffering effects of pelagic food scarcity.

4.4 Predation

Juveniles of saithe are preyed upon by other gadoids e.g. Cod (Reinsch 1976).

4.5 Competition

Saithe in their juvenile phase have a great dietary overlap with mackerel (Nedreaas 1987, Langøy et al. 2012) and since the 1980s western mackerel extended their summer feeding areas along the west coast of Norway (Corten & Kamp 1992). As these areas are important nursery habitat for saithe competition between these two species is likely (Nedreaas 1987).

5. Summary

Saithe is a highly migratory species with its life cycle extending far beyond the North Sea. Mixing of spawners as well as recruits with the adjacent Barent Sea stock can therefore bias the perception of the stock-recruitment relationship within the North Sea. As most of the life stages thrive within the North Atlantic current system (Norwegian coastal current, North Sea inflow) effects of wind, current pattern and temperature are likely to be related to recruitment. Positive effects of nutrients and plankton (see Table A.1.5) might be linked to coastal nursery habitat. However, pinpointing one particular environmental driver to recruitment of saithe might pose considerable challenge as recruits enter the scientific survey as well as commercial catches in the North Sea late (at age 3) and might therefore experience a magnitude of different influences, also related to their dispersal during that time. Large scale indices like the SPG or the NAO summarize dynamics over larger areas and might therefore correlate well with saithe recruitment. On the contrary, they mostly lack a mechanistic understanding compared to more localised indices. Still relationship with large scale as well as localised environmental drivers might break down, as it is shown with temperature in the North Sea and the SPG for Faroe Shelf saithe. The challenge lies in finding mechanistic links (or at least promising proxies), which incorporate the complex stock structure of saithe and connecting ecosystem knowledge beyond the conventional stock boundaries. Trophic interactions like the link with feeding migrations of herring and blue whiting, as well as competition with hake over Norway pout pose another pitfall, as they are highly dynamic in time and space. In conclusion, highly migratory species like saithe require more "ecosystem-thinking" and likely spatial dynamics have to be taken into account.

Table A.1.5: Correlative/statistical Recruitment studies for North Sea saithe

Environmental variable	Life-stage	Region	Time period	Relationship	Author
SSB	Age-2-recruits	North Sea, Skagerrak, West of Scotland	1967-2001	-	(Cardinale & Hjelm 2003)
	Age-3-recruits	North Sea, Skagerrak, West of Scotland	1967-2005	-	(Ottersen et al. 2013)
Temperature (SST)	Age-1-recruits	North Sea	1968-1990	+	(Svendsen et al. 1991)
	Age-1-recruits	North Sea/NCC	1972-1991	+	(Dippner 1997)
	Age-1-recruits	North Sea, Skagerrak, West of Scotland	1967-1999	+	(Cook & Heath 2005)
	Age-3-recruits	North Sea, Skagerrak, West of Scotland	1967-1984	+	(Ottersen et al. 2013)
	Age-3-recruits	North Sea, Skagerrak, West of Scotland	1967-2005	none	(Ottersen et al. 2013)
	SSB	North Sea, Skagerrak, West of Scotland	1967-2007	+	
Wind	Age-1-recruits	North Sea	1968-1990	+	(Svendsen et al. 1991)
Currents	Age-3-recruits	North Sea, Skagerrak,	1967-2011	+	(Pécuchet et al. 2015)

		West of Scotland			
Nutrients (PO4)	Age-3-recruits	North Sea, Skagerrak, West of Scotland	1967-2011	+	(Pécuchet et al. 2015)
Phytoplankton:					
Diatom abundance	Age-1-recruits	North Sea	1960-1980	-	(Pepin 1990)
Dinoflagellates	Age-1-recruits	North Sea	1960-1980	+ (weak)	(Pepin 1990)
Chlorophyll	Age-3-recruits	North Sea, Skagerrak, West of Scotland	1967-2011	+	(Pécuchet et al. 2015)
Zooplankton:					
Zooplankton-index	Age-3-recruits	North Sea, Skagerrak, West of Scotland	1967-2011	+	(Pécuchet et al. 2015)
Calanus abundance	Age-1-recruits	North Sea	1960-1980	-	(Pepin 1990)
Herring abundance	Age-1-recruits	North Sea	1960-1980	-	(Pepin 1990)
Cod recruitment	Age-1-recruits	North Sea	1960-1980	-	(Pepin 1990)
Cod abundance	Age-1-recruits	North Sea	1960-1980	+	(Pepin 1990)
NAO	Age-1-recruits	North Sea	1972-1991	+	(Dippner 1997)
	Age-2-recruits	North Sea, Skagerrak, West of Scotland	1967-2001	none	(Cardinale & Hjelm 2003)

6. Knowledge gaps

Most research of saithe focuses on older life stages, their migratory behaviour and general life cycle with a paucity of studies on early life stages. The life cycle of saithe in the North Sea in part follows the theory of a “migration triangle”, with life cycle closure between spawning, nursery grounds and the adult stock through favourable drift in early life stages and return migrations of adults. Research in the early life stages (eggs and larvae, juveniles) might therefore help in gaining insight which phase might be the “recruitment-bottleneck”. Stock mixing, being the case particularly in the North Sea, however might make it hard to track these effects. As mentioned earlier understanding spatial effects are of paramount importance and need to be taken into account even beyond stock boundaries.

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Annex A.1.5 Recruitment of North Sea whiting

Life cycle of North Sea whiting (*Merlangius merlangus*) and processes that might affect recruitment variability

1. Effect of the spawning population

1.1 Stock structure

Several studies indicate that the stock structure of whiting managed as North Sea (Subarea 4) and eastern English Channel (Division 7d) stock is not a good representation of the underlying population structure. The spatial structure of adult whiting in the North Sea and adjacent Seas studies were inferred by methods of otolith chemistry (Tobin et al. 2010), vertebra counts (Gamble 1959), parasite infestation (Kabata 1967, Hislop & MacKenzie 1976, Pilcher et al. 1989), tagging experiments (Williams & Prime 1966, Hislop & MacKenzie 1976, Tobin et al. 2010), genetic markers (Rico et al. 1997, Charrier et al. 2007), catches and link with environmental variables (Kerby et al. 2013) as well as trends in substock dynamics (de Castro et al. 2013, Holmes et al. 2014, Barrios et al. 2017). An extensive review from Miethe & Wright (2018) in the ICES WKNSEA report 2018 (ICES 2018) summarized these information about the mismatch between stock and population structure. The whiting stock seems to be separated into three sub-populations: A southern and a northern sub-population within in the North Sea, separated approximately by the Dogger Bank along the 50m depth contour and a population west of Scotland. Adult movement between West of Scotland and the North Sea stock is restricted, however an exchange of juveniles is frequently happing with the West of Scotland acting as a net source for the North Sea (Tobin et al. 2010). Reasons for this separation might be hydrographic processes during the early life stages together with homing behaviour of adults (Charrier et al. 2007).
An analysis of SSB and recruitment for the different sub-regions found differing trends in the time series (de Castro et al. 2013, Holmes et al. 2014). SSB in the northern North Sea and West of Scotland increased until a peak in the 1990s, but is decreasing since then (de Castro et al. 2013) and again a slight increase since 2005 for the northern North Sea (Holmes et al. 2014). Both regions exhibit a synchronised pattern in both SSB and recruitment, however with a lag of around five years (de Castro et al. 2013). The southern North Sea sub-stock shows an increasing trend over the time period, but with considerable oscillations. The overall SSB of the whole region is driven by the large northern North Sea sub-stock. Recruitment trend in the northern North Sea and West of Scotland also showed a peak in the 90s and are decreasing since then, while in the southern North Sea recruitment is decreasing over the whole period (de Castro et al. 2013). However, the asynchrony between regions was less distinct than in SSB.

1.2 SSB effect

In the whiting stock a negative effect from stock size on subsequent recruitment has been observed in the past (Cook & Armstrong 1984, 1986), probably related to competition in younger year classes or cannibalism in the stock (see Juveniles paragraph).

1.3 Parental effects and fecundity

Studies concentrating on the investigation of maternal effects in whiting are sparse. Data on spawning whiting in captivity indicate that larger whiting invest more energy into reproduction than younger fish (Hislop 1975). However, effects on offspring viability are not known. Fecundity in North Sea whiting increases in an allometric fashion with length (Hislop & Hall 1974, Barneche et al. 2018). Hislop & Hall (1974) noticed spatial differences between the southern and the northern North Sea with fish in the southern North Sea experiencing slower growth and lower fecundities than fish in the North. There is a general tendency of fish in the northwest to be larger at a given age than fish in the southeast (see Grubbe & Gislason (1997) and references therein), indicating a larger contribution of the north-western sub-stock to SSB and recruitment of the whole stock than the southern sub-stock (de Castro et al. 2013). As whiting are batch spawners and egg size decreases with prolonged season (Hislop 1975) reduced viability of later egg batches as reported for other gadoids (e.g. Trippel & Neil (2004) for haddock), is likely.

1.4 Maturation

Age and size of maturation decreased from 1970s to the 2000s in whiting, however, not as strong as for cod and haddock (Marty et al. 2014). The authors explained this due to fisheries induced evolution. A decrease in age and length of maturation between 1986-2009 was observed for whiting in the Firth of Clyde area and the western Shelf (Hunter et al. 2015), but here rising temperatures and density-dependent effects seemed to play a role.

1.5 Timing of Spawning

Spawning times of whiting differ between the northern and southern subpopulations. In the English channel spawning starts in January and lasts to April, whereas in the northern North Sea spawning lasts from March to June (Daan et al. 1990, Gibb et al. 2004, Loots et al. 2010, Sundby et al. 2017 and also references therein). Shift in spawning times follows a latitudinal pattern, possibly related to temperature.

1.6 Spawning grounds

Whiting spawning grounds are widely distributed around the North Sea and their occupation is highly variable between years. Studies of Loots et al. (2010, 2011) looking at spawner distribution during the first quarter IBTS survey between 1980 – 2007 found high prevalence in the north-western North Sea along the east coast of Scotland and the Southern Bight and English Channel. The central and eastern North Sea were classified as unfavourable. González-Irusta & Wright (2017) found a similar distribution of IBTS Q1 catches from 2009 - 2015 with a high concentration of adults towards the shallow parts of the English coast in the Thames estuary, between Lincolnshire and Norfolk Banks as well as southern Bight and English Channel. Occupation of northern spawning grounds, however, might be underestimated in these studies as the IBTS Q1 survey does not cover the complete spawning season in the North. Results from Ichtyoplankton studies found eggs in the southern North Sea to be wider distributed, also covering the Doggerbank (Lelièvre et al. 2014, Höffle et al. 2017), indicating drift. In the northern North Sea and to the West of Scotland main spawning grounds have been reported to be in a broad band between 58° N and 61 °N from east of Shetland and Buchan to Viking Bank (Gibb et al. 2004, Höffle et al. 2017). Analysis of spawner as well as egg abundance indicated high current velocities due to residual currents and springtide to be favourable for whiting, indicating strong reliance on transport processes of early life stages (Loots et al. 2011, Lelièvre et al.

2014, González-Irusta & Wright 2017). Preferences for shallow regions (0 – 100m), medium and broad bottom structure, temperatures (2 -10 °C) as well as salinities in broad range (Lelièvre et al. 2014, Höffle et al. 2017) reflect the ubiquitous nature of whiting spawning habitats across the North Sea (e.g. estuaries vs. region of northern Atlantic water inflow).

1.7 Environmental effects on reproduction potential

1.7.1 Food availability and effects on fish condition

Resources acquired through feeding within the reproductive season are partly transferred to reproduction outcome (Hislop 1975). Changes in prey abundance before and during the spawning season can therefore directly affect the quality/quantity of eggs. Diet of adult whiting is highly selective, comprising almost only crustacean and fish (Hislop et al. 1991, Greenstreet et al. 1998, Pedersen 1999) with sandeel, Norway pout, sprat, young cod, herring and haddock being the most important forage fish species. Temming et al. (2004) reported whiting in some regions in the North Western North Sea to prey almost exclusively on sandeels. Body condition in whiting was shown to be closely linked to inter-annual differences in sandeel availability (Engelhard et al. 2013). Lauerburg et al. (2018) linked the period of 2000 – 2007 in the North Sea, which was characterised by a low abundance in several forage fish, to reduced length-at-age and condition of adult whiting. However, temperature and fishing could also play a role in the observed changes.

1.7.2 Temperature and Atlantic inflow

Zheng et al. (2001, 2002) modelled spatial abundance of adult whiting in relation to environmental variables and found a strong association with temperature in the region of North Atlantic inflow during winter and spring. The authors suggest whiting aggregations to be positively related to influences on growth and food intake in this area. Changes in inflow and/or temperature in this area might therefore indirectly affect recruitment through effects on reproductive outcome. Indeed Svendsen & Magnusson (1992) explained more than 70 % of recruitment variability in age-0 whiting to an index of Atlantic Water inflow in winter and spring. However due the extended spawning period of whiting and spatial overlap of different life stages, it could not be resolved if this was due to a direct effect on early life stages or indirect through effects on the spawning stock.

2. Eggs

To date no studies have been conducted looking explicitly on the egg stage of whiting in the North Sea and environmental influences. The extended spawning period of whiting with eggs present from January to June in the southern North Sea (van der Land 1990) results in a multitude of influences with possibly great interannual variability.

3. Larvae

3.1 Diet

Whiting larvae in the yolk-sac stage largely feed on tintinnids with a lesser extent on diatoms and dinoflagellates in the southern North Sea (Last 1978). With increasing size, they showed preference for nauplii and copepodid stages of the copepods *Pseudo/Paracalanus spp*. and *Temora longicornis*. In the northern North Sea small whiting larvae preyed almost exclusively on calanoid nauplii and later additionally on the copepods *Oithona sp.* and *Pseudocalanus elongates* (Economou 1991). *Calanus finmarchicus* became most important at the end. Nielsen & Munk (1998) found whiting larvae to feed on neritic zooplankter (*Acartia sp., Temora sp., Para/Pseudocalanus sp. and Evadne sp.*) at the coastal side of a frontal zone in the central North Sea, opposite to cod, which fed on the oceanic side on *Calanus*.

3.2 Atlantic water inflow

Correlative studies found whiting recruitment positively related to increased temperature (Cook & Heath 2005) as well as an index of warm, saline Atlantic water inflow (Svendsen & Magnusson 1992) (see also Table A.1.6). The spawning grounds of whiting in the southern North Sea lie directly in the vicinity of warm Atlantic water inflow coming from the English Channel. Associated with the intrusion of these warm water masses are neritic zooplankton (Beaugrand et al. 2001, Beare et al. 2002), which form an important part of the diet in whiting larvae. The negative correlation with *Calanus* found by Pepin (1990) might indicate an association with the inflow path over the English Channel. *C. finmarchius* normally enters the North Sea via the northern inflow over the Norwegian Trench (Beare et al. 2002). The Norwegian Trench inflow and the English Channel inflow show opposite pattern of activity with strong English Channel inflow associated with weak northern boundary inflow and vice versa (Winther & Johannessen 2006).

3.3 Transport and the role of Frontal zones

Various studies of Munk et al. looked at the occurrence of whiting larvae near fronts in the North Sea (Nielsen & Munk 1998, Munk et al. 1999, Munk 2014). Whiting larvae were found on the coastal side of the front in the central and eastern part of the North Sea (Nielsen & Munk 1998, Munk et al. 1999), mostly in depth of 0 to 30m (Economou 1991, Höffle et al. 2013, Munk 2014). Abundance of whiting larvae in the region varied with the strength of the front (Munk et al. 1999). Observed differences between distribution of cod and whiting larvae across the front were suggested to be attributed to association of different water masses in spawning as well as drift of eggs and larvae (Nielsen & Munk 1998). Indeed, oceanographic structures seem to play a major role for North Sea whiting as it is suggested by genetic analysis. Charrier et al. (2007) found differences between whiting north vs. south of the Doggerbank associated with limited mixing between water masses during the egg and larval stage. Additionally the authors suggested the front at Flamborough as limit for dispersal.

3.4 Predation

Haddock larvae took newly hatched whiting larvae (Economou 1991), however spatial overlap is limited as haddock and whiting show different presence at a frontal zone (Munk et al. 1999). Additionally whiting and haddock do only co-occur in the northern and central North Sea.

4. Juveniles

4.1 Habitat and density dependent effects

As other gadoids, 0-group whiting change from a pelagic to a benthic lifestyle in summer of their first year. Whiting juveniles settle much later and over a longer period (June to August) compared to other gadoids (cod and haddock) (Demain et al. 2011, Bastrikin et al. 2014). Hislop (1996) mentioned that whiting and haddock do not occupy a specific nursery habitat like the gadoids cod and saithe, which stay in particular inshore nursery grounds. However in the Skagerrak area 0-group whiting were usually found in shallow waters and fjords co-occurring with cod in sheltered areas (Fromentin et al. 1997). Whiting showed a clear preference for sandy substrate (Bertelli & Unsworth 2014, Elliott et al. 2017) and was shown to occupy seagrass during night (Bertelli & Unsworth 2014). As suitable habitats are limited competition for food and space is likely to occur. With increasing age whiting moved to deeper areas (Fromentin et al. 1997, Bastrikin et al. 2014, Elliott et al. 2017).

4.2 Association with medusa (jellyfish umbrellas)

Pelagic 0-group whiting with its extended pelagic phase were observed to hide under jellyfish umbrellas as an effective protection from predation (Dahl 1961, Thiel 1978). Correlative analysis found a positive association between 0-group whiting abundance and survival and two species of the jellyfish *Cyanea* namely *C. lamarckii* and *C. capillata* in the North Sea (Hay et al. 1990, Lynam & Brierley 2007). Largest overlap with the scyphomedusae *Cyanea* and juvenile whiting in summer was between Orkney and Shetland, east of Shetland and at the outlet of the Skagerrak around Fisher Bank (Hay et al. 1990). Analysis of CPR data by Attrill et al. (2007) found an increasing occurence of jellyfish in the central North Sea positively related to the NAO and Atlantic water inflow from 1958 - 2000.

4.3 Diet

Whiting is an opportunistic feeder with prey items reflecting their general surrounding environment (Shaw et al. 2008). Pelagic juvenile whiting feed almost exclusively on copepods after metamorphosis (Robb & Hislop 1980, Robb 1981, Hamerlynck & Hostens 1993, Rowlands et al. 2008, Shaw et al. 2008). However, which copepods dominate in their diet depended on the region and time sampled. *Temora longicornis* was the dominant copepod in most studies for the northern and eastern North Sea (Robb & Hislop 1980, Shaw et al. 2008, Bastrikin et al. 2014). Other prey items were dominant including *Centropages typicus* (Robb & Hislop 1980) and *Calanus finmarchicus* (Bastrikin et al. 2014) in the North and *Para/Pseudocalanus* in the eastern North Sea (Shaw et al. 2008) and to a lower extend in the North (Robb & Hislop 1980, Robb 1981). In the southern North Sea also copepods were dominant food items in May, but information on species level is not available (Hamerlynck & Hostens 1993). Pelagic fish eggs were also present in the diet of whiting juveniles (Robb 1981). With increasing size whiting feed on crustaceans like mysids (Hamerlynck & Hostens 1993), amphipods (Hamerlynck & Hostens 1993, Bastrikin et al. 2014) and euphasids (Robb & Hislop 1980) and then on a variety of prey items mainly crustaceans and fish (Robb & Hislop 1980, Hamerlynck & Hostens 1993, Bromley et al. 1997, Bastrikin et al. 2014). In the southern as well as northern North Sea whiting were preying on larval to postlarval stages of herring and sprat as well as crustaceans such as brown shrimp (*Crangon crangon*) (Hamerlynck & Hostens 1993, Greenstreet et al. 1998). Goby was only an important prey item in the south (Hamerlynck & Hostens 1993), whereas in the North also sandeel was consumed (Greenstreet et al. 1998, Bastrikin et al. 2014).

4.4 Competition

As the diets of cod and whiting overlap especially in the first pelagic juvenile phase, where they consume mostly copepods, competition is highly likely (Rowlands et al. 2008, Shaw et al. 2008). Although cod settles earlier to the bottom habitat as whiting, both species overlap in time during May and June in the pelagial (Bastrikin et al. 2014). Which species has the competitive advantage over the other is, however, not clear (e.g. Fjøsne & Gjøsæter 1996, Shaw et al. 2008).

4.5 Predation

Cannibalism in whiting is common especially on the youngest age classes (Hislop et al. 1991, Bromley et al. 1997, Greenstreet et al. 1998). Additionally, cod and haddock prey on early age-classes of whiting (Bromley et al. 1997). However, after 1960 cannibalism was comprising the largest amount of predation mortality from gadoids on the whiting stock (Pope & Macer 1996). Dahl & Kirkegaard (1987) found also horse mackerel in the eastern North Sea largely preying on 0-group whiting in the summer of 1986. Grey gurnard was also shown to prey frequently on juvenile whiting (De Gee & Kikkert 1993), explaining over 44% of variability in whiting recruitment (Floeter et al. 2005). Contrary to cod, which seems to be experience higher predation pressure by grey gurnard since the late 1980s, whiting recruitment was always largely affected by grey gurnard predation (Floeter et al. 2005).

5. Summary

Whiting showed a more stable recruitment pattern of the commercial gadoids in the North Sea, compared to cod and haddock, although with a slight downward trend. The ability to cope with varying environmental conditions could explain the more stable recruitment of this species. The extended spawning season inherent in whiting also smoothes over episodic adverse effects (e.g. low prey availability at the onset of the season), but also makes it harder to pinpoint one environmental effect responsible for a particular year class dynamic. Indication for a positive relation to temperature, a wide feeding niche and less reliance on boreal *C. finmarchius* in the diet than cod may have buffered to some extent against the observed North Sea regime shift with higher temperatures and a change in the zooplankton community. Additionally, the unique behaviour hiding under jellyfish umbrellas comes in handy with the North Sea predicted to become more gelatinous in the future.

Table A.1.6: Correlative studies taking into account environmental effects on whiting recruitment in the North Sea

Environmental variable	Life-stage	Region	Time period	Relationship	Author
Temperature (SST)	Age-0-recruits	North Sea/ Norwegian Coastal Current	1972-1991	-	(Dippner 1997)

		(NCC)			
	Age-0-recruits	North Sea	1960-1998	+	(Cook & Heath 2005)
	Age-0-recruits (Ricker residuals)	North Sea	1971-1986	none	(Lynam & Brierley 2007)
Warm Atlantic water inflow (winter)	Age-0-recruits	North Sea	1970-1988	+	(Svendsen & Magnusson 1992)
Currents	Age-0-recruits	North Sea	1990-2011	Non-linear	(Pécuchet et al. 2015)
Wind turbulence (Cubed wind speed)	Age-0-recruits	North Sea	1970-1988	-	(Svendsen & Magnusson 1992)
Salinity	Age-0-recruits (Ricker residuals)	North Sea	1971-1986	none	(Lynam & Brierley 2007)
Phytoplankton	Age-0-recruits	North Sea	1960-1980	+	(Pepin 1990)
	Age-0-recruits	North Sea	1990-2011	Non-linear	(Pécuchet et al. 2015)
Calanus abundance	Age-0-recruits	North Sea	1960-1980	-	(Pepin 1990)
Jellyfish biomass	Age-0-recruits	North Sea	1974-1983	+	(Hay et al. 1990)
	Age-0-recruits (Ricker residuals)	North Sea	1971-1986	+	(Lynam & Brierley 2007)
Herring biomass	Age-0-recruits	North Sea	1960-1980	+	(Pepin 1990)
	Age-0-recruits	North Sea	1990-2011	Non-linear	(Pécuchet et al. 2015)
Plaice/Sole recruitment	Age-0-recruits	North Sea	1960-1980	-	(Pepin 1990)
Cod biomass	Age-0-recruits	North Sea	1960-1980	-	(Pepin 1990)
Gadoids biomass	Age-0-recruits	North Sea	1990-2011	Non-linear	(Pécuchet et al. 2015)
NAO	Age-0-recruits	North Sea/ Norwegian Coastal Current (NCC)	1972-1994	-	(Dippner 1997)
	Age-0-recruits (Ricker residuals)	North Sea	1971-1986	none	(Lynam & Brierley 2007)

6. Knowledge gaps

Taking both correlative studies (Table A.1.6) and information of whiting life cycle into account points towards the importance of temperature and currents, especially warm Atlantic water inflow for whiting recruitment. However if the positive effect is due to increased feeding conditions for various life stages, transport, temperature effects on growth and spawning potential, changes in predator fields, competitive advantage over cod or attributed to increased jellyfish abundance is not resolved. Additionally, most of the correlative relationships were done with time series until the late 90s, with only Pécuchet et al. (2015) examining the time period after. Information if the proposed relationship hold true with increasing time series length is therefore missing. There is also a paucity of studies examining the effects of transport on early life stages of whiting. The ubiquitous distribution of spawning grounds over the North Sea and the extended spawning season, however, poses a challenge for a systematic investigation. The same is true for a link of recruitment with environmental variables as effects on life stages are integrated over a longer time, which might cancel each other out and causes only population effects to remain. In summary, which particular environmental variables drives recruitment in North Sea whiting is still poorly understood.

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Task 1.2. North Sea case study

Annex 2. Review on stock structure of North Sea cod and plaice

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4. Stock/Spatial structure of commercially important North Sea stocks – Atlantic cod and European plaice

One of the emergent themes in the published literature and recent ICES (International Council for the Exploration of the Sea) reports and advice is the topic of stock structure (e.g. Hunter *et al.*, 2004c; Neat *et al.*, 2014; ICES, 2015a). This topic is multi-faceted, but some of the key questions surrounding stock structure consider how a species in a certain area is distributed, how the population of individuals interacts with conspecifics in adjacent areas and how their presence affects predator-prey dynamics. Answering these questions, and many others, are fundamental steps in conservation and management, particularly in the stock assessment process; any new information feeds into estimates of abundance, recruitment and Spawning Stock Biomass (SSB), and allows catch/landings allocations to be increasingly more reflective of the underlying dynamics of the resource.

In the North Sea, two species that have seen considerable research effort are Atlantic cod (*Gadus morhua*) and European plaice (*Pleuronectes platessa*). Both are widely distributed, have experienced altered abundance levels due to historical and current fishing pressure and have substantial commercial value (ICES, 2018a, 2018b). Levels of exploitation and the state of the stock are assessed, predicted and managed annually by ICES at a stock and species level (e.g. ICES, 2018a, 2018b). Both exhibit resident, migratory and aggregating behaviours that can lead to fine-scale population sub-structuring (e.g. Hunter *et al.*, 2004b, 2004a; Robichaud and Rose, 2004; Neat *et al.*, 2014). Further, both species have, and are predicted to, experience changes to their individual-level processes (e.g. growth, maturation and survival; Brander, 1995; Teal *et al.*, 2008; Kjesbu *et al.*, 2010) and spatial distribution under a changing climate (Drinkwater, 2005; Dulvy *et al.*, 2008; Engelhard *et al.*, 2011, 2014).

In the following review we will describe the existing knowledge concerning stock structure in these two demersal fish species and highlight any data gaps or research needs. Drawing on several information sources, ranging from genetics to tagging studies, we will demonstrate how our understanding of stock structure in the North Sea has changed and how the rate of mixing can vary at the scale of ICES Divisions (4.a, 4.b, 4.c, 3.a20, 3.a21 and 7.d; Figure A.2.1) due to behavioural differences. Furthermore, we will briefly discuss the age structure of each North Sea stock and summarise existing knowledge on growth, maturity and recruitment; the latter phase will be by no means an exhaustive review, primarily because these topics are covered elsewhere in this document (linked to other sections needed here), but it will provide some of the building blocks for future work.

4.1 Atlantic cod

Cod is a highly mobile marine species, with adults roaming over a seasonal scale of approximately 200km (Neat *et al.*, 2014). Spawning typically takes place in the spring, occurring in January through to April. Following spawning, individuals re-distribute to feeding grounds for the duration of the summer and autumn months. Adult cod are top predators in the North Sea food web, feeding on a range of crustaceans and other small fish (Magnussen, 2011), whilst smaller cod are prey for grey gurnard (*Eutrigla gurnardus*), whiting (*Merlangius merlangus*), herring (*Clupea harengus*) and seabirds, as well as larger cod (Floeter *et al.*, 2005; ICES, 2015a). The 2017 key model run from the Working Group on Multispecies Assessment Methods also highlights that grey seals (*Halichoerus grypus*) and harbour porpoises (*Phocoena phocoena*) exert significant predation pressure on cod below 4kg (ICES, 2017a). Within sub-area 4, cod are caught by virtually all demersal gear types, including beam trawls, otter trawls, seine nets, gill nets, trammel nets and lines (ICES, 2017b). At the scale of the North Sea, the abundance and SSB of cod is low compared to historical levels, and is currently estimated to be below reference points (e.g. B_{lim}, B_{pa} and MSY $B_{trigger}$; (ICES, 2019a)).

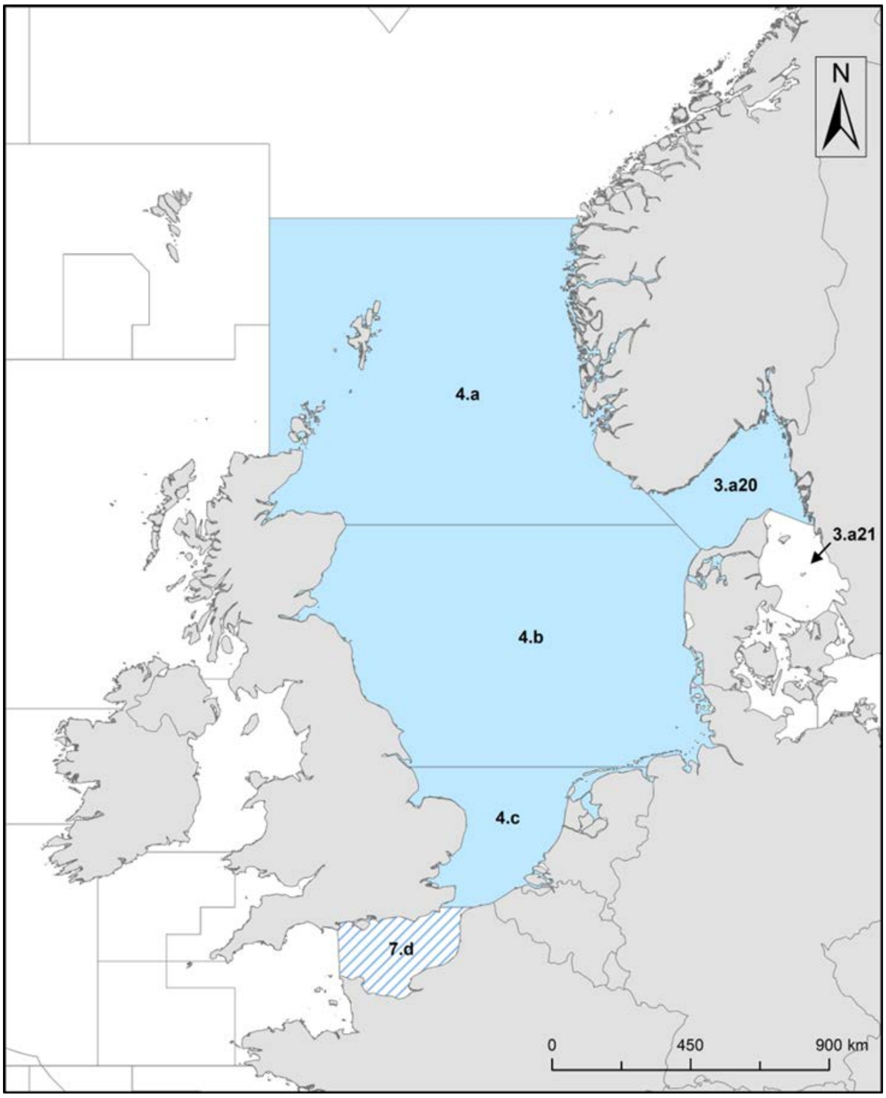

Figure A.2.1. North Sea management areas, including ICES Divisions (shown in blue and labelled) 4.a, 4.b, 4.c (sub-area 4) and subdivision 3.a20. ICES Division 7.d is partially coloured as it is considered part of the North Sea cod stock but not part of the North Sea plaice stock. ICES subdivision 3.a21 is also shown.

4.1.1 Stock/Spatial structure

Cod in the North Sea, including ICES Divisions 4.a, 4.b, 4.c, 7.d and subdivision 3.a20, is currently assessed as a single functional unit. However, recent examination, most notably during the 2015 Benchmark Workshop on North Sea Stocks (WKNSEA; ICES, 2015), highlights that cod stock structure is an area of uncertainty, concluding that 'strong evidence from several studies shows that the North Sea cod population structure is complex, and at least two distinct stocks could be confidently assumed for the assessment area'. One of these stocks occurs in the northern North Sea whereas the second inhabits the shallower waters of the central and southern North Sea. An infographic illustrating how these two cod stocks are structured, in terms of spatial distribution and movement, is provided in Figure A.2.2. The uncertainties associated with the complex structure of the cod stock may have played a role in the deteriorating performance of the assessment model in recent years (José De Oliveira, *pers. comm.*), although further research is required to test this theory. Contributors to WKNSEA (ICES, 2015a) also highlighted the need for further research into the extent of mixing between stocks in different quarters and life stages is a key research need.

4.1.1.1 Genetic studies

Genetic studies are increasingly being used to help tackle the stock structure problem (Mariani and Bekkevold, 2014). These studies make use of genetic markers, typically microsatellite DNA or Single Nucleotide Polymorphisms (SNPs) to effectively classify fish into unique stocks and/or populations based on their genetic composition. For instance, we might expect the genetic profile of cod in the northern North Sea to differ from their southern conspecifics, especially if the rate of mixing during the spawning season is low.

Microsatellites are small segments of repetitive, noncoding DNA, found throughout the genomes of all eukaryotes. They contain motifs composed of two to six base pairs which repeat sequentially several times in a given allele. Several characteristics of microsatellite DNA make them very suitable genetic markers for studies of population structure and stock identification, for example, codominance, Mendelian inheritance, neutrality, high levels of genetic variation and their relative ease of analysis (Abdul-Muneer, 2014).

Recent advances in next-generation sequencing (NGS) have also facilitated the discovery of SNPs; i.e. the occurrence of alleles with different nucleotide bases at a specific point in a DNA sequence. This advancement allows population structure to be determined at a far higher resolution compared to alternative methods (Davey *et al.*, 2011; Hemmer-Hansen *et al.*, 2014). One of the most valuable aspects of SNPs as genetic markers is the variation they exhibit between neutral regions and those under selection. SNPs in regions under selection pressure may reveal adaptive divergence even when neutral regions show genetic homogeneity between populations (Hauser and Carvalho, 2008; Milano *et al.*, 2014). This final point highlights why it is important to use different genetic markers and different regions when the aim is to accurately determine population structure and define stock boundaries.

Population genetic research illustrates that cod populations are structured over both small and large spatial scales. For instance, Nielsen *et al.* (2003) identified differences in the genetic profile of North Sea and Baltic Sea cod within transitional waters. Several other studies, which make use of both microsatellite DNA (Nielsen *et al.*, 2009) and SNPs (Poulsen *et al.*, 2011; Heath *et al.*, 2014; Wright *et al.*, 2018), support the presence of two distinct cod stocks in the North Sea. Such distinctions can be driven by a number of competing factors, including reproductive isolation, limited mixing, natal homing and behavioural differences.

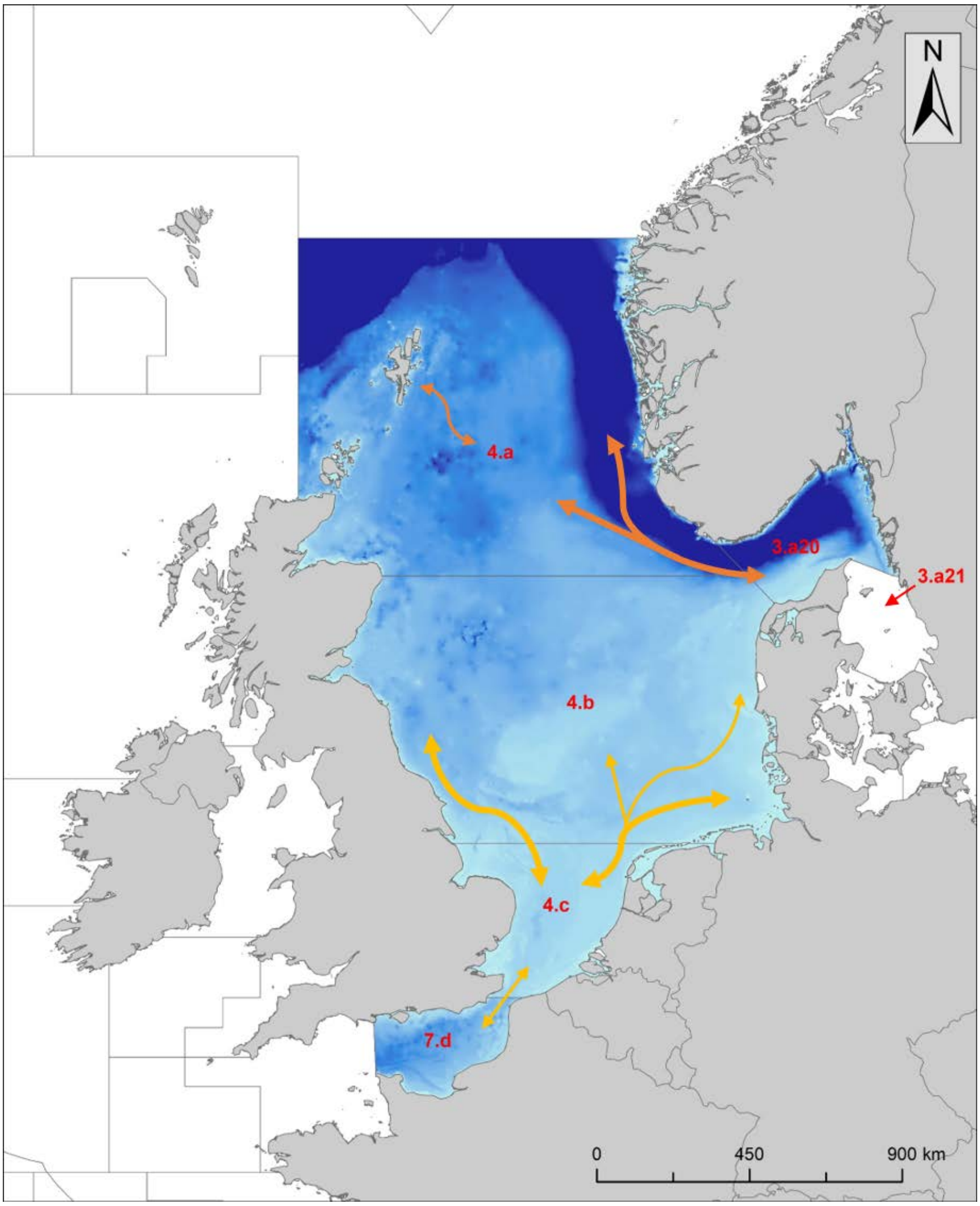

Figure A.2.2. Cod movement and stock structure in the North Sea assessment area. The directionality of the arrows is designed to illustrate our existing knowledge and the width is representative of our confidence i.e. the amount of evidence we have to support such knowledge. The southern and central North Sea cod stock is shown in yellow and the northern Viking cod stock is shown in orange. The underlying bathymetric data is sourced from the General Bathymetric Chart of the Oceans (GEBCO) and is gridded at a one-minute spatial resolution (GEBCO, 2017; www.gebco.net).

Within the North Sea, one distinct stock appears to inhabit the much deeper waters of the northern North Sea, centred on the Viking Bank in ICES Division 4.a (hereafter referred to as Viking). Conversely, the second occurs in the much shallower central (ICES Division 4.b), southern (ICES Division 4.c) North Sea and eastern English Channel (ICES Division 7.d). Such separation might be driven by differences in depth utilisation, as adults in the Viking stock appear to remain exclusively in waters >100 metres (Wright *et al.*, 2006b, 2006a; Neat *et al.*, 2014). Moreover, investigations into early life stage connectivity also suggest that such isolation in North Sea cod may have arisen through oceanographic features that either characterise favourable spawning grounds (Munk *et al.*, 2009) or influence the rate and/or directionality of dispersal (Heath *et al.*, 2008).

Interestingly, recent work by Wright *et al.* (2018) using genetic and otolith microchemistry illustrates that many Viking juveniles disperse towards and settle in the western Skagerrak (ICES subdivision 3.a20), before making return migrations prior to spawning. Such natal homing may explain why previous studies have noted high abundance of 0- and 1-group cod in the Skagerrak but a distinct lack of abundance at age 2+ (Svedäng and Svenson, 2006). It also explains why the strong juvenile year class of 2001 within the Skagerrak was genetically attributed to the North Sea stock as opposed to local adults (Knutsen *et al.*, 2004). Furthermore, Wright *et al.* (2018) show that adults in the eastern English Channel (ICES Division 7.d) and the southern North Sea have otolith microchemistry values that are consistent with juveniles sampled in the southeastern North Sea. This finding supports the hypothesis that southern North Sea cod are mostly recruited from adjacent nursey grounds (Munk *et al.*, 2002, 2009; Gonzalez-Irusta and Wright, 2015) and exhibit minimal spatial overlap with more northern stock units (Wright *et al.*, 2006b; Righton *et al.*, 2007; Neat *et al.*, 2014).

4.1.1.2 Tagging studies

Several tagging studies have been conducted in the North Sea to investigate long-term movement patterns, migratory highways and the geographical distribution of cod populations (e.g. Bedford, 1966; Daan, 1978; Righton *et al.*, 2007, 2008; Hobson *et al.*, 2009; Neat *et al.*, 2014; Griffiths *et al.*, 2018). These studies consider both electronic (predominantly Data Storage Tags; DSTs) and mark-recovery tags and often indicate a strong seasonal cycle. Typically, cod separate to local spawning grounds during the late winter and early spring and then re-distribute and often intermix with conspecifics during the summer feeding season (Metcalfe, 2006; Neuenfeldt *et al.*, 2013).

In the southern North Sea, Righton *et al.* (2007) re-analysed historical mark-recovery data (dating back to the 1960s) as well as electronic tags (n = 30) to investigate the movement patterns of cod. The authors show that the spatial distribution of tag returns depends on both season and age. Fish recaptured during the spawning season (Q1 and Q4) were typically caught within their release area, whereas recapture outside of their release area was much more common during the summer foraging season (Q2 & Q3). Adults were found to displace further than juveniles (body length < 50 cm) and movement northwards into 4.b was a lot more frequent than movement into the eastern English Channel. The authors used electronic tags to further explore these trends. The authors attributed a lack of mixing between 4.c and 7.d to behavioural differences, as cod in 4.c typically make use of strong tidal streams during migration, whereas cod tagged in 7.d display minimal evidence of this behaviour. Further, they linked patterns of northern displacement to homing migration, as individuals move away from natal spawning grounds and return later on in the year. Such findings highlight the ability of behavioural and environmental differences to cause fine-scale stock structuring despite any physical barrier to re-distribution (Righton *et al.*, 2007). The role that movement behaviour plays in cod stock structure is also explored in Robichaud and Rose (2004), Hobson *et al.* (2009) and Griffiths *et al.* (2018).

It is noteworthy that cod tagged in 4.c move an average distance of 135 km (± 135 km) from release to recapture, but their northern range does not extend beyond the geographical extent of 4.b. This finding is consistent with the work of Neat and Righton (2007) who show that 129 adult cod tagged with electronic tags in the southern North Sea showed no evidence of northward expansion. This result is discussed in a thermodynamic perspective, with the authors highlighting that cod within the southern North Sea currently operate in thermal conditions that are super-optimal for growth. These cod show no evidence of a northward dispersal to cooler waters even though they appear more than capable of such re-distribution. The findings could point towards a local preference for environmental/seabed conditions (e.g. high salinity waters and coarse sandy bottoms during spawning; Gonzalez-Irusta and Wright (2015)) or a reliance on prey species that display patchy spatial distributions (e.g. the lesser sandeel, *Ammodytes tobianus*; Magnussen (2011)), both of which may limit the potential re-distribution of the southern North Sea cod stock. Moreover, we might expect such patterns to change as sea temperatures continue to rise (Peck and Pinnegar, 2018), subsequently imposing greater thermal pressures on metabolism, growth and survival.

In the northern North Sea, extensive mark-recovery work has indicated that cod located in Norwegian coastal waters (northeast part of 4.a) display high rates of site fidelity, with very little movement south (Nedreaas *et al.*, 2008). Some evidence does exist to support mixing between Viking cod and cod that inhabit the shallow waters to the east of Shetland (Neat *et al.*, 2014). However, such mixing only occurs during the summer foraging season (Neat *et al.*, 2014). Further tagging work in the northern North Sea is limited, however it is clear that movement south is infrequent and that the amount of mixing between the two hypothesized North Sea stocks is minimal.

4.1.1.3 Survey and landings data

Holmes *et al.* (2014) investigated how survey-based indices of SSB varied across the North Sea. The authors opted to spilt the North Sea in three core areas: Viking, the northwest and the south, noting that the most significant difference occurred between Viking and the shallower areas of the southern North Sea. Further, a similar approach is frequently employed during the annual ICES assessment, with International Bottom Trawl Survey (IBTS) data for North Sea cod being spilt into four areas: Viking (ICES Division 4.a), Viking (3.a20), northwest and southern North Sea (ICES, 2019a). Results show that the Viking (ICES Division 4.a), Viking (3.a20) and northwest areas show similar trends in biomass through time, whereas the biomass of cod in the southern area has declined at a steeper trajectory since 2008. Such findings further bolster a two-stock hypothesis.

Cod spawn throughout the North Sea. Data from ichthyoplankton surveys and fisherman's observations indicate a number of spawning aggregations, in particular around the southern and eastern edge of the Dogger Bank, in the German Bight, the Moray Firth and to east of the Shetland Isles (Fox *et al.*, 2008). Interestingly, Fox *et al.* (2008) failed to detect any significant spawning activity on the northeast coast of England, an area that historically was a highly productive spawning ground for cod in the central North Sea.

Re-digitisation of historical fisheries data (1913-2012) by Engelhard and colleagues (2014), revealed that the current spatial distribution of cod is almost completely the opposite of its distribution throughout much of the 20th century. Currently, catch per unit effort (CPUE) for cod peaks in the deeper, northern and north-eastern North Sea, whereas prior to the 1980s CPUE was mainly concentrated in the western North Sea (off the English and Scottish coast). The authors show that this change has predominantly occurred over the last 30 years (1980-2010). Statistical analysis links the northward shift of CPUE to deeper waters to a warming of sea surface temperature. Conversely, the eastward shift is attributed to spatial differences in fishing pressure.

4.1.2 Age structure

4.1.2.1 Young fish (ages 0-2)

Young cod have historically been found in large numbers in the south-eastern parts of the North Sea, especially in the German Bight (ICES, 2015a). More recently, the western Skagerrak has become increasingly more important (ICES, 2015a). Interestingly, despite differences in the spatial abundance of young cod, their mean catch weight-at-age has showed little absolute variation through time (ICES, 2015a). This is not the case in adult cod (see section 4.1.2.2).

Over the last five years, young cod have, on average, made up 71% of all international landings by number in the North Sea (ICES, 2015a). The proportion of catch made up of young cod could even be as high as 85% when discards are considered (ICES, 2015a).

4.1.2.2 Adult fish (ages 2+)

Adult cod have historically been distributed throughout the Southern Bight, the northeast coast of England, in the German Bight, the east coast of Scotland and in the north-eastern North Sea. However, as the abundance of the stock has declined through time, the area occupied by these groupings has contracted and they have become increasingly more discrete (ICES, 2015a). Based on landings and survey data the highest densities of older cod currently occurs within the deeper waters of the central and northern North Sea (ICES, 2015a).

Over the last thirty years, the mean catch weight-at-age for age 3-6 cod in the North Sea has remained fairly consistent (ICES, 2018c). In terms of absolute abundance, older cod continued to decline up to 2006 due, in part, to the very weak year classes of 2000, 2002 and 2004. Despite recent increases, the abundance of cod has again declined since 2016 (ICES, 2019a).

4.1.3 Growth

Growth parameters of North Sea cod presented in ICES (1994) demonstrate that cod in the southern North Sea grow faster than those in the northern North Sea but reach smaller maximum body lengths (Oosthuizen and Daan, 1974; ICES, 2005). Past work has linked cod growth to variation in temperature and prey availability (Blanchard *et al.*, 2005; Righton *et al.*, 2010). Age and maturity also play a role, as older and larger cod have lower optimal temperatures for growth (Björnsson and Steinarsson, 2002) and mature cod of each sex are, on average, larger than immature cod (Hislop, 1984). Moreover, in the context of space use and stock structure, temperature and local depth have been indirectly linked to the distribution of cod (Ottersen *et al.*, 1998; Swain, 1999; Blanchard *et al.*, 2005).

4.1.4 Maturity

Until 2015, the North Sea cod assessment assumed a constant maturity ogive, where maturity occurred infrequently at ages 1 and 2, becoming more common at age 3+. This maturity ogive was originally estimated using the International Bottom-trawl Survey series for 1981-1985 (ICES, 2015a). However, several studies have now shown that the maturity-at-age of cod in the North Sea has changed, with cod maturing at a younger age and at smaller sizes compared to historical levels (Cook *et al.*, 1999; Yoneda and Wright, 2004; ICES, 2015a). As of 2015, maturity-at-age is allowed to vary with time and is estimated annually during the assessment as described in Walker and Poos (2017).

Interestingly, the spatial differences that have been observed in terms of distribution, age structure and growth are also reflected in maturation rates. For example, Wright *et al.* (2011) show that the rate at which cod achieve maturation in the more northern Viking stock remained fairly constant between 1976-2005. In comparison, cod in the southern North Sea and north-western North Sea, in particular on the east coast of Scotland, have displayed an increasingly positive relationship between age and the proportion of individuals that are mature. Wright *et al.* (2011) conclude that temperature is a principle explanatory variable underpinning these spatial differences. Moreover, their work on maturation reaction norms suggests that temperature effects on gonad maturation could be a contributory factor and merits further investigation (Wright *et al.*, 2011).

The issue of temperature-mediated maturity-at-age is further exacerbated by findings that older and larger fish contribute disproportionally to population replenishment (Beldade *et al.*, 2012; Barneche *et al.*, 2018). Consequently, any reduction in the age and size of an average adult will presumably reduce a stock’s potential for recovery. In fact, differences in the fecundity of North Sea cod have already been documented by Rijnsdorp *et al.* (1991) and Yoneda and Wright (2004). In both studies, the relative fecundity of cod is shown to vary with age, size and time. For instance, Yoneda and Wright (2004) show that the fecundity-size relationship in northwest North Sea cod changed considerably between the late 1960s and the early 2000s. Differences were also found between spatial areas, with cod in the north-western North Sea having, on average, a 37% greater relative fecundity than cod in Viking. Rijnsdorp *et al.* (1991) found similar trends in the central and southern North Sea.

4.1.5 Recruitment

The recruitment of North Sea cod has previously been linked not only to SSB, but also temperature (Dickson and Brander, 1993; Myers *et al.*, 1995; Planque and Frédou, 1999; O’Brien *et al.*, 2000), plankton production and mean prey size (Beaugrand *et al.*, 2003), the North Atlantic Oscillation (Brander and Mohn, 2004; ICES, 2005) and the demographic composition of spawners (Wright, 2014). Since 1998, cod recruitment in the North Sea has been relatively low, reaching minima in 1998, 2003, 2016 and 2018 (ICES, 2019a). The large 1996-year class was the last to contribute substantially (above a billion new recruits) to the fishery (ICES, 2015a).

Historically, the SSB of the North Sea cod stock peaked in the early 1970s and has since steadily declined (ICES, 2018b). SSB reached its lowest known values, approximately 45,000 tonnes, in 2004, 2005 and 2006 (ICES, 2018b). Such declines have been linked to a series of poor recruitment classes, as well as high fishing mortality and discard rates (ICES, 2015a). SSB did show increases between 2007 and 2015, mainly due to some strong recruitment classes (e.g. in 2010) and marked efforts to reduce the fishing pressure imposed on the stock (ICES, 2015a). That said, this trend has been reversed since 2016 (ICES, 2019a).

4.1.6 Research needs

Based on the previously discussed existing knowledge of cod stock structure and spatial distribution in the North Sea, there are two clear research needs. First, as stipulated in the 2015 benchmark report (WKNSEA; ICES, 2015) there is a need to investigate the 'extent of mixing of stocks in different quarters and life stages'. This topic has been largely covered in the southern North Sea and eastern English Channel by Righton *et al.* (2007). A similar level of knowledge is currently unavailable in 4.a, 4.b and 3.a20, however patterns of space use and the extent of mixing could be readily investigated using the same data sources as Righton *et al.* (2007). For instance, the Cefas tagged fish database in both the northern and central North Sea dates back to the early 1960s and includes over 7,000 juvenile and adult fish, thus representing an untapped resource with significant scientific value. Moreover, any findings will add evidence, for or against, the two-stock hypothesis and will allow exploration into whether stock structure in the North Sea assessment area has changed through time.

Second, given the potential impacts of temperature on cod growth, maturity and recruitment, there is a clear research need regarding the propagation of these impacts at the stock level both now and into the future. This topic is also discussed in (add some link/text to other sections). However, given that any changes in sea temperature are unlikely to be spatially uniform and will undoubtedly impose different pressures on the entire North Sea food web (e.g. Beaugrand *et al.*, 2003), we propose to revisit the match/mismatch hypothesis (Cushing, 1990). Using the experimental work of Kjesbu *et al.* (2010) we plan to build a deterministic individual-based maturation model for North Sea cod, where the rate of maturation and the date of spawning will be modelled as a function of temperature and body length. Temperature data through time will be sourced from IPCC simulations (1900 to 2090) and will vary based on ICES Division (i.e. 4.a, 4.b and 4.c). Any findings will be compared to the Continuous Plankton Recorder (CPR) database (1958 to present), allowing the timing of spawning and timing of primary/secondary production in the North Sea to be compared.

4.2 European plaice

Behaviourally, plaice display periods of migration interspersed with prolonged periods of residency (Hunter *et al.*, 2004c, 2004b; Griffiths *et al.*, 2018). As in cod, spawning typically takes place in late winter and early spring, occurring in February through to April. Following spawning, individuals use strong tidal flows to migrate to feeding grounds for much of the summer and autumn months (Hunter *et al.*, 2003). Plaice feed on a range of benthic organisms, including a number of polychaetes, bivalve and crustacean species (Rijnsdorp and Vingerhoed, 2001). Within sub-area 4, plaice are mainly caught by beam trawlers in mixed fisheries in the southern and south-eastern North Sea. Beam trawlers also target plaice in the central North Sea (ICES, 2017b, 2018c). An emergent issue facing plaice stocks involves the large discard rates of undersized fish, a trend that seems to be driven by a decoupling between an enforced minimum mesh size of 80 mm and a minimum landing size of 27cm (ICES, 2018c). That said, plaice abundance is currently experiencing a large outburst in the North Sea, a topic that was investigated by the Working Group on the Ecosystem Effects of Fishing Activities in 2014 (ICES, 2014). Plaice is also the subject of a long-standing closed area, the so called 'plaice box', which has been in operation within the German Bight since 1989 (ICES, 2018c).

4.2.1 Stock/Spatial structure

As in cod, plaice in the North Sea, including sub-area 4 and ICES subdivision 3.a20, are currently assessed as a single stock unit. This has only been the case since 2015, prior to which plaice in the North Sea and the Skagerrak (ICES subdivision 3.a20) were assessed separately (ICES, 2015a, 2015b). The decision to extend the North Sea assessment area was primarily due to the work of Ulrich *et al.* (2013), who completed a comprehensive review of plaice stock structure in the Skagerrak and the Kattegat (ICES subdivision 3.a21) and concluded that plaice (both adults and juveniles) in the Skagerrak are highly associated with plaice in the North Sea, although local populations are present. An infographic illustrating the structure of the North Sea plaice stock, in terms of spatial distribution and movement, is provided in Figure A.2.3.

A similar issue exists between 4.c and 7.d, as North Sea plaice have been shown to move in and out of the eastern English Channel during the spawning season (in particular Q1; ICES (2010)). Consequently, the assessment now assigns part of the landings and estimated discards of mature fish in 7.d during Q1 to the North Sea stock (50%; ICES (2010b)). Although the stock structure and spatial distribution of North Sea plaice has not received the same level of attention as North Sea cod, i.e. no recent ICES benchmark request, it is clear that the subject is of interest and remains uncertain. This is especially true if recent increases in stock biomass and abundance (ICES, 2012), coupled with temperature and density dependent drivers, lead to range expansions or further re-distribution to the north (a trend already shown in Engelhard *et al.* (2011)).

A wider question surrounds whether or not plaice inhabiting the North Sea and Irish Sea can be considered a single stock. From a fisheries management perspective, the general consensus suggests that this is unlikely, although the evidence remains conflicting.

4.2.1.1 Genetic studies

A number of studies have investigated the genetic population structure of plaice within European waters (Hoarau *et al.*, 2002, 2004, 2005; Was *et al.*, 2010; Watts *et al.*, 2010). These studies, using both microsatellite and mitochondrial DNA, reveal strong genetic differentiation between plaice occupying shelf waters and those from Iceland and the Faeroe Islands (Hoarau *et al.*, 2002; Was *et al.*, 2010). Such findings suggest that deep water might serve as an oceanographic barrier to large-scale population mixing (Hoarau *et al.*, 2002). Within shelf waters, minimal differentiation was observed, suggesting that plaice from the North Sea, Irish Sea and other waters, notably the Baltic and the Bay of Biscay, are genetically similar (Hoarau *et al.*, 2002, 2005; Was *et al.*, 2010). The only notable difference, albeit small, occurred between plaice from the North and Irish Seas and plaice found in the western Baltic (Hoarau *et al.*, 2002, 2005).

A first review of available biological data (both published and unpublished) was carried out by Ulrich and colleagues (2013), to better understand the population structure of plaice from the eastern North Sea to the Baltic Sea. This review showed that plaice in the Skagerrak are closely associated with plaice in the North Sea (Ulrich *et al.*, 2013). Afterwards, using a multidisciplinary approach the same research team clarified stock identity and connectivity patterns in the transition area (Skagerrak-Kattegat) between the eastern North Sea and the Baltic Sea (Ulrich *et al.*, 2017). Although previous studies (e.g. Hoarau *et al.*, 2002; Was *et al.*, 2010) identified only low levels of genetic differentiation between samples taken in the North Sea and the Baltic Sea, thanks to advances in molecular methodology, new data were generated using the SNP approach (see section 4.1.1.1; Ulrich *et al.*, 2017). The analysis of this new data demonstrated that multiple populations are present in the Skagerrak to Kattegat transitional area. Furthermore, by combing multiple approaches, Ulrich and colleagues (2017) were able to show that North Sea plaice migrate to feeding grounds in the Skagerrak and it might represent a significant proportion of the catches in the area. Overall, genetic work on sub-stock structuring in the North Sea and the Skagerrak is clearly a research need moving forward to quantify the level of mixing between populations across different seasons and to avoid the depletion of the local population in the Skagerrak (Ulrich *et al.*, 2017). Such work may benefit from alternative genetic markers, some of which have evolved towards targeting genes subject to environmental selection (as discussed in Nielsen *et al.*, 2009; Ulrich *et al.*, 2013, 2017).

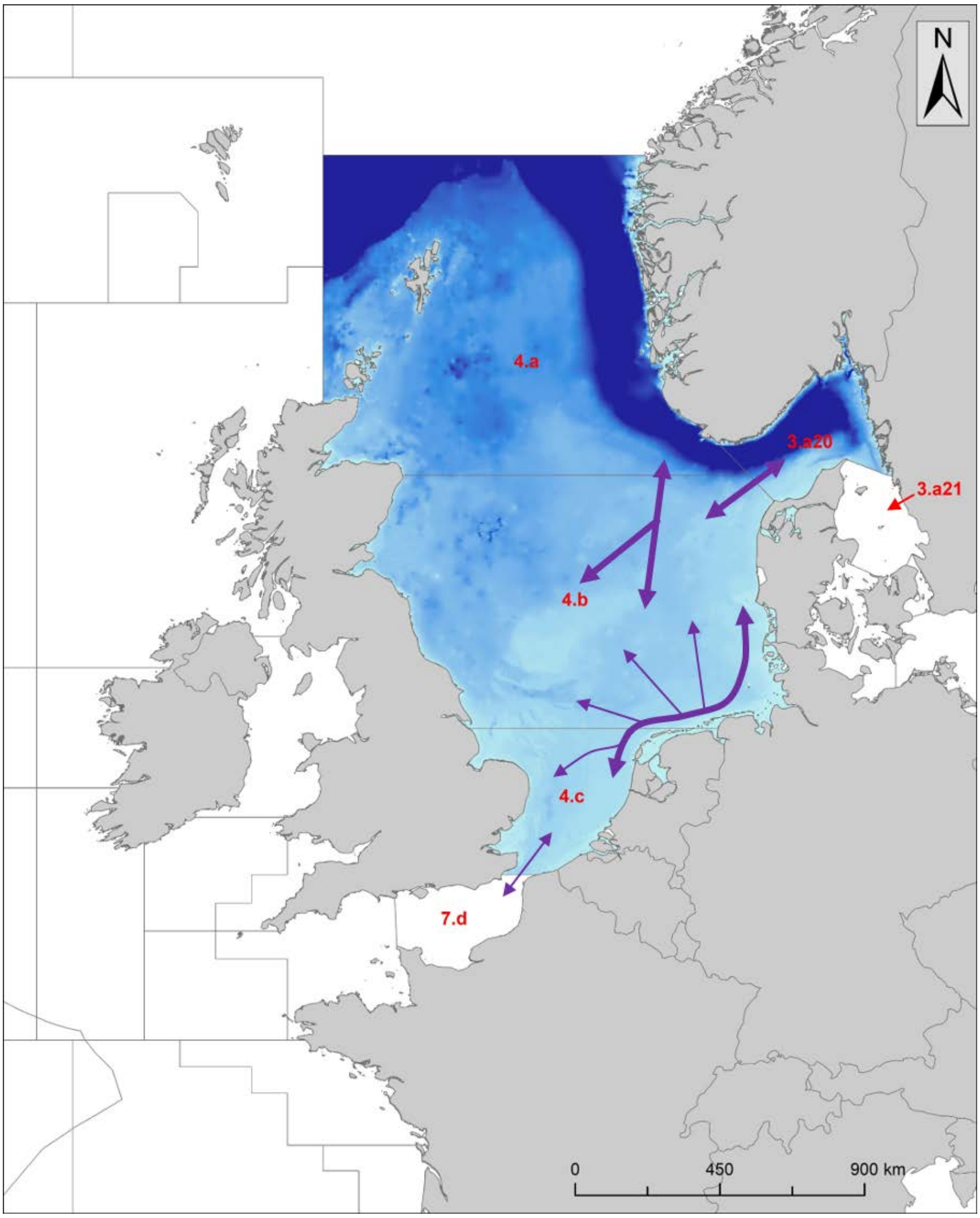

Figure A.2.3. Plaice movement and stock structure in the North Sea. The directionality of the arrows is designed to illustrate our existing knowledge and the width is representative of our confidence i.e. the amount of evidence we have to support such knowledge. The underlying bathymetric data is sourced from GEBCO (www.gebco.net).

4.2.1.2 Tagging studies

The tagging of plaice in the North Sea has been ongoing for almost a century. Mark-recovery data from the North Sea dates back to the early 1950s (Cefas legacy data) whilst records in the Skagerrak/Kattegat stretch back to the early 1900s (Trybom, 1905, 1908; Molander, 1944). As in cod, these sources of data have been used alongside electronic tag deployments (e.g. Hunter *et al.*, 2003, 2004b, 2004c; Bolle *et al.*, 2005) to investigate long-term movement patterns, migratory highways and space use. Generally, these studies suggest that the North Sea plaice stock is made up of several different spawning components. Individuals are shown to move towards spawning grounds during the winter and display minimal mixing on feeding grounds throughout the summer and autumn months (Bolle *et al.*, 2005; Hunter *et al.*, 2009). Migration is a topic of significant interest in plaice, as electronic tag returns in the southern North Sea consistently yield depth profiles that are indicative of Selective Tidal Stream Transport (STST). STST is an adaptive movement strategy that uses strong tidal flows to both minimise energy expenditure and maximise the speed and distance of travel (Metcalfe *et al.*, 1990; Hunter *et al.*, 2009).

Electronic tag returns reveal that one third of plaice released in 4.c visit the eastern parts of 7.d in December and January (Bolle *et al.*, 2005). Similar trends were found in Hunter *et al.* (2004c), with 13% of plaice released in 4.c being recaptured in 7.d during the late winter and early spring. These findings highlight that plaice in the southern North Sea do leave sub-area 4, re-distributing to spawning grounds in eastern English Channel, although most exhibit post-spawning migration back into 4.c (Hunter *et al.*, 2003; Bolle *et al.*, 2005). Plaice tagged on spawning grounds in the central North Sea (4.b and southern parts of 4.a) are shown to move in a southerly direction towards the Dogger Bank. In comparison, plaice within the German Bight re-distribute north and west during the summer. Therefore, it is likely that plaice from the German Bight and central North Sea display some mixing on foraging grounds within 4.b. Past studies have linked such population structuring to the distribution of thermal stratification during the summer, illustrating the influence that physical factors can have at the scale of the North Sea (Hunter *et al.*, 2003, 2004c). That said, STST is rarely observed in plaice within the German Bight and central North Sea (Hunter *et al.*, 2003, 2004c, 2004a), likely due to a lack of strong tidal flows, suggesting that oceanographic features can also play a critical role in the population sub-structuring of North Sea plaice.

In 3.a20, tagging studies have shown that the Skagerrak acts as a transitional area for plaice, with individuals moving both east and west post-release (Ulrich *et al.*, 2013). For example, the work of Cardinale *et al.* (2011) suggests that plaice from the Skagerrak stock undergo spawning migrations towards the Skagen peninsula. Conversely, Ulrich *et al.* (2013) show that plaice undertake summer migrations, moving from spawning grounds in western areas or in the North Sea towards feeding grounds in the Skagerrak. The latter movement pattern has significantly more support in the scientific literature. For example, Swedish tagging studies demonstrate that maturing fish (ages 2-4) re-distribute towards the western Skagerrak and to various locations in the North Sea (Molander, 1923; Jacobsson, 1982). Furthermore, parasite data from the time period 1969 to 1978 show that adult plaice residing in the Skagerrak during the summer were characterised by a high infection rate with the parasite *Myxabolis aeglefinus* (van Banning *et al.*, 1978). The same parasitic infection was common within North Sea plaice and the infection rate was highest during the spawning season. Thus, the authors conclude that adult plaice may migrate into the North Sea to spawn.

The lack of genetic differentiation between Irish Sea and North Sea plaice is refuted by tagging studies. For example, over a 17-year mark-recovery tagging program, Dunn and Pawson (2002) found the exchange rate between the North Sea and the Irish Sea was very low (approximately 0.36%). Moreover, the work of Kell and colleagues (2004) concludes that migration in and out of sub-area 4 is a minimal compared to the effect it can have on assessment efforts in smaller adjacent areas. Such findings highlight how different types of evidence (from genetic and tagging studies) can lead to alternative conclusions about fish population structure over both large and small spatial scales.

4.2.1.3 Survey and landings data

Similar to their work on cod, Engelhard et al. (2011) re-digitised historic catch and effort data (1913-2007) for British North Sea trawlers. The authors demonstrate that the maximum CPUE of plaice has shifted northward and offshore towards deeper waters. These findings are consistent with the work of Dulvy et al. (2008) who estimate that plaice have moved into deeper waters at a rate of 3.96 metres per decade. As in cod, this change in distribution is a recent one (since the 1980s). Statistical analysis indicates that changes in plaice CPUE have largely been driven by warming as opposed to fishing pressure. Moreover, the authors comment that such changes are ‘in line with expectations assuming a north-south sea surface temperature gradient in the northern hemisphere’ (Engelhard et al. 2011).

4.2.2 Age structure

4.2.2.1 Young fish (ages 0-2)

Juvenile plaice remain in inshore coastal waters and gradually move offshore as they become larger (Lockwood and Lucassen, 1984; Gibson N., 1999; Power *et al.*, 2000). Nursey grounds are typically characterised by shallow (water depth: 0-3 metres) sediment substratum and are distributed throughout the eastern English Channel, eastern North Sea and in the western Skagerrak. Current estimates suggest that nursery grounds in the eastern North Sea contribute most to total recruitment within subarea 4.

The distribution of young plaice has moved increasingly offshore in recent years. For instance, surveys in the Wadden Sea have found an absence of age 1 plaice in areas where they were previously very abundant (van Keeken *et al.*, 2007). Such re-distribution could be linked to a number of casual factors, most notably increases in sea temperature, lower levels of eutrophication or declines in turbidity (Vorberg *et al.*, 2005), although no conclusive evidence is currently available.

4.2.2.2 Adult fish (ages 2+)

As described in section 4.2.1.2, adult North Sea plaice have an annual migration cycle between spawning and feeding grounds that is characterised by a tendency for strong natal homing. Despite occupying similar waters during the foraging season, evidence of mixing between sub-stocks is minimal (e.g. de Veen, 1978; Rijnsdorp and Pastoors, 1995).

Age 4 plaice dominate current landings data (ICES, 2018c), a trend that was also observed in the 1960s. Conversely, age 3 dominated throughout the 1970s, 1980s and the 1990s. Current landings data also show a relatively high abundance of age 5 and age 6 plaice and a very low abundance of age 2 plaice. This was also noted during the 1960s, demonstrating that the age distribution of the

North Sea plaice stock is trending back towards historic levels (ICES, 2018c). Interestingly, fishing pressure was low in the 1960s, but ramped up in the 1970s, 1980s and the 1990s, before declining again recently. Thus, changes in the age distribution of North Sea plaice appear to have tracked changes in fishing pressure (ICES, 2018c).

4.2.3 Growth

Growth coefficients computed over a 46-year period (1956 – 2002) have shown that plaice growth has experienced a strong declining linear trend (albeit with significant variation) in the North Sea. As in cod, the decline in growth rate has been linked to increasing sea temperatures and decreasing prey availability (van Walraven *et al.*, 2010; Baudron *et al.*, 2014). For instance, WGNSSK (ICES, 2018c) theorise that declines in growth could be driven by food limitation, as their benthic invertebrate food supplies are being continually consumed by an increasingly large North Sea plaice stock.

4.2.4 Maturity

As in cod, the North Sea plaice stock has experienced a shift in age and size at maturation, with individuals becoming mature at a younger age and at smaller sizes over recent years (Grift *et al.*, 2003, 2007). This shift is thought to be fisheries-induced, as high fishing pressure sustained over a prolonged period will theoretically favour individuals that mature earlier and contribute to the next generation prior to their removal.

Currently, a fixed maturity ogive is used for assessment purposes, where maturity-at-age 1 is zero, maturity-at-age 2 is 0.5 and all other age groups are assumed to be mature. That said, the work of Grift et al. (2003; 2007) suggests that the maturity-at-age is unlikely to be constant through time.

4.2.5 Recruitment

Over the last eight years the SSB of the North Sea plaice stock has rapidly increased and was estimated to be 1,052,266 tonnes in 2019 (ICES, 2019b). This estimate is well above current B_{pa} and $MSYB_{trigger}$ values.

Recruitment seems to vary interannually, with peaks in 1964, 1986, 1997, 2002 and 2017 and troughs in 1968, 1972 and 2003. Broadly speaking, recruitment appears to have been low during the 1960s and 1970s. Since the 1980s recruitment has trended upwards toward an average of just over 1 million recruits per year.

4.2.6 Research needs

A clear research need for North Sea plaice surrounds population sub-structuring within the North Sea. From both a genetic and tagging perspective, we know much about the difference between plaice in the North Sea, Irish Sea and the Skagerrak but very little about the degree of mixing that takes place at a regional or local scale (e.g. between the central and southern North Sea). Individual studies do exist, for example the electronic tagging work of Hunter *et al.* (2003, 2004c, 2009) and Griffiths *et al.* (2018), however these only provide a small snapshot into the spatial distribution the stock. We already suspect that the stock has moved northwards in response to anthropogenic warming and has experienced a large population outburst in recent years. The potential causes of this population outburst will be explored elsewhere within the Pandora project. Within the WP1 North Sea case study we plan to utilise Cefas' tagged fish database (Burt *et al.*, 2006) to further investigate the movement patterns of North Sea plaice. The tagged fish database dates back to the early 1950s, including just under 19,000 individual records (all with release and recapture information), with recapture locations spanning the entirety of the North Sea stock unit, the English Channel, west of Scotland, the Irish Sea and Celtic Sea. To our knowledge, previous use of the dataset is minimal and as in cod it represents an untapped resource with significant scientific appeal. We expect that this research will add evidence, for or against, the hypothesis of a climate driven re-distribution of the stock. Moreover, any knowledge gained will contribute to future stock assessment efforts and help inform management actions.

Continuing on from the above, there is also a clear need for regional and local scale genetic work. In cod, the use of SNPs and microsatellite DNA has greatly advanced our understanding of stock structure and spatial dynamics within the North Sea stock unit (Nielsen *et al.*, 2003, 2009; Poulsen *et al.*, 2011; Heath *et al.*, 2014; Wright *et al.*, 2018), both contributing to, and advancing the knowledge gained from more conventional data sources (e.g. tagging data, landings data and survey indices). In plaice, genetic work has occurred at the broad scale, for example in European waters (Hoarau *et al.*, 2002, 2004, 2005; Was *et al.*, 2010; Watts *et al.*, 2010) and in transitional waters between the North Sea and the Baltic Sea (Ulrich *et al.*, 2013, 2017), but is lacking at the sub-stock level. In line with this research need, Gary Carvalho and his research team at the University of Bangor will conduct an in-depth review of available genetic information on population structuring in exploited species including possible pipelines for implementation of genetic data into the general framework for resources assessment. This will be presented as part of the 30-month 1.3 WP1 deliverable. Such work is critical in commercially exploited species that are experiencing climate driven range shifts, as any redistribution of the stock, or parts of it, can lead to either sub-stock fragmentation or increased levels of mixing. Further, any changes in the spatial dynamics of a stock will presumably have consequences on fishing and it's sustainability, and will require careful management.

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Annex 3. Review of available knowledge on North Sea food web interactions relevant for stock assessments and fisheries management.

Introduction

The North Sea has a complex food-web which leads to many trade-offs in yield between predator and prey species as well as competitors compared to simpler food-webs (e.g., Baltic foodweb). If managers decide to adopt a multispecies/ecosystem based management approach, this will be very challenging as politicians often try to avoid making decisions on trade-offs between species or fisheries of different countries (e.g., Kempf et al. 2016, Rindorf et al. 2018). So far, the main management approaches in the North Sea still focus on single species although at least variable natural mortality estimates from the stochastic multi-species stock assessment model SMS (Lewy and Vinther 2004) are incorporated in single stock assessment models of commercially important fish stocks (WGNSSK 2018, HAWG 2018).

This review work is meant to illustrate current work in the North Sea area on modelling predation mortality as input for stock assessments and forecasting stock dynamics and management implications. It aims to highlight the most important implications of available knowledge for fisheries management and to identify knowledge gaps. In this work, the focus is on the interactions between important commercially exploited fish stocks in the area and does not attempt to provide a full food-web description.

The review starts with an overview of available modelling approaches and input data followed by a description of the main interactions covered by available models. Finally, the main implications of species interactions for fisheries management in the North Sea are highlighted based on ICES advice, publications and the EU project MYFISH.

Available modelling approaches

One of the TORs of the working group on multi species stock assessment methods (WGSAM) is to provide an overview on important multi species/ecosystem modelling work in different ecoregions. The WGSAM reports of the last five available years (2014 – 2018) were screened and relevant modelling approaches for assessments and fisheries management simulations in the North Sea area were extracted.

Over the last 5 years, three modelling approaches can be identified as most influential in providing input to North Sea stock assessments or strategic forecasting of species interactions and management implications: SMS (Lewy and Vinther 2004), Ecopath with Ecosim (Christensen and Walters 2004) and the LeMans model (Thorpe et al. 2015, 2016, 2017).

The input of time dynamic natural mortality estimates has been provided in the last five years based on so called keyruns (WGSAM experts agree on input data, model settings, the modelling approach etc.) with the stochastic multi species assessment model SMS. This model is an assessment model with the addition of a diet-selection and predation mortality sub-model. Next to stomach data, it uses the same input as the respective single species assessments used to provide advice by ICES. The last keyrun with SMS has been finalized in 2017 (WGSAM 2017) and details can be found in a stock annex under: http://www.ices.dk/sites/pub/Publication%20Reports/Stock%20Annexes/2017/StockAnnex_ICES_NS_SMS_Configuration.pdf.

Although SMS natural mortality estimates from the hindcast part are used directly in single species assessments, the forecast part has so far not been used for tactical advice but has been used to strategically analyse e.g., maximum sustainable yield in a multi species context (ICES 2013, Kempf et al., 2016).

In the greater North Sea region several Ecopath with Ecosim (EwE) models are known to WGSAM. EwE is a time dynamic mass balance ecosystem model and is mainly used for strategic analyses and advice. There is a model for the whole North Sea (Subarea 4) and one for the southern part only (Divisions 4c and 4b) as well as several EwE models in the English channel (7d). A WGSAM keyrun exists for the whole North Sea model and details can be found in the WGSAM report (WGSAM 2015). EwE has been used in the North Sea region e.g., to analyse MSY in a multi species and mixed fisheries context (Mackinson et al. 2009), to evaluate the fishery and ecological consequences of a proposed North Sea multi-annual plan (Mackinson et al. 2018), the impact of subsidies (Heymans et al. 2011) or trade-offs between objectives in the common fisheries policy and the marine strategy framework directive (Staebler et al. 2016).

The LeMans model is a size and species based multi species simulation model that utilizes an assemblage approach by selecting realistic models from a large set of parameter combinations. The model simulates the North Sea food web with a focus on commercially important target and by-catch species as well as fishing fleets in demersal mixed fisheries in a course manner. The LeMans model has been used in recent years e.g., to analyse management implications of uncertainty in a multispecies size-structured model (Thorpe et al. 2015), to analyse trade-offs in risk and benefits between management strategies as pretty good yield ranges and Nash equilibria (Thorpe et al. 2016, 2017) or to compare conceptual frameworks for a fish community MSY (Thorpe and DeOliveira 2019).

Next to these three models, an Atlantis model (Fulton et al. 2011) has been set up for the English Channel (Girardin et al. 2016) and one for the North Sea and Skagerrak (Subarea 4 and Subdivision 3a.20) during the Vectors project (EU-FP7-VECTORS, http://www.marine-vectors.eu/). Their usage for management related questions is so far limited.

Other multi species modelling approaches applied in the North Sea area include delay difference models (WGSAM 2014), tGAMs (Lynam et al. 2017) or size spectra models to evaluate targets and trade-offs among fisheries and conservation objectives (Blanchard et al. 2014).

Available data as input for multi species modelling

The most important input to parameterize food web models are stomach data. Most of the available modelling approaches use the so called Years of the stomach as main source of information on species interactions in the North Sea. Observed relative stomach contents (weight based) are available from five years (1981, 1985, 1986, 1987 and 1991) of North Sea wide stomach sampling exercises (Anon, 1988; Daan,1989; Hislop et al., 1997) coordinated by the International Council for the Exploration of the Sea (ICES). Data from these years are mainly available for cod, whiting, haddock, saithe, mackerel, horse mackerel, grey gurnard and starry rays. Since the early 90ies no similar large internationally coordinated stomach sampling exercise has taken place. Additional stomachs from seals and harbor porpoise were sampled to a minor extent and in 2012-2013 new information on stomach contents were collected for mackerel and grey gurnard as well as hake as new emerging predator in the North Sea ecosystem via an EU tender. The data from the Years of the stomach and the EU tender are available from the ICES database under http://www.ices.dk/marine-data/data-portals/Pages/Fish-stomach.aspx

Another valuable source for diet information is Dapstom (Pinnegar 2014). This database can be accessed via https://www.cefas.co.uk/cefas-data-hub/fish-stomach-records/. DAPSTOM (integrated database and portal for fish stomach records) is an ongoing initiative (supported by Defra and the EU) to digitise and make available fish stomach content records spanning the past 100 years. The online database contains information (226,407 records from 254,202 individual predator stomachs) on 188 predator species and can be searched by **predator name** or by **prey name** for given sea areas (not only North Sea) and years. The database does not include as many parameters as the ICES database (i.e. no relative share by weight) and the samples are not from a coordinated sampling program in space and time leading potentially to difficulties and bias when using the data for the parameterization of food web models. Never the less, it is a very valuable source of information on general prey preferences and on who eats whom.

Main interactions between commercially important species included in North Sea food web models

The North Sea SMS model has a clear focus on higher trophic levels and commercially important fish species (WGSAM 2017). It includes the main species interacting with commercially important fish stocks through predation (Figure A.3.1). All other prey organisms eaten by predators in the model are represented as so called "Other Food" assuming a constant in time biomass pool. The predator and prey populations in the model are age based. The model covers life stages from the 0-group onwards, but no dynamics in the egg and larval phase. Top predators form an important part of the SMS foodweb, including numerous charismatic species such as seabirds and marine mammals that eat fish. Within the fish community a number of fish eat other fish, and some of those spend only part of their time in the North Sea. The fish species can be divided into four categories: forage fish, fish that eat small fish, benthic-feeding fish, and fish that eat large fish (top predators). Forage fish feed on plankton in the water column. The majority of forage fish are also targeted directly by the fishery (herring, sandeel, sprat, Norway pout). Together with typical forage fish, juvenile gadoids are also an important food source in the North Sea foodweb. Fish that eat small fish belong to a wide range of species, including some that are targeted by fisheries (e.g. whiting, haddock), some that are only occasionally landed (e.g. grey gurnard, starry ray), and some that enter the North Sea only in specific seasons (e.g. western horse mackerel and mackerel). Benthic-feeding fish include all kinds of flatfish that feed on prey in or near the bottom. The majority of flatfish species only eat a small amount of commercially important fish species and have not been included as a fish predator. Fish that eat large fish are mainly large cod, hake and saithe, which also have almost all other fish in their diet. Elasmobranchs (e.g. spurdog) are also important top predators in the North Sea foodweb, but the abundance of most species is currently at a low level and/or data on their diet is scarce, so they have not been included so far.

In the keyrun with EwE a wider range of species/functional groups is included (WGSAM 2015). Compared to SMS, the EwE keyrun includes e.g., functional groups like Spurdog, different ray and skate species, monkfish, several flatfish species and crustaceans like Nephrops and brown shrimp. In addition, as full ecosystem model it also covers lower tropic level plankton and benthic functional groups down to primary producers. However, while EwE covers more species interactions, the populations are less detailed than in SMS and only for some commercially important species like cod and herring so called stanzas differentiate juvenile and adult life stages and associated changes in prey composition and vulnerability to predation and fisheries.

The LeMans model covers like SMS interactions between commercially important fish species, however, also bycatch species like witch, turbot and anglerfish are included. A total of 21 fish species is represented in 32 equal length classes of 5 cm (Thorpe et al. 2019). Also the LeMans model uses a constant "Other Food" pool to take into account predation on prey not explicitly included in the model. The main driver of species interactions in the LeMans model is size preference while species preference (or vulnerability) is not explicitly modelled like in SMS or EwE.

Overall, it becomes evident that the main available models used to provide input to assessments or strategic discussions about management strategies focus on the upper trophic levels of the North Sea food web. Only EwE covers the whole food web including also lower trophic levels but at the cost of a courser representation of stock dynamics inside functional groups. This leads to the fact, that the dynamic of natural mortalities in North Sea models relevant for the input to assessment and management advice is more top-down driven while bottom-up effects originating from the dynamic in lower tropic levels are not well covered especially by SMS and the LeMans model.

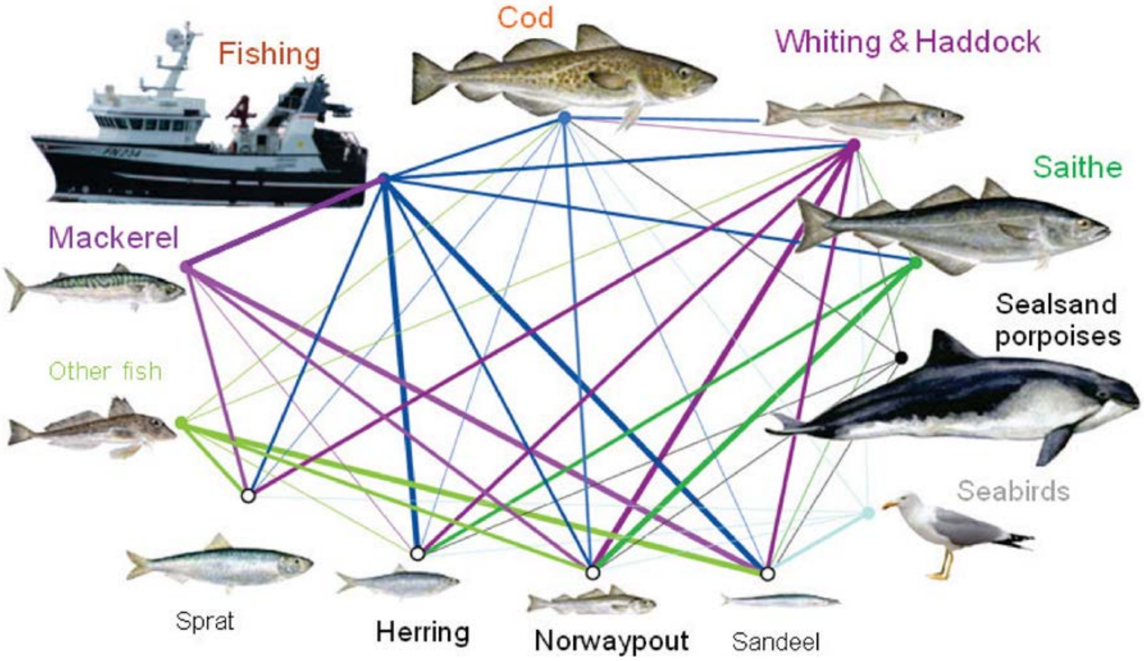

Figure A.3.1. Overview of important predator and prey in the North Sea SMS model food web. Other fish include grey gurnard, North Sea and western horse mackerel, and starry ray. Seabirds include fulmar, gannet, great blackbacked gull, guillemot, herring gull, kittiwake, puffin, and razorbill. Seals and porpoises include grey seal and harbour porpoise. An "Other food" pool with constant biomass is included in the model to represent all prey types that are found in the stomachs but that are not modeled explicitly (e.g., crustaceans, mollusks, other prey fish).

Implications for management

Based on the ICES advice on multi species considerations (ICES 2013), published literature (e.g., Mackinson et al. 2009, Kempf et al. 2016, Thorpe et al. 2017 and 2019) and results from projects (i.e. EU project MYFISH; http://www.myfishproject.eu) conclusions can be made on the main impacts of species interactions on management relevant questions in the North Sea area:

- Potential target multispecies FMSY depends on the management objectives and SSB constraints used. There is no single maximum sustainable yield solution in a multispecies context, and policy choices will have to be made. These results are common for all three main multi species applied in the North Sea area (SMS, EwE, LeMans). An analysis of trade-offs caused by species interactions can inform on the possible consequences of various policy decisions. To decide on trade-offs, however, is often avoided by politicans making any implementation of a multi species approach difficult.

- Yield of virtually all species were affected by the abundance of cod and saithe in model simulations with SMS. They are the main predator fish species in the SMS North Sea configuration. Changing management target fishing mortality (target F) for cod and saithe therefore influenced the yield of all other stocks.

- Indirect predation effects may be also important in the complex North Sea food. For example, a lower F on cod increases cod biomass, which can lead to a decrease in SSB and yield for whiting and haddock (direct predation effect), which in turn can lead to an increase in SSB and yield e.g., for herring, sandeel, Norway pout, and sprat. The increase in SSB for these prey species is caused in simulations with the model SMS due to the reduction in predation pressure from whiting and haddock, which more than compensates the increase in direct predation from a larger cod stock (indirect effect).

- Due to predation, it is no longer guaranteed that all stocks can be maintained above precautionary single-species biomass reference points simultaneously. A new approach may be needed to define what precautionary means in a multispecies context.

- Target fishing mortalities leading to close-to-maximum average yield (F_{MSY}) in a multispecies context can be derived similar to F_{MSY} ranges calculated by ICES in a single species context and implemented in the EU plan for mixed fisheries in the North Sea. Management based on Nash equilibria, however, turned out to be superior over these ranges in simulations with the LeMans model (Thorpe and De Oliveira 2019).

- It happens that multi species F_{MSY} is higher than the agreed single-species F_{MSY} values because of density dependent effects like cannibalism or competition. Also a reduction of predators increases the yield from more productive prey species. This highlights the previous point that the target multi species F_{MSY} depends on defining agreed constraints and acceptable risk levels for all species involved.

- Due to a successful reduction in fishing, natural mortality is an increasingly important source of mortality in the North Sea. This means that the stock dynamics are increasingly more influenced by natural processes. At the same time, improving estimates of consumption of fish by top predators, such as seals and cetaceans, is important, particularly when these predator populations are expected to increase further.

Conclusions and main knowledge gaps

There exists a wealth of multi species and ecosystem models in the North Sea area that are able to inform on consequences of species interactions for fisheries management. In the North Sea mainly three models are currently used to estimate natural mortalities and to perform analyses on the impacts of management decisions: The stochastic multi species model SMS, Ecopath with Ecosim (EwE) and the length structured multi species model LeMans. As one of the few examples worldwide, natural mortality estimates from the stochastic multi species model SMS are used as input to single species ICES assessments for commercially important fish stocks. The various models have been also used for various strategic analyses on fisheries management options. However, forecasting capabilities have so far not been used for tactical advice on quotas and only to a minor extent for management plan evaluations that are still mainly conducted with single species management strategy evaluations (MSEs). Approaches are also missing that are able to predict the impact of management options for mixed fisheries in detail taking into account biological interactions in short- to medium term projections for tactical advice on quotas. Next to biological interactions also technical interactions in mixed fisheries are highly relevant for North Sea demersal fisheries.

The bottleneck for a successful application of multi species assessments and forecasts are stomach data. The last internationally coordinated stomach sampling program in the North Sea is from 1991. An international coordination for a new stomach sampling program is missing substantially preventing multi species models becoming a serious alternative to single species approaches. The lack of a time series of data does not only hinder analyses of processes behind dynamics in species interactions, it is also a main argument against using multi species approaches for advice due to a perception of too large uncertainties and potential bias. A coordinated stomach sampling program inside the data collection framework is needed based on already existing best practice guidelines on how to sample and analyse stomach data in a cost effective way.

The main models available focus on the main interactions between commercially important species. There is a lack of representation of dynamics in lower trophic and benthic food webs. Therefore, the available models are suitable to simulate top-down effects but especially SMS and the LeMans model are not built to simulate bottom-up effects e.g. from changes in primary production. EwE is able simulate such effects, but the representation of lower trophic levels could be also improved for the available North Sea models. Processes acting on the egg and larval phase are also not directly implemented and only captured via stock recruitment relationships. An improvement in our understanding the dynamics determining stock recruitment relationships will also be beneficial for the available multi species models. A review of processes influencing recruitment can be found in Annex 1.

The main impacts of multi species interactions on fisheries management have been analysed in various analyses and studies. The main issues are trade-offs between yield from different species that emerge when moving from single species to multi species approaches. Such trade-offs are difficult to handle in a political context. However, it could be proved that also in a multi species world it is possible to calculate pretty good yield F_{MSY} ranges providing at least 95% of the maximum sustainable yield from each stock. Another interesting approach are Nash equilibria that outperformed F_{MSY} ranges in a risk and benefit analysis with the LeMans model. The lack of uptake of such management options can be found in a general mistrust in complex multi species and ecosystem models. To some extent this mistrust could be elevated by more rigorous skill assessments. Best practice guidelines on what needs to be included in such a skill assessment would be beneficial.

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